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Circumpolar and Regional Seascape Drivers of Genomic Variation in a Southern Ocean Octopus

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Received: 5 February 2024 | **Revised:** 31 October 2024 | **Accepted:** 12 November 2024

Handling Editor: Shotaro Hirase

Funding: This work was supported by Australian Research Council (ARC) Discovery grant DP190101347 (to J.M.S., N.G.W); Thomas Davies Research grant (Australian Academy of Science) (to J.M.S.); David Pearse bequest, Antarctic Science Bursary, Antarctic PhD student support grant (Antarctic Science Foundation) (to S.C.Y.L.); CoSyst grant (to J.M.S. and P.C.W.); Research Council of Finland grant 305532 (to P.C.W.); and the Australian Research Council (ARC) SRIEAS Grant SR200100005 Securing Antarctica's Environmental Future.

Keywords: Antarctica | Cephalopoda | genotype–environment association | isolation-by-environment | seascape genomics

ABSTRACT

Understanding how ecological, environmental and geographic features influence population genetic patterns provides crucial insights into a species' evolutionary history, as well as their vulnerability or resilience under climate change. In the Southern Ocean, population genetic variation is influenced across multiple spatial scales ranging from circum-Antarctic, which encompasses the entire continent, to regional, with varying levels of geographic separation. However, comprehensive analyses testing the relative importance of different environmental and geographic variables on genomic variation across these scales are generally lacking in the Southern Ocean. Here, we examine genome-wide single nucleotide polymorphisms of the Southern Ocean octopus *Pareledone turqueti* across the Scotia Sea and the Antarctic continental shelf, at depths between 102 and 1342 m, throughout most of this species' range. The circumpolar distribution of *P. turqueti* is biogeographically structured with a clear signature of isolation-by-geographical distance, but with long-distance genetic connectivity also detected between East and West Antarctica. Genomic variation of *P. turqueti* was also associated with bottom water temperature at a circumpolar scale, driven by a genotype-temperature association with the warmer sub-Antarctic Shag Rocks and South Georgia. Within the Scotia Sea, geographic distance, oxygen and fine-scale isolation-by-water depth were apparent drivers of genomic variation at regional scales. Putative positive selection of haemocyanin (oxygen transport protein), calcium ion transport and genes linked to RNA modification, detected within the Scotia Sea, suggest physiological adaptation to the regional sharp temperature gradient (~0–+2°C). Overall, we identified seascape drivers of genomic variation in the Southern Ocean at circumpolar and regional scales in *P. turqueti* and contextualised the role of environmental adaptations in the Southern Ocean.

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1 | Introduction

Knowledge of the determinants of spatial genetic structure provides information about key evolutionary processes that occurred during a species' history (Pittman et al. 2021) and is particularly important for building roadmaps for species' conservation and management. Landscape (=seascape for marine environments) genomics provides a conceptual framework to understand how environmental and geographic features influence contemporary patterns of neutral and adaptive variation, which may, in turn, reveal the potential for different populations to adapt to future environmental changes (Dauphin et al. 2023). A putative consequence of current global climate change is that genetic diversity will be reduced or restructured (Exposito-Alonso et al. 2022). Also, there are concerns that future climate change can outpace the ability of some species to adapt (Grummer et al. 2022). It is uncertain how marine ecosystems will respond due to the variability of individual level and local scale responses, as well as the synergistic effects between different climate and human drivers (Gissi et al. 2021). Understanding the seascape drivers of population genomic variation is urgently needed to characterise species and ecosystem responses, including vulnerability or adaptive potential, to any future changes.

The Southern Ocean covers ~10% of the world's oceans and encompasses diverse habitats (e.g., islands, the Antarctic continental shelf, pelagic and deep-sea habitats) and complex seascape features (Post et al. 2014; Xavier et al. 2016). Most of the Southern Ocean biodiversity is comprised by benthic fauna (~88% of extant marine species; De Broyer et al. 2011). Currently, the Southern Ocean is a rapidly changing environment, with ~86% of its ecosystem projected to experience diverse climate change stressors, including warming (Gutt et al. 2015; Strass et al. 2020). The underlying physical-ecological dynamics across the Southern Ocean seafloor are sensitive to climate change (Fabri-Ruiz et al. 2020), and this impacts current conservation efforts that are directed towards protecting distinct regions. For example, the Southern Ocean is generally characterised as thermally stable with limited seasonal variation, albeit with thermal gradients associated with latitude and between shelf and deep-sea habitats (Clarke et al. 2009; Post et al. 2014). Future environmental change, such as warming, will impact benthic habitats and the biota within them (Chapman et al. 2020; Constable et al. 2014).

So far, the relationship between Southern Ocean seascape and population genetic variation is often discussed in the context of how dispersal is influenced by oceanic currents at regional and circumpolar levels, including regional currents (Galaska et al. 2017; Levicoy et al. 2021; Muñoz-Ramírez et al. 2020), and the continental-wide Antarctic Circumpolar Current (ACC) (Hemery et al. 2012; Moore et al. 2018; Raupach et al. 2010). For example, the regional Scotia Sea contains an island arc system separated by deep-water channels (>1000 m), crossed by the ACC and is influenced by local currents that have various circulatory patterns (Thompson et al. 2009). Within the Scotia Sea, the current dynamics could be linked to regional gene flow (Hoffman et al. 2012; Levicoy et al. 2021; Muñoz-Ramírez et al. 2020) or genetic discontinuities (Hoffman et al. 2011; Linse et al. 2007; Moore et al. 2018) in some benthic species. However, the distribution of genetic variation in the Scotia Sea can also be impacted by other features of the seascape, such as isolation-by-bathymetry (Linse et al. 2007; Strugnell, Allcock, and Watts 2017). Beyond the Scotia Sea, connectivity across the continental scale is also noted in benthic species with circumpolar distribution and is often linked to the influence of the ACC (e.g., Lau et al. 2023; McLaughlin, Wilson, and Rouse 2023; Moore et al. 2018; Soler-Membrives et al. 2017).

Emerging studies have highlighted a role for seascape, mostly the influence of oceanic currents, in driving genetic structure in Southern Ocean benthic fauna. However, knowledge of the relative contribution of seascape features in driving neutral and adaptive genetic structuring at contrasting spatial scales (i.e., circumpolar and regional) is scarce (Brasier et al. 2021). How genetic diversity is structured across both circumpolar and regional levels is poorly understood for Southern Ocean benthic species. It is generally also unclear how Southern Ocean benthic fauna will respond to environmental changes resulting from climate change, such as temperature, at a functional or molecular level (Brasier et al. 2021; Gutt et al. 2018; Ingels et al. 2012). Evidence of genetic adaptation to the environment is limited for Southern Ocean benthic species. Understanding how the complex seascape of the Southern Ocean distributes adaptive genetic diversity could support comprehensive conservation efforts in maintaining existing genetic diversity and connectivity to preserve evolutionary resilience (Lau and Strugnell 2022), as well as informing the design of Marine Protected Area networks (Leiva et al. 2022).

The Southern Ocean octopus *Pareledone turqueti* (Joubin, 1905) is an excellent model to examine the influence of circumpolar and regional seascapes on genomic variation. *Pareledone turqueti* has a circumpolar distribution and occurs around some Antarctic islands south of the Polar Front and on the Antarctic continental shelf from shallow water to the continental slope (Allcock et al. 1997; Strugnell et al. 2012; this study). This species is a direct developer with benthic hatchlings (Barratt et al. 2008) and is therefore associated with limited dispersal capability. Populations of *P. turqueti* from the Scotia Sea are likely isolated by water depth, raising the prospect that seascape is an important structure of genetic differentiation in this species (Strugnell, Allcock, and Watts 2017). However, these data are based on a small panel of microsatellite loci ($n=10$), thus lacking statistical power to identify environmental drivers of differentiation as well as any associated adaptive genetic signal. Here, we quantify the population genomic variation of *P. turqueti* using double-digest restriction-associated DNA (ddRAD) loci (Peterson et al. 2012) on samples collected throughout most of this species' distribution (Lau et al. 2023). The historic spatial genomic structure of *P. turqueti* across the Southern Ocean was described in Lau et al. (2023) in relation to Pliocene-Pleistocene demographic events. Here, we describe recent patterns of dispersal and evidence for adaptation in *P. turqueti* across the contemporary Southern Ocean seascape. Specifically, we examined (1) how the genomic variation of *P. turqueti* is structured at both circumpolar and regional (Scotia Sea) scales, (2) whether genomic variation among *P. turqueti* can be explained by present variation in the environment and oceanic currents at both regional and circumpolar scales and (3) whether putative adaptive regions (outlier loci) are linked to Southern Ocean seascape adaptation, such as temperature, in *P. turqueti*.

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2 | Materials and Methods

2.1 | Target Capture Sequencing of ddRAD Loci in Degraded *P. turqueti* Samples

Genomic DNA of *Pareledone turqueti* ($n = 96$) samples from the Antarctic continental shelf and Antarctic islands (Figure 1; Tables S1 and S2), between the depths of 102–1342 m, was sequenced with target capture sequencing with probes designed from ddRAD sequencing; these were performed by, and are detailed in Lau et al. (2023). Samples were sequenced using target capture as the DNA was degraded due to long-term storage in collections, a characteristic for many Antarctic marine specimens due to logistical challenges in accessing fresh samples in the remote Southern Ocean. Sample locations around the Antarctic continental shelf include the South and East Weddell Sea, Prydz Bay, East Casey Station, Adélie Land, Ross Sea and Amundsen Sea. Sample locations from within the Scotia Sea include locations of Shag Rocks, South Georgia, South Orkney Islands, Bransfield Strait, Elephant Island, the South Shetland Islands group (King George Island, Robert Island, Livingston Island and Deception Island) and the West Antarctic Peninsula. Two outgroup species (*P. aequipapillae* and *P. cornuta* from the Ross Sea and Adélie Land, respectively) were included in the dataset.

A total of 8877 ddRAD loci were sequenced using target capture in all samples (Lau, Wilson, et al. 2023). In brief, these loci were previously identified via ddRAD sequencing and site calling across 285 samples of Southern Ocean octopus species, including *Adelieledone adelieana* ($n = 4$), *A. polymorpha* ($n = 1$), *Adelieledone* sp. ($n = 12$), *P. turqueti* ($n = 204$), *P. aequipapillae* ($n = 28$), *Pareledone* sp. ($n = 15$), *Megaleledone setebos* ($n = 3$) and *Graneledone* sp. ($n = 1$) (Lau et al. 2023). Demultiplexed ddRAD reads (enzyme set: *MseI* and *EcoRI*) with phred quality less than 20 ($Q < 20$) were discarded using *fastp* v.0.20 (Chen et al. 2018) to remove low-quality base calls (Chen et al. 2017). Potential contaminants (humans and microorganisms) were identified using *Kraken* v.1.0 (Wood and Salzberg 2014), and reads that matched those of the contaminant database (MiniKraken 8GB 2017) were removed. Clean reads were then mapped to a *P. turqueti* draft genome via *bowtie2* v.2.3.4.1 (--very-sensitive-local) (Langmead and Salzberg 2012), processed through *Samtools* v.1.7 (Li et al. 2009) and SNPs called using the *Stacks* v.2.3d *gstacks* module (Catchen et al. 2013). Sites that were present in 50% of the samples (-R 0.5) with at least a minor allele frequency of 0.01 (-min-maf 0.01) were retained using the *Stacks population* module, which resulted in 31,142 loci. The parameter -R 0.5 (50% missing data) was chosen to allow effective capture of interspecies relationships across the 285 samples, while a minor allele frequency filter was applied to exclude potential sequencing errors (-min-maf 0.01, following Rochette and Catchen 2017). The consensus fasta sequences of the 31,142 loci were aligned against the draft *P. turqueti* genome using *bowtie2* (--sensitive), leaving 8942 ddRAD loci that uniquely aligned just once to the draft genome. The number of target capture loci were reduced subsequently to 8877 loci after filtering for bait design following the Arbor Bioscience (Ann Arbor, MI, USA) in-house filtering pipeline.

For the target capture sequencing of ddRAD loci in *P. turqueti*, libraries with index adapters were built and pooled into single capture reactions (six libraries per capture). Libraries were enriched in capture reactions using myBaits following the manufacturer's protocol, and the resulting capture reactions were sequenced on Illumina NovaSeq S4 flow cells with 150 bp paired end reads. Sixty-five out of the 96 *P. turqueti* samples and the two outgroup samples were previously genotyped at COI and 10 microsatellite loci (Strugnell et al. 2012; Strugnell, Allcock, and Watts 2017).

Raw target capture reads were demultiplexed with adapters and barcodes removed using *process_shortreads* in *Stacks*. Bases with quality less than 20 ($Q < 20$) were discarded, and polyG in read tails were trimmed using *fastp*. Potential contaminants were identified using *Kraken* v.1.0 (Wood and Salzberg 2014), and reads that matched those of the contaminant database (MiniKraken 8GB 2017) were removed.

2.2 | Read Mapping and Variant Calling

Cleaned target capture reads were mapped to the consensus sequences of the 8877 ddRAD loci used for bait design using *bwa* v.0.7.17 *mem* with default parameters (Li and Durbin 2009). *Samtools* was used to sort reads, and PCR duplicates were marked and removed using *picard* v.2.18.1 (Broad Institute 2019). Variants and short indels were called across all samples using *bcftools* v.1.7 *mpileup* (Li 2011).

Variant filtering was performed in *VCFtools* v.0.1.13 (Danecek et al. 2011). First, indels were removed, and high-quality SNPs were retained based on the following steps. Sites with a quality score > 30 were kept (--minQ 30), and sites with a mean read depth $< 16\times$ (one third the average depth (48.2×)) and $> 96\times$ (2× average depth) were removed (--min-meanDP 16, --max-meanDP 96); only biallelic sites were kept (--min-alleles 2, --max-alleles 2). Sites were kept if present in at least 50% of all samples (--max-missing 0.5). Sites with a minor allele frequency of at least 5% were kept (--maf 0.05). To remove artificial SNPs arising from paralogous regions, those with observed heterozygosity > 0.5 removed (Gargiulo, Kull, and Fay 2020; Hohenlohe et al. 2011) via the R package *adegenet* v.2.1.3 (Jombart and Ahmed 2011). Lastly, only one site per ddRAD locus was kept (--thin 1000; an arbitrary number larger than the longest locus (in bp) used in the bait set). Subsets of this dataset were generated by removing individuals based on including (1) all *P. turqueti* samples ($n = 96$) without outgroups and (2) samples from the Scotia Sea ($n = 52$) without outgroups.

2.3 | Analyses of Genomic Structure in *P. turqueti*

Discriminant Analysis of Principal Components (DAPC) was performed using the R package *adegenet* v.2.1.10 (Jombart and Ahmed 2011) to explore population structure. Genetic differentiation between sample locations was examined with pairwise F_{ST} values (Weir and Cockerham 1984), calculated using the R package *hierfstat* v.0.5-11 (Goudet 2005). Locations with low sample size ($n \leq 2$) were omitted from F_{ST} analysis (i.e., South Orkney Island, Bransfield Strait, the West Antarctic Peninsula and East Casey Station). A post hoc sequential Bonferroni correction (Rice 1989) was applied to account for multiple pairwise comparisons. Individual admixture proportions were also estimated via

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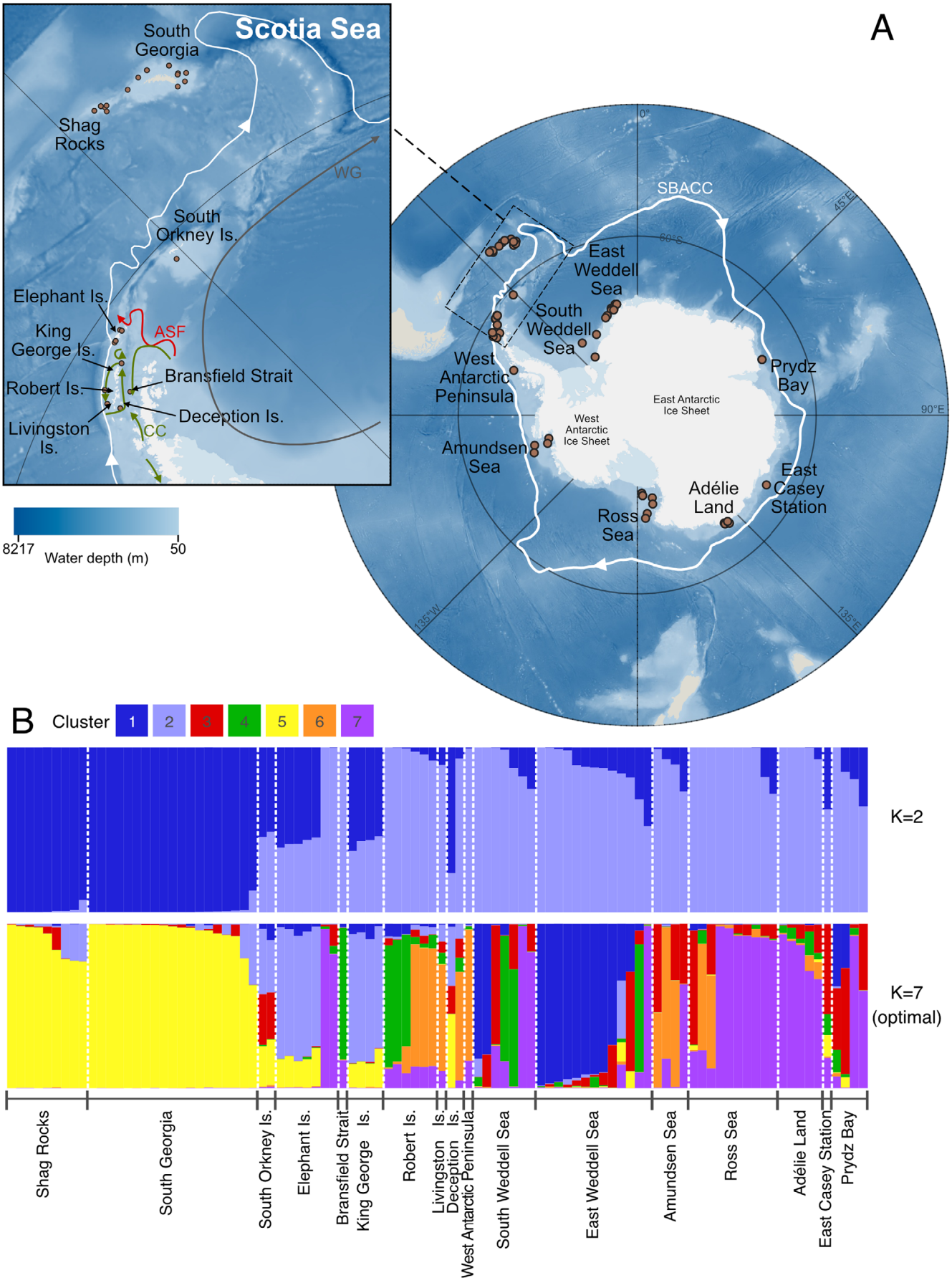

FIGURE 1 | Legend on next page.

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FIGURE 1 | (A) Map of the Southern Ocean with bathymetry and sample distribution of the octopus *Pareledone turqueti* examined in this study. Bathymetry data was obtained from ETOPO1/IBCSO/RAMP2 elevation model in Quantarctica (Matsuoka et al. 2021). The location of the southern boundary of the Antarctic Circumpolar Current (SBACC) (Matsuoka et al. 2021) is illustrated. Major currents in the Scotia Sea, including Weddell Gyre (WG) (Vernet et al. 2019), Antarctic Slope Front (ASF) and Antarctic Coastal Current (CC) (Moffat and Meredith 2018), are also illustrated. Arrows indicate current directions. (B) Admixture proportions of *Pareledone turqueti* across the Southern Ocean. Each vertical bar represents one individual sample; colours correspond to admixture proportion estimations derived from *Structure*. The two best K values ($K=2$ and 7) are presented based on deltaK and log-likelihood values, respectively. [Colour figure can be viewed at wileyonlinelibrary.com]

Structure v.2.3.4 (Pritchard, Stephens, and Donnelly 2000), which was run for values of $K=1$ through to 10, with 10 replicates per value of K using *Structure_threader* (Pina-Martins et al. 2017). Each run was performed with 500,000 iterations and a burn-in of 100,000. Meaningful values of K were evaluated based on the highest mean log likelihood [mean LnP(K)] and deltaK statistics using *Structure Harvester* (Earl and VonHoldt 2012).

2.4 | Seascape Genetic Analyses

2.4.1 | Isolation-By-Distance, Isolation-By-Water Depth and Isolation-By-Environment at Circumpolar and Regional Scales

Partial Mantel tests examined isolation-by-environment, with geographic distance and water depth defined as controlled factors, in order to evaluate the effect of each environmental variable on genetic distance. To evaluate whether the genetic variation of *P. turqueti* can be explained by isolation-by-distance, a partial Mantel test was performed to evaluate the relationship between genetic distance and geographic distance while controlling for the effects of water depth. To evaluate whether the genetic variation of *P. turqueti* can be explained by isolation-by-water depth, a partial Mantel test was performed to evaluate the relationship between genetic distance and water depth while controlling for the effects of geographic distance. Pairwise genetic distances between samples were first estimated via *ngsDist* v.1.0.10 (Vieira et al. 2016). Partial Mantel tests were then performed separately for (1) all *P. turqueti* samples ($n=93$; three continental shelf samples were excluded due to missing precise coordinate information [ID: JS_40, JS_44, NIWA87470]) and (2) *P. turqueti* samples from the Scotia Sea ($n=52$), using the R package *ecodist* v.2.1.3 (Goslee and Urban 2007) with 1000 permutations.

For geographic distance between samples, least-cost physical distances in kilometres (via the ocean only, avoiding the Antarctic ice sheets) were calculated using the *lc.dist* function of the R package *marmap* v.1.0.10 (Pante and Simon-Bouhet 2013). Least-cost distances between samples were calculated based on a class bathy object on R obtained from Kelly (2019), which represents the spatial bathymetry information of the Southern Ocean. All coordinates and surface were converted to WGS 84/Antarctic Polar Stereographic (EPSG:3031) projection before geographical distance calculations.

Environmental variables considered for isolation-by-environment included bottom water temperature, bottom water salinity, as well as silicate, phosphate, nitrate and oxygen (winter and summer values, at sea surface and at 500 m depth). We incorporated these environmental variables in genotype–environmental association analyses as they are considered potential drivers of spatially varying benthic ecological patterns globally and in the Southern Ocean (Belanger et al. 2012; Teschke et al. 2020). Information on water depth was obtained from the sample's metadata. Values of bottom water temperature and salinity were calculated from the decadal means of annual average bottom temperature and salinity at 1°C spatial resolution between 1955 and 2010 from World Ocean Atlas 2018 (Locarnini et al. 2018; Zweng et al. 2019). Bottom temperature and salinity data were estimated based on the information at the depth interval closest to the maximum depth available for each point using *QGIS* v.3.16 (QGIS.org 2024). Values of silicate, phosphate, nitrate and oxygen (summer and winter values, at the sea surface and 500 m) were extracted from existing interpolated GIS layers from *Quantarctica* (Matsuoka et al. 2021), generated based on World Ocean Atlas 2013 datasets (Garcia et al. 2013), gridded at 25 km spatial resolution. These values were extracted from existing GIS layers from *Quantarctica* rather than directly from the World Ocean Atlas, as they required additional care in achieving the statistically best interpolation, which was performed by *Quantarctica*. Since Southern Ocean bottom temperature and salinity exhibit limited seasonal variation, decadal means of annual averages were used in this study. However, Southern Ocean biological production varies seasonally following summer sea ice melting (which influences nutrient parameters) (Post et al. 2014); therefore, both summer and winter values of nutrient profiles at different depths were utilised in this study. For partial Mantel tests, multicollinearity between environmental variables was assessed using the R package *psych* v.1.9.12 (Revelle 2020), and we retained variables with low collinearity ($r<0.7$) following Dormann et al. (2013). All retained variables are presented in Table S3.

2.4.2 | Genotype–Environment Association Analyses at Circumpolar and Regional Scales

Redundancy analysis (RDA) is a constrained ordination approach that uses multiple linear regression to summarise the linear relationships between genotypes by a set of explanatory predictors. Here we performed partial redundancy analyses (pRDA) and full redundancy analyses (RDA_{full}) to detect genome-wide adaptations to environmental variables and spatial distance in the Southern Ocean for (1) all *P. turqueti* samples ($n=93$) and (2) *P. turqueti* samples from the Scotia Sea ($n=52$). For each dataset, two pRDA models ($pRDA_{ENVD}$, $pRDA_{ENV}$) and one full RDA model (RDA_{full}) were performed. First, $pRDA_{ENVD}$ were performed to explore genotype–environment associations, including water depth and other environmental variables, corrected for the effects of spatial distance. We also performed $pRDA_{ENV}$ to further explore genotype–environment associations only on environmental variables, which was corrected for both the effects of spatial distance and water depth.

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Finally, RDA_{full} was performed to explore the combined effects of water depth, environmental variables and spatial distance on genetic variations. All RDA models were performed using the R package *vegan* v.2.5-6 (Oksanen et al. 2013), and significance ($\alpha = 0.05$) was assessed with ANOVA (999 permutations).

Least-cost geographic distances between samples were considered as spatial distances in the pRDA and RDA_{full} models and were represented by distance-based Moran's eigenvector maps (dbMEMs). A pairwise least-cost geographical distance matrix between samples was used to calculate dbMEMs using the *dbmem* function of the R package *adespatial* v.0.3-23 (Dray et al. 2023). Environmental variables considered for pRDA and RDA_{full} models included bottom water temperature, bottom water salinity, as well as silicate, phosphate, nitrate and dissolved oxygen (winter and summer values at the surface and 500 m). For each dataset, only significant dbMEMs and environmental variables correlated with genetic variation were considered in the pRDA and RDA_{full} models. Significant dbMEMs and environmental variables were selected by separate analyses using the function *ordistep* of the R package *vegan* via a forward selection with 10,000 permutations, followed by an ANOVA with 999 permutations.

For each pRDA/RDA_{full} model, variance inflation factors (VIFs) were examined to further detect multicollinearity between variables. Only variables with VIF < 10, an indication of limited collinearity (Oksanen 2012), were retained in the final models. All retained variables for each pRDA/RDA_{full} model are presented in the results.

For the $pRDA_{ENVD}$, $pRDA_{ENV}$ and RDA_{full}, SNP loadings in the ordination space were also identified to assess whether certain SNPs might be associated with predictors (i.e., SNPs under selection as a function of predictors). Outlier SNPs were identified via the distribution of SNP loadings on each significant axis, with SNPs that exhibited more than ±3 standard deviations from the mean loading identified as putative outliers (see Forester et al. 2018). Pearson's correlation coefficient was used to evaluate associations between putative outlier SNPs and predictors.

2.4.3 | Regional Migration Patterns Across the Scotia Sea

Contemporary migration rates (i.e., over the last few generations) among locations within the Scotia Sea were examined using *BA3-SNP* v.3.0.5 (Mussmann et al. 2019). Samples from the South Weddell Sea were also included to consider the influence of the Weddell Gyre into the Scotia Sea. Locations with a sample size of $n = 1$ were removed from *BA3-SNP* analysis, including Bransfield Strait, Livingston Island and the West Antarctic Peninsula. *BA3-SNP* was run for 60,000,000 iterations, with a burn-in of 6,000,000 iterations and a sampling frequency of 10,000. Mixing parameters were adjusted (-a 0.95 -f 0.8 -m 0.9) with the aim of achieving 20%–60% acceptance rate for each parameter. BA3-SNP was repeated five times with different starting seeds to ensure Markov Chain Monte Carlo (MCMC) convergence with effective sample size > 200, which was evaluated using *Tracer* v.1.7.2 (Rambaut et al. 2018). Results from the best run, determined based on the lowest Bayesian deviance (Meirmans 2014), were presented. Only significant migration rates (i.e., 95% confidence interval did not overlap with zero) are presented in the main text.

Directional relative migration between locations across the Scotia Sea was examined using *divMigrate* (Sundqvist et al. 2016) in the R package *DiveRsity* v1.9.90 (Keenan et al. 2013), which reflects both historic and recent migration patterns (Sundqvist et al. 2016). Samples from the South Weddell Sea were also included in *divMigrate* analysis. *divMigrate* evaluates the directional migration rates by comparing the geometric means of allele frequencies between user-defined populations (Sundqvist et al. 2016). Genetic differentiation between locations was calculated using *Nm* (i.e., effective number of migrants) (Alcala, Goudet, and Vuilleumier 2014). Ten thousand bootstrap iterations were used to assess whether gene flow between populations was significantly asymmetric. Samples from Bransfield Strait, Livingston Island and the West Antarctic Peninsula were excluded due to insufficient sample size ($n = 1$) at these locations.

2.4.4 | Outlier Loci Detection and Gene Ontology at Circumpolar and Regional Scale

Alongside $pRDA_{ENVD}$, $pRDA_{ENV}$ and RDA_{full}, SNPs under putative selection were identified using outlier detection analyses including *OutFLANK* v.02 (Whitlock and Lotterhos 2015), *BayeScan* v.2.1 (Foll and Gaggiotti 2008) and *PCAdapt* v.4.3.2 (Privé et al. 2020). Outlier detection analyses were performed separately across (1) all *P. turqueti* samples ($n = 96$) and (2) only *P. turqueti* from the Scotia Sea ($n = 52$).

OutFLANK analyses were performed using default parameters and a *q*-value threshold of 0.01. *BayeScan* analyses were performed with prior odds set to 100, followed by 20 pilot runs and 100,000 iterations with 5000 samples, burn-in length of 50,000 and thinning interval of 10, with outlier SNPs identified with a *q*-value threshold of 0.01. *PCAdapt* analyses were performed with scree plots used to select the optimal principal component (*K*), and outlier SNPs were determined via the Benjamini-Hochberg Procedure with a *p*-value threshold of 0.01. SNPs that were identified as outliers by two or more tests (*OutFLANK*, *BayeScan*, *PCAdapt*, $pRDA_{ENVD}$, $pRDA_{ENV}$ and RDA_{full}) were considered to be putatively under selection to minimise selection of false positives (Ahrens et al. 2021).

For *OutFLANK* and *BayeScan*, individuals can be pre-defined as different populations. For outlier detection analyses across all *P. turqueti* samples, samples were grouped within the Scotia Sea or Antarctic continental shelf. For outlier detection analyses across *P. turqueti* only from the Scotia Sea, samples were grouped within sample locations.

The functional roles of putative outliers were evaluated by subjecting 1000 base pairs upstream and downstream of each of the identified outlier ddRAD loci, using the contig information from the draft partial *P. turqueti* genome (Lau et al. 2023). Sequences were queried against the UniProtKB/Swiss-Prot database (release 2023_05) using the *BLASTx* (Altschul et al. 1990) search tool to determine whether homologous sequences were present with a known function. The best hits per search

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(*E*-value threshold of 1×10^{-5} and bit-score at least 50 following Pearson (2013)) were considered as significant matches. Gene ontology (GO) functional annotations of the significant matches were assigned using the *QuickGO* webserver (GO version 2023-11-06) (Binns et al. 2009). To visualise GO terms, redundant GO terms were filtered and clustered based on SimRel semantic measure and similarity of 0.7, using *REViGO* with the default whole UniProt database (Supek et al. 2011).

3 | Results

3.1 | Sequencing Data and SNP Calls

A total of 1,519,910,163 raw reads were obtained from 96 *P. turqueti* samples and two outgroup samples (*P. aequipapillae* and *P. cornuta*) during target capture sequencing of ddRAD loci, with an average of 15,509,287 reads (±5,974,298 SD) per sample. After SNP filtering, the final dataset included *P. turqueti* ($n = 96$) and outgroups ($n = 2$) with 37,322 SNPs (all SNPs per locus) and 5188 SNPs (single SNP per locus). Across the 37,322 SNPs, the dataset had near-zero missingness (i.e., average proportion of missing SNP per individual was 0.003 between 0 and 1), and average depth per SNP across all individuals was 42.5×. Across the 5188 SNPs, the dataset also had near-zero missingness (i.e., average proportion of missing SNP per individual was 0.004 between 0 and 1), and average depth per SNP across all individuals was 33.3×.

3.2 | Population Genomic Structure

Genetic clustering using *Structure* suggested all *P. turqueti* samples can be represented by $K = 2$ or 7, based on delta$K$ and log-likelihood values, respectively (Figure 1B). $K = 7$ is supported as the optimal value as the admixture proportions correspond to the genomic patterns observed in DAPC (Figure 2). Visualisation of samples grouped by collection year indicates this dataset is unlikely to be influenced by cohort structure (e.g., similar admixture proportions are observed across South Georgia samples over 16 years; Figure S1). At $K = 2$, samples from Shag Rocks and South Georgia were distinct from the rest of the locations, with samples from South Orkney Island, Elephant Island and King George Island (locations within the Scotia Sea) exhibiting a high level of admixture with Shag Rocks and South Georgia (Figure 1B). Sub-optimal K values at $K = 3$ and 4 (Figure S2) revealed broad patterns of substructure within the Scotia Sea (e.g., King George Island versus Robert Island), as well as admixture between the Scotia Sea and the Antarctic continental shelf (e.g., between Elephant Island—King Georgia Island—Weddell Sea). Higher sub-optimal K values at $K = 5$ and 6 further reveal admixture between Scotia Sea and the Antarctic continental shelf (e.g., between Ross Sea–Amundsen Sea–Robert Island).

At $K = 7$, samples from Shag Rocks and South Georgia were also distinct from other sampled locations, with a lower level of admixture detected with South Orkney Islands, Elephant Island and King George Island (Cluster 5 in Figure 1B). Furthermore, three distinct genetic clusters were observed in the Scotia Sea (Figure 1B), including between the South Orkney Islands, Elephant Island, King George Island and Deception Island (Cluster 2), Robert Island, Livingston Island, Deception Island and the West Antarctic Peninsula (Cluster 6) and between Bransfield Strait and Robert Island (Cluster 7). When grouped by water depths, these three genetic clusters can be differentiated by depths across these locations (Figure S3). At $K = 7$, on the Antarctic continental shelf, circumpolar connectivity is observed between Ross Sea and Adélie Land, as well as South and East Weddell Sea, Amundsen Sea and Prydz Bay individuals (Clusters 3 and 7 in Figure 1B). Distinct admixture was detected between the East and South Weddell Seas and Prydz Bay (Cluster 1 in Figure 1B). Admixture was also observed between the Antarctic continental shelf and the Scotia Sea (Figure 1B), including between Ross Sea, Amundsen Sea and the West Antarctic Peninsula, Deception Island, Livingston Island and Robert Island (Cluster 6) and between East and South Weddell Sea and Bransfield Strait and Robert Island (Cluster 4).

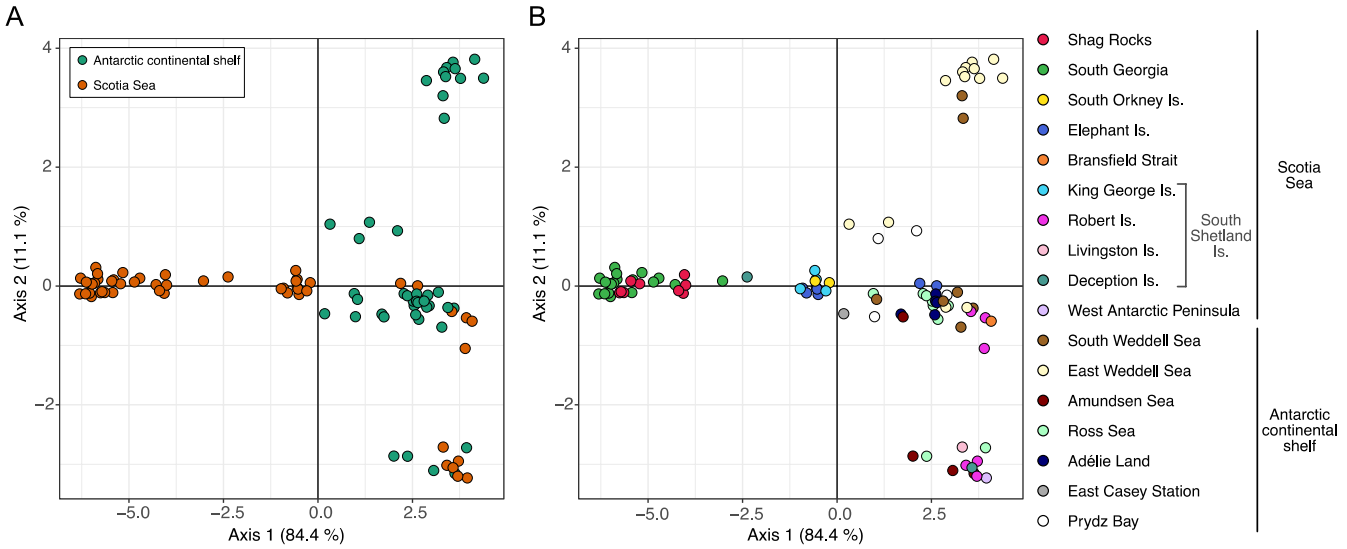

FIGURE 2 | Discriminant Analysis of Principal Components (DAPC) results on the first two axes of *Pareledone turqueti* across the Southern Ocean based on ddRAD loci data, labelled by broader geographical region (A) and sample location (B). [Colour figure can be viewed at wileyonlinelibrary.com]

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DAPC detected structured populations within *P. turqueti* (Figure 2A,B). Samples collected from Shag Rocks and South Georgia clustered together and were distinct from other locations on the first axis (Figure 2B). The second axis indicated a clear differentiation between most (but not all) samples from the South/East Weddell Sea and other localities (Figure 2B). Some samples from the South/East Weddell Sea, Prydz Bay and Elephant Island exhibited limited differentiation from the Ross Sea and Adélie Land samples on the second axis (Figure 2B). Pairwise F_{ST} values indicated samples from South Georgia and Shag Rocks exhibited clear differentiation with other locations in the Scotia Sea and on the Antarctic continental shelf (F_{ST} between 0.069 and 0.129) (Table S4), which was also reflected by DAPC (Figure 2A).

3.3 | Isolation-By-Distance, Isolation-By-Water Depth and Isolation-By-Environment

Partial Mantel tests revealed significant isolation-by-geographical distance based on pairwise genetic distance between *P. turqueti* individuals for both datasets, including all circumpolar samples and also only samples collected from the Scotia Sea (Table S3). For the dataset including all samples, significant relationships between genetic distance and environment variables were also observed, including bottom water temperature, as well as silicate at 500 m during winter (Mantel's r between 0.202 and 0.299, $p = 0.001$). For the dataset that only included samples from the Scotia Sea, partial Mantel tests revealed no significant correlation between genetic and environmental distances. No significant correlation between genetic and bathymetric distances was observed for both datasets.

3.4 | Genotype–Environment Association at a Circumpolar Scale

For the dataset of all *P. turqueti* samples across the Southern Ocean ($n = 93$), RDA_{ful} was first performed to explore the combined effects of spatial distance, water depth and environmental variables (Figure 3A, Table S5). RDA_{full} explained 9.9% (adjusted R^2, $p < 0.001$) of the total genetic variation. The first five constrained PCs significantly explained 22.12% ($p < 0.001$), 9.67% ($p < 0.001$), 7.72% ($p < 0.001$), 7.20% ($p < 0.001$) and 6.07% ($p < 0.001$) of the total adjusted R^2. Bottom water temperature ($p = 0.044$), winter oxygen values at 500 m ($p = 0.032$), MEM2 ($p = 0.011$) and MEM4 ($p = 0.006$) were found as significant predictors in the final RDA_{full} results. On RDA1, samples from South Georgia and Shag Rocks displayed a positive association with temperature (Figure 3A). On RDA2, samples from the Ross Sea, Adélie Land, Prydz Bay, East Casey Station and the Amundsen Sea displayed a positive association with MEM2, whereas Scotia Sea localities including South Orkney Islands, Elephant Island and King Gorge Island displayed a clear negative association with MEM2 (Figure 3A).

To further explore the relationship between genotype–environment association, effects of spatial distances were controlled in $pRDA_{ENVD}$ (Figure 3A, Table S5) and $pRDA_{ENV}$ (Figure 3A, Table S5). In the $pRDA_{ENVD}$ model comparing individuals collected across the Southern Ocean, with water depth considered as a testable environmental variable, $pRDA_{ENVD}$ explained 3.5% (adjusted R^2, $p < 0.001$) of the total genetic variation. The first three constrained PCs significantly explained 24.43% ($p < 0.001$), 14.89% ($p < 0.001$) and 12.00% ($p = 0.011$) of the total adjusted R^2. Bottom water temperature ($p = 0.021$), water depth ($p = 0.047$), bottom water salinity ($p = 0.031$), winter phosphate values at 500 m ($p = 0.029$) and winter oxygen values at 500 m ($p = 0.011$) were found as significant variables in the final $pRDA_{ENVD}$ results. On RDA1 and 2, samples from South Georgia and Shag Rocks displayed a positive association with temperature, and samples from Robert Island and Deception Island displayed a positive association with water depth (Figure 3A). Samples from King George Island and some samples from Elephant Island ($n = 5$) displayed a positive association with winter oxygen values at 500 m (Figure 3A).

When water depth was also controlled as a covariate alongside spatial distances, $pRDA_{ENV}$ explained 2.7% (adjusted R^2, $p < 0.001$) of the total genetic variation (Figure 3A). The first three constrained PC significantly explained 25.32% ($p < 0.001$), 14.12% ($p = 0.011$) and 3.27% ($p = 0.037$) of the total adjusted R^2. Bottom water temperature ($p = 0.022$), bottom water salinity ($p = 0.025$), winter phosphate values at 500 m ($p = 0.028$) and winter oxygen values at 500 m ($p = 0.012$) were significant variables in the final $pRDA_{ENV}$ results. When the effects of both geographical distances and water depth are controlled on RDA1 and 2, samples from South Georgia exhibited a negative association with bottom water salinity (Figure 3A). Samples from Elephant Island exhibited a position association with winter oxygen values at 500 m, as well as a negative association with temperature (Figure 3A).

3.5 | Genotype–Environment Association Within the Scotia Sea

For the dataset of *P. turqueti* within the Scotia Sea ($n = 52$), RDA_{full} was performed to explore the combined effects of spatial distance, water depth and environmental variables. RDA_{full} explained 19.07% (adjusted R^2, $p < 0.001$) of the total genetic variation (Figure 3B, Table S5). The first three constrained PCs significantly explained 37.53% ($p < 0.001$), 17.86% ($p = 0.015$) and 14.04% ($p = 0.021$) of the total adjusted R^2. Water depth ($p = 0.003$), summer oxygen values at sea surface ($p = 0.028$) and MEM1 ($p = 0.002$) were significant predictors in the final RDA_{full} results. On RDA1, samples from South Georgia and Shag Rocks displayed a positive association with MEM1 (Figure 3B). On RDA2, samples from Robert Island, Bransfield Strait and the West Antarctic Peninsula exhibited a positive association with water depth (Figure 3B).

Effects of spatial distances were then controlled in $pRDA_{ENVD}$ and $pRDA_{ENV}$. $pRDA_{ENVD}$ considered water depth as a testable environmental variable, which the model explained 2.9% (adjusted R^2, $p < 0.001$) of the total genetic variation (Figure 3B, Table S5). The first two constrained PC significantly explained 33.12% ($p = 0.002$) and 27.36% ($p = 0.014$) of the total adjusted R^2. Water depth ($p < 0.001$), winter nitrate values at sea surface ($p = 0.0.34$) and summer oxygen values at sea surface ($p = 0.021$) were recovered as significant variables in the final $pRDA_{ENVD}$

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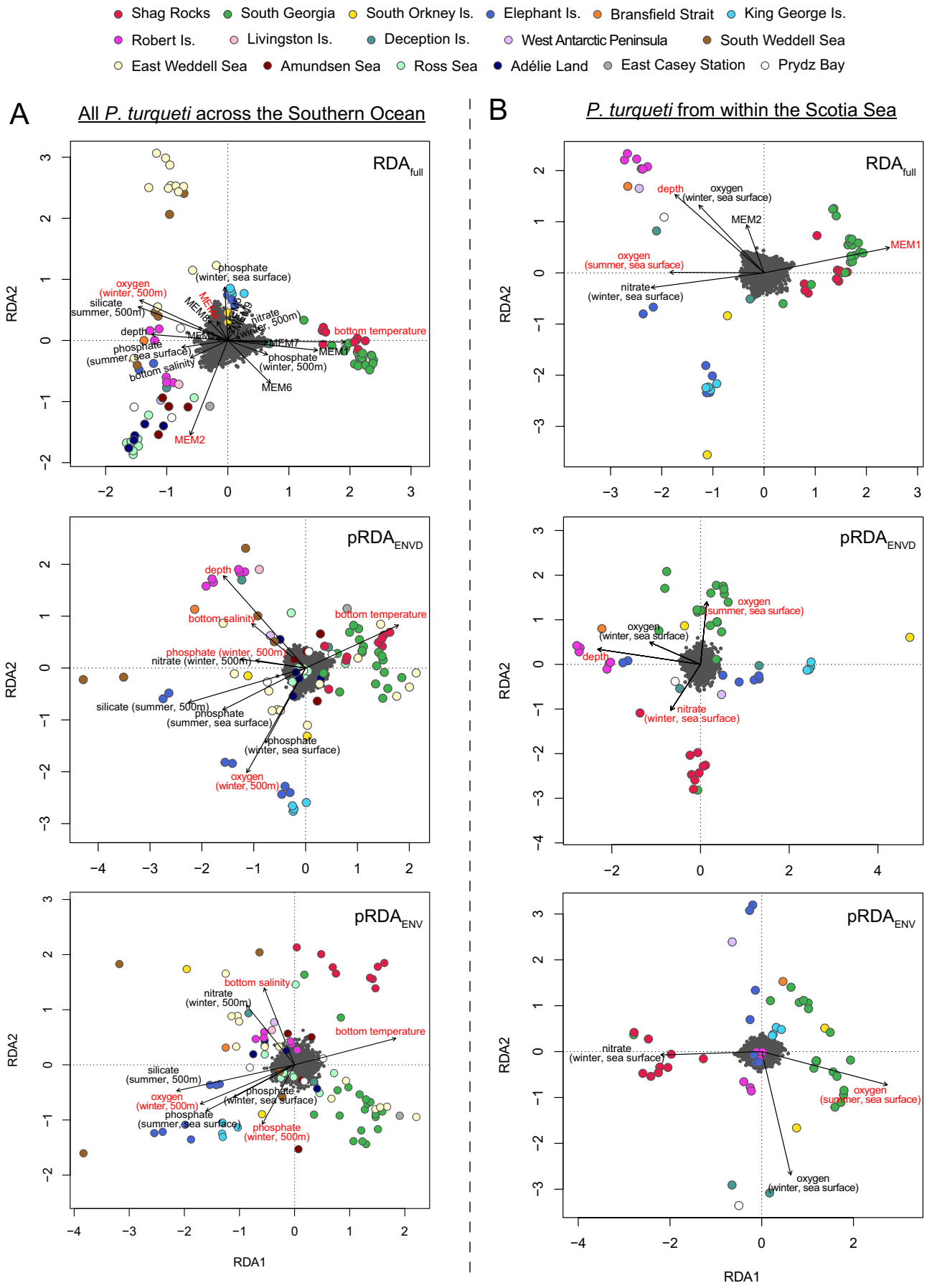

FIGURE 3 | Legend on next page.

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FIGURE 3 | Redundancy analysis (RDA) and partial redundancy analysis (pRDA) models showing genotype-environment association in (A) *Pareledone turqueti* collected across the Southern Ocean and (B) *P. turqueti* collected within the Scotia Sea, based on ddRAD loci data. RDA_{full} model incorporates spatial vectors (distance-based Moran's eigenvector maps [dbMEMs]), water depth and environmental variables as predictors. $pRDA_{ENVD}$ models incorporate water depth and environmental variables as predictors, while controlling for the effects of dbMEMs. $pRDA_{ENV}$ models incorporate environmental variables as predictors, while controlling for the effects of dbMEMs and water depth. Only significant predictors identified by *ordistep* are considered as input predictors in the models. Predictors highlighted in red are the significant predictors ($p < 0.05$) in the results. Grey dots represent SNPs, and coloured circles represent individual samples defined by assigned location labels. [Colour figure can be viewed at wileyonlinelibrary.com]

results. On RDA1 and 2, samples from South Georgia showed a positive association with summer oxygen values at sea surface, with samples from Shag Rocks showing a positive association with winter nitrate values at sea surface (Figure 3B). Samples from the Robert Island also displayed a positive association with water depth (Figure 3B).

When water depth was controlled as a covariate alongside spatial distances, $pRDA_{ENV}$ explained 1.4% (adjusted R^2, $p = 0.003$) of the total genetic variation (Figure 3B, Table S5). Only the first axis was significant, which explained 40.9% ($p = 0.009$) of the total adjusted R^2. Only summer oxygen values at sea surface ($p = 0.020$) were a significant variable in the final $pRDA_{ENV}$ results. On RDA1, samples from South Georgia showed a positive association with summer sea surface oxygen values (Figure 3B).

RDA_{full} and $pRDA_{ENVD}$ both revealed significant fine-scale positive genotype associations to water depth in the samples from around Robert Island. When the effects of spatial distance are controlled, $pRDA_{ENVD}$ also revealed significant positive genotype–water depth association in samples from the deep-water Scotia Sea, including those from Elephant Island collected at 343 m ($n = 2$), from Deception Island collected at 352 m ($n = 1$), from Bransfield Strait collected at 666 m ($n = 1$) and from Livingston Island collected at 363 m ($n = 1$). The findings suggest fine-scale isolation-by-water depth in locations within and around the South Shetland Islands.

3.6 | Outlier SNP Detection and Gene Ontology

A contrast between the Scotia Sea and Antarctic continental shelf (dataset of all *P. turqueti* samples) revealed a total of 276 loci containing putative outlier SNPs, identified by at least two methods (*OutFLANK*, *BayeScan*, *PCAdapt*, $pRDA_{ENVD}$, $pRDA_{ENV}$ and RDA_{full}) (Table S6). In the full dataset, 28 loci were annotated against the UniProtKB/Swiss-Prot database under the search criteria (Table S7). Among the annotated 28 contigs, seven were proteins related to transposable elements (TE), including retrotransposons (LTR; $n = 2$), putative domesticated TE ($n = 4$) and proteins that interact with TE ($n = 1$). GO analyses of biological functions highlighted annotated outlier loci were associated with mRNA processing and tRNA modification, protein modification, signalling pathways, regulation of metabolic processes and UV response (Figure S4).

In the dataset containing only *P. turqueti* samples from the Scotia Sea, a total of 143 contigs containing putative outlier SNPs were identified when individuals were separated between sample locations (Table S6). Of the 143 contigs, 14 were annotated with support of the UniProtKB/Swiss-Prot database under the search criteria, and three were related to TE, including putative domesticated TE ($n = 2$) and protein that interacts with TE ($n = 1$) (Table S7). GO analyses of biological functions highlighted annotated outlier loci were related to calcium ion transport, lactate and pyruvate metabolic processes, cell cycle regulation, oxygen transport, protein folding, UV response and DNA processes (Figure S5). The locus (CLocus_56272) that corresponded to haemocyanin G-type (units Oda to Odg) (Uniport ID: O61363) was detected as an outlier in both datasets (i.e., across all *P. turqueti* samples and in the samples from within the Scotia Sea) and notably returned the lowest *e*-value (0.00) and highest BitScore (652.90) among all of the annotated outlier loci (Table S7).

3.7 | Migration Across the Scotia Sea

Inference of contemporary migration (i.e., the last few generations) via BA3-SNP detected significant migration events between some locations across the Scotia Sea and between the Scotia Sea and the South Weddell Sea (Figure 4A, Table S8). The highest migration rate was detected from South Georgia to Shag Rocks, where 20% (posterior mean, 95% CI between 11.9 and 27.3) of the individuals per generation from Shag Rocks were detected to be migrants derived from South Georgia. Near the continental shelf, migration was detected from Elephant Island to each of South Orkney Island, King George Island and the South Weddell Sea; 8%–14% of individuals per generation (posterior mean) in these sink locations are migrants derived from Elephant Island. Migration was also observed from Robert Island to the South Weddell Sea (7% of individuals per generation (posterior mean) in the South Weddell Sea are migrants from Robert Island). Migration was also observed from the South Weddell Sea to Elephant Island (7% of individuals per generation (posterior mean)) in Elephant Island are migrants from the South Weddell Sea.

Bi-directional migration was detected by *divMigrate* between all locations across the Scotia Sea and South Weddell Sea (*Nm* between 0.08 and 1.00), with significant asymmetry between them (Table S9). The highest migration values ($Nm = 0.65$ and 1.00) were detected between the sub-Antarctic islands Shag Rocks and South Georgia (Figure 4B). Between the sub-Antarctic and locations near the continental shelf, relatively high migration values (when filtering for $Nm > 0.3$) were also present from Elephant Island to Shag Rocks and from Elephant Island, King George Island and the South Weddell Sea to South Georgia (Figure 4B). This highlights the sub-Antarctic Shag Rocks and South Georgia populations have been a major sink for *P. turqueti* near the continental shelf. Between locations near the Antarctic continental shelf, relatively high bi-directional migration values (when filtering for *Nm* at least 0.3) were also observed between Elephant Island and the South Weddell Sea, between Elephant

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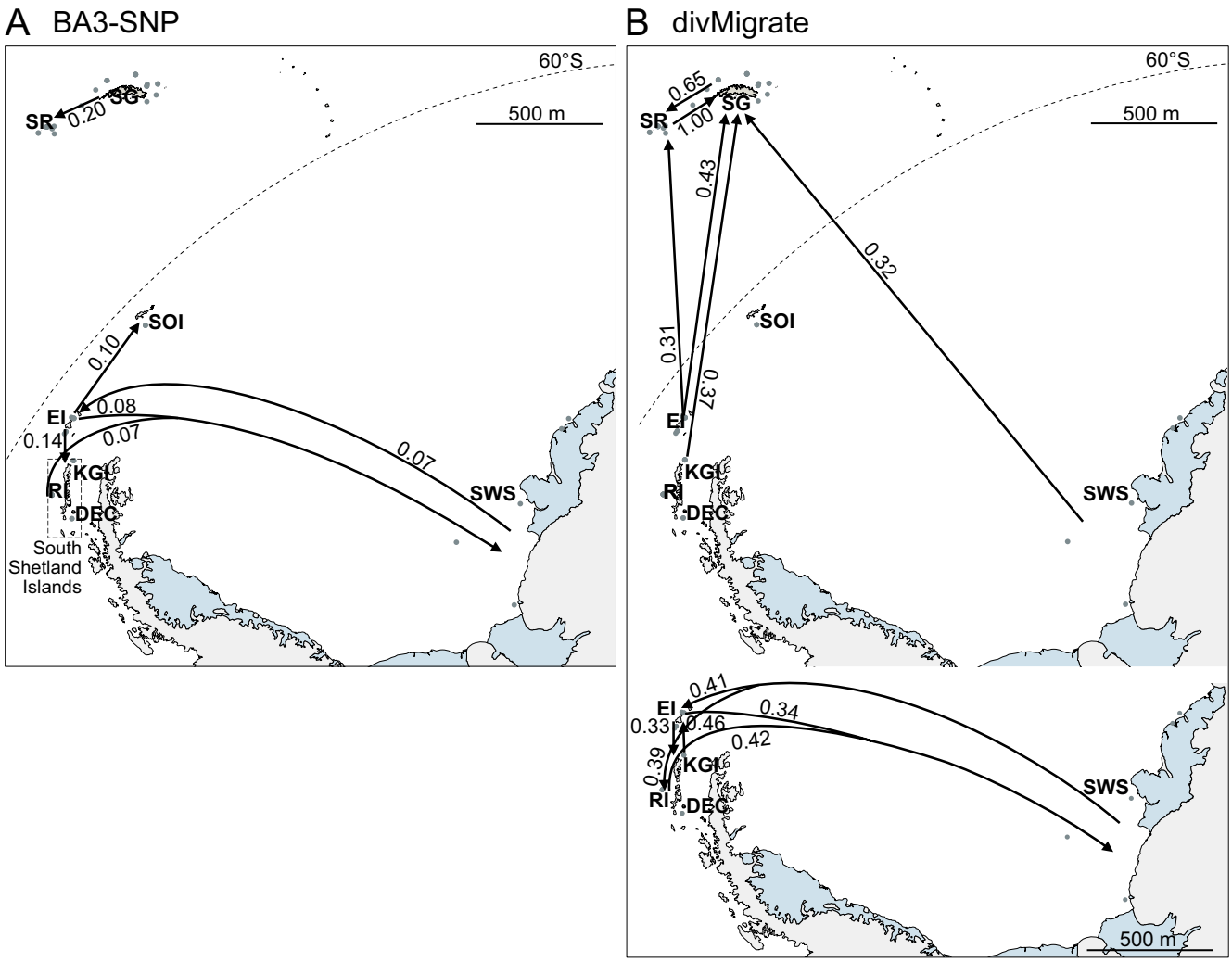

FIGURE 4 | Analyses of migration between Scotia Sea locations and the South Weddell Sea in *Pareledone turqueti*. Directions of migration are represented by arrows, with the inferred migration rate of each migration pathway placed next to the arrows. DEC, Deception Island; EI, Elephant Island; KGI, King George Island; RI, Robert Island; SG, South Georgia; SR, Shag Rocks; SWS, South Weddell Sea. Grey dots on the map represent individual sample locations. (A) Inferred contemporary migration rates in the last few generations by BA3-SNP. Values are posterior means representing the fraction of individuals in the sink population that are migrants derived from the source population per generation. Only significant migration rates are displayed. (B) Inferred relative migration (*Nm*; effective number of migrants) between locations by divMigrate. Only *Nm* values above the filter threshold of 0.3 are displayed. Top: Only showing migrations between sub-Antarctic locations (Shag Rocks and South Georgia) and locations around the Antarctic continental shelf. Bottom: Only showing migrations between locations around the Antarctic continental shelf. [Colour figure can be viewed at wileyonlinelibrary.com]

Island and King George Island and between Robert Island and the South Weddell Sea (Figure 4B).

4 | Discussion

The Southern Ocean is characterised by a diverse seascape, with the Antarctic islands, Antarctic continental shelf and deep sea presenting a complex series of dispersal barriers and corridors, as well as environmental features that could promote genetic connectivity and diversification. Understanding how the contemporary genomic patterns of *P. turqueti* can be related to seascape dynamics at both circumpolar and regional scales offers crucial ecological and evolutionary knowledge for establishing genetically-informed Southern Ocean biodiversity conservation practices across the Southern Ocean.

4.1 | Contemporary Drivers of Long-Distance Connectivity in a Benthic Direct Developing Octopus

The benthic environment of the broad Southern Ocean can be separated into distinct regions based on geomorphic features, temperature, sea ice extent and productivity, all of which can act as barriers to dispersal (Douglass et al. 2014). Isolation-by-geographic distance leading to genetic differentiation between geographically distant locations is also expected for benthic taxa with direct development species in the Southern Ocean (Poulin and Féral 1996). Genetic dissimilarities between distant locations are a feature of Southern Ocean benthic taxa with direct development (Baird, Miller, and Stark 2011; Collins et al. 2018; Hoffman et al. 2011; Moreau et al. 2019), including species of *Pareledone* (Allcock et al. 2011), and was also supported in this study of *P. turqueti*.

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Despite evidence for general geographical structure and isolation-by-distance in *P. turqueti*, signals of long-distance connectivity detected here are comparable with other Southern Ocean benthic taxa that have non-pelagic dispersal (González-Wevar et al. 2018; Leese, Agrawal, and Held 2010; Lau et al. 2021; Maroni and Wilson 2022). These observed patterns often involve connectivity between locations separated by deep sea that are outside of the depth range of the focal species, as well as over long geographical distances. For *P. turqueti*, the detected long-distance connectivity is superimposed on an overall genetic structure that reflects biogeographical patterns. Possible long-distance connectivity (e.g., between Scotia Sea and Prydz Bay) by *P. turqueti* could have been facilitated via rafting of adults or egg masses (e.g., on macroalgae or ice) or by egg masses being dislodged and dispersed via currents (Strugnell et al. 2012). In this study, evidence for long-distance connectivity was detected via admixture between the South Orkney Islands and Prydz Bay individuals; also, two individuals from Elephant Island exhibited admixture proportions that are otherwise found only within continental shelf locations. Genetic connectivity between the Scotia Sea and East Antarctic locations (including Heard Island and Prydz Bay) is apparent in other Southern Ocean benthic taxa (Moore et al. 2018; Strugnell et al. 2012; Baird, Miller, and Stark 2011; Hemery et al. 2012; Lau et al. 2021), with a probable current-driven seascape corridor hypothesised to be linking the two regions (Lau et al. 2021). Elephant Island has also been described as a 'choke point' for ocean current drifters entering the Scotia Sea (Renner et al. 2012; Thompson et al. 2009), with a larval dispersal study of Antarctic fish also indicating genetic connectivity around the Antarctic Peninsula can be achieved by stepping stone transport via Elephant Island (Young et al. 2018). Elephant Island as a major contemporary biological source and sink location is also supported in this study. Despite the hypothesised rafting by *P. turqueti* (Lau et al. 2023; Strugnell et al. 2012; Strugnell, Allcock, and Watts 2017), there is no direct support for this type of dispersal in this species, implying that the opportunities for long-distance travel via rafting are limited. Direct observations of rafting by Antarctic benthic taxa are rarely captured (e.g., see González-Wevar et al. 2024) but have been reported for sub-Antarctic benthic taxa (Waters et al. 2018). Direct observations are needed to verify the role of oceanic currents and the means of travelling along these currents in facilitating long-distance connectivity in Antarctic benthic taxa with direct development.

4.2 | Drivers of Migrations and Structure Within the Regional Scotia Sea

That five out of seven genetic clusters observed of all sampled *P. turqueti* samples had a major presence within the Scotia Sea supports the idea of the Scotia Sea as a highly diverse seascape that promotes population genetic differentiation (Strugnell, Allcock, and Watts 2017; Bernal-Durán et al. 2024). The distinct distributions of genetic clusters within the region appear to be linked to different oceanographic regimes known to the Scotia Sea and surrounding areas. For example, the connectivity observed between the Amundsen Sea—the West Antarctic Peninsula—Deception Island—Livingston Island—Robert Island coincides with the pathway of Circumpolar Deep Water intrusion onto the continental shelf of the Amundsen and Bellingshausen Seas, along the West Antarctic Peninsula to the South Shetland islands (Nakayama et al. 2018; Tarakanov 2010). The close affinities observed between East and South Weddell Sea, Elephant Island, Bransfield Strait and Robert Island coincide with the direction of the counter-clockwise Antarctic Coastal Current and Antarctic Slope Front (Collares et al. 2018; Moffat and Meredith 2018) and the clockwise Antarctic Circumpolar Current (ACC).

Connectivity between King George Island and Elephant Island could be attributed to the fast-moving near-surface circulation between the two areas and its role in facilitating rafting of individuals (Bartlett et al. 2021). An alternative explanation of the connectivity pattern between King George Island and Elephant Island could also be related to the genetic equilibrium that has yet to be reached between the two locations, as hypothesised in *P. charcoti* (Strugnell, Allcock, and Watts 2017).

Genetic distinctiveness of the sub-Antarctic islands of Shag Rocks and South Georgia, with some apparent contemporary migration from South Georgia to adjoining Shag Rocks, indicates their general isolation from other parts of Antarctica. This corresponds to previous evidence (based on analysis of mitochondrial DNA) that *P. turqueti* from Shag Rocks and South Georgia are considered a separate lineage from other locations around the Antarctic continental shelf (Strugnell et al. 2012). No contemporary migration was detected between Shag Rocks/South Georgia to other locations near the Antarctic continental shelf. However, *divMigrate* suggested relatively high migration ($Nm > 0.3$) from some locations around the Antarctic Peninsula (Elephant Island, King George Island and the South Weddell Sea) to Shag Rocks/South Georgia. It is likely that the northward migration to Shag Rocks/South Georgia from areas around the Antarctic Peninsula could be related to historical events. For example, *P. turqueti* could have experienced quaternary population expansion to sub-Antarctic island refugia from maritime Antarctica, as observed in the evolutionary history of the Antarctic limpet *Nacella concinna* (González-Wevar et al. 2013). The hypothesised historical migration also supports the previous interpretation that Shag Rocks and South Georgia served as sub-Antarctic glacial refugia for *P. turqueti*, among other identified refugia for the species located around the Antarctic continental shelf far away from the Antarctic Peninsula (Weddell Sea, Ross Sea and around Adélie Land) (Strugnell et al. 2012). However, additional samples would be needed to verify the sub-Antarctic island refugia hypothesis as proposed through *divMigrate* results.

The influence of regional currents is striking for *P. turqueti*, a benthic species with direct development, as gene flow in the Southern Ocean is often discussed in the context of pelagic dispersal (Muñoz-Ramírez et al. 2020; Galaska et al. 2017; Lau et al. 2021). Generally, genetic isolation between Scotia Sea localities has been reported in species with direct development (Linse et al. 2007; Lörz et al. 2012; Wilson, Schrödl, and Halanych 2009), and sometimes in species with pelagic larval dispersal (Demarchi et al. 2010; Young et al. 2015). It is important to note that the overall values of migration are low across the Scotia Sea and South Weddell Sea, relative to other Antarctic benthic species with pelagic larvae. For example, ddRADseq data of the Antarctic sponge *Dendrilla antarctica* with pelagic larvae indicated migration values > 0.8 (Nei's G_{ST} of *divMigrate*) between many Scotia Sea locations (Leiva et al. 2019). The overall observed migration rates in *P. turqueti* support the concept

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that dispersal is generally weak for a benthic direct-developing octopus. Finally, the interpretation of migration to and from South Orkney Island and Deception Island is also difficult due to low sample sizes from these areas ($n = 2$). Additional gene flow inferences with a high and balanced sample size ($n > 10$) (Sundqvist et al. 2016) between source-sink locations would be necessary to verify the roles of contemporary oceanic currents and historical demographic factors in facilitating connectivity in benthic species with direct development.

4.3 | Genotype–Environment Association Analyses Across the Circumpolar and Regional Seascape

The overall genetic structure of *P. turqueti* at a circumpolar scale can be most explained by geographic distance and bottom temperature. Given that bottom temperature is correlated with latitude in the Southern Ocean (Clarke et al. 2009), the observed association between temperature and genetic variation in *P. turqueti* could reflect general adaptation to temperature across the lower latitude sub-Antarctic zone and the higher latitude Antarctic continental shelf. Although the seafloor around the Antarctic continental shelf is thermally stable and cold (−2°C to 0°C), warmer temperatures are displayed along the regional Scotia Arc, from west of the Antarctic Peninsula at ~0°C to sub-Antarctic Shag Rocks/South Georgia at ~+2°C (Post et al. 2014). Further outlier loci analyses of *P. turqueti* samples also revealed evidence linked to potential physiological adaptations to warmer temperatures around the sub-Antarctic South Georgia and Shag Rocks (see below).

Across the circumpolar seascape, *P. turqueti* genotypes from the Scotia Sea showed a positive association with bottom temperature and oxygen and phosphate levels at 500 m, reflecting the general deep-water depths this species can be found. Oxygen is understood to be a tracer of meridional circulations in the Southern Ocean (Post et al. 2014), and samples from Elephant Island displayed a clear positive association with oxygen at 500 m. This further supports the role of currents in influencing benthic biota around Elephant Island, echoing the above interpretation that Elephant Island is a choke point for biological connectivity as seen through migration analyses.

Within the regional Scotia Sea, the full RDA indicates South Georgia and Shag Rocks are spatially distinct from the rest of the Southern Ocean. When the effects of geographic distances are removed, partial RDAs further revealed samples from South Georgia distinctly displayed a positive association with summer oxygen level at sea surface. The influence of summer oxygen levels or other variables that could be represented by such gradient may explain the observed small genetic differences between Shag Rocks and South Georgia on DAPC.

4.4 | Relationship Between Water Depth and Fine-Scale Genomic Variation Around the South Shetland Islands

Previous microsatellite data of *P. turqueti* highlighted genetic differentiation among samples from the Antarctic Peninsula, Elephant Island and South Orkney Islands, which could be associated with sampling collection depth (Strugnell, Allcock, and Watts 2017). In this study, while no general, significant association was found between genetic distance and water depth across samples from the Scotia Sea, signatures of fine-scale isolation-by-water depth were detectable in locations within and around the South Shetland Islands. *Structure* analyses further indicated that, within the Scotia Sea, clusters 6 and 7 were only found at depths > 340 m around Robert Island, Deception Island, Livingston Island, Bransfield Strait and Elephant Island. The association between clusters 6 and 7 and deeper water within the Scotia Sea does not seem to be explained by sampling bias, as these samples were collected from five different trawls over three expeditions. The sampling distribution of *P. turqueti* in the Scotia Sea in the present study was more comprehensive than previous microsatellite data analyses of *P. turqueti* (Strugnell et al. 2012; Strugnell, Allcock, and Watts 2017). The present study suggests that water depth may only be a driver of genetic variation of *P. turqueti* in the areas surrounding the South Shetland Islands group (including Bransfield Strait, Robert Island, Deception Island, Livingston Island and Elephant Island).

Within the sampled South Shetland Islands group (King George Island, Robert Island, Livingston Island and Deception Island), the sharp genetic discontinuity between King George Island and other islands is comparable with the pattern of spatial genetic structure in the sponge *Dendrilla antarctica* (Leiva et al. 2019). For *P. turqueti*, the genetic discontinuity between King George Island and Robert Island (and other South Shetland localities) does not seem to be explained by oceanic currents, as previous drifter data indicated that water could travel from the north of King George Island to Robert Island within 10 days (Bartlett et al. 2021). Topographic data indicate King George Island and other islands within the South Shetland Islands group are separated by the Nelson Strait (Capella et al. 1992). However, the waters of the Nelson Strait do not exceed ~500 m and its seafloor is characterised by bedrock and thin sediments (Simms et al. 2011), which are within the distributional and habitat range of *P. turqueti*. Given that the *P. turqueti* samples from King George Island were collected at shallow depths of 111 m, and samples from Robert Island, Livingston Island and Deception Island were collected at depths between 352 and 804 m, a plausible explanation of this genetic break could be fine-scale genetic isolation-by-water depth within the South Shetland Islands group.

The genotype–water depth association in some parts of the Scotia Sea could be correlated with other unaccounted factors that drive the genetic variation of *P. turqueti*. Other biological explanations include competition with other papillated *Pareledone* species, some of which only inhabit shallow depths in the Scotia Sea (e.g., down to 286 m in *P. charcoti*) (Strugnell, Allcock, and Watts 2017). Additional uncharacterised factors include palaeobiogeographical evolution (Bastías et al. 2023) and glacial survival in deeper waters throughout the Quaternary. During the last glacial maximum, the Southern Shetland Ice Cap was grounded down to ~400 m (Simms et al. 2011), which could be related to the observed upper depths of genetic clusters 6 and 7 (i.e., only found in areas > 340 m around the South Shetland Islands). More samples from the Scotia Sea across space and depths are needed to examine the relationship between genetic patterns and water depth at regional and local levels.

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4.5 | Outlier Loci Detection Across the Circumpolar Seascape

At a circumpolar scale, outlier loci detection analyses likely suggest potential selective signals related to genome interactions with transposition in *P. turqueti*. Transposable elements (TEs) are mobile genetic sequences that may change positions within a genome and are major components of many eukaryotic genomes (Etchegaray et al. 2021), including cephalopods (Whitelaw et al. 2020). Within an ecological context, the activity of TEs is hypothesised to promote genotypic variation leading to diversification within and between species (Niu et al. 2019; Serrato-Capuchina and Matute 2018). The propagation of TEs has been hypothesised to be favoured during local adaptation (Serrato-Capuchina and Matute 2018), genetic isolation and drift (Jurka, Bao, and Kojima 2011), small population size (Belyayev 2014) and/or response to environmental stress (Pimpinelli and Piacentini 2020).

It should be noted that reduced representation genomic data (i.e., ddRAD) are likely of low resolution for adaptive loci detection relative to whole genome sequencing (Hoban et al. 2016). However, the outlier loci, identified across multiple detection methods in this study, should represent a meaningful foundation for searching key loci of adaptation in future inferences. The potential selection for TEs and related genes in *P. turqueti* potentially unlocks a new perspective on understanding the long-standing questions regarding the genomic mechanisms of diversification and evolution in the Southern Ocean. Future long read- and whole genome sequencing would be required to investigate how TE and TE-interacting genes, or other adaptative signals and mechanisms such as inversions (Wellenreuther and Bernatchez 2018), contribute to genome evolution across evolutionary timeframe and space.

4.6 | Outlier Loci Associated With Temperature Gradient in the Regional Scotia Sea

In octopus, an increase in oxygen transport in haemolymph and RNA editing are apparent strategies for warm and cold temperature adaptation, respectively (Garrett and Rosenthal 2012; Oellermann, Strugnell et al. 2015). Our results show *P. turqueti* around Shag Rocks/South Georgia likely exhibit distinct adaptation to warmer sub-Antarctic temperatures. Evidence of warm temperature adaptation can also be inferred via outlier loci associated with haemocyanin G-type (units Oda to Odg) and RNA editing function detected at the circumpolar scale. Within the Scotia Sea, additional loci linked to immune and environmental stress response in marine invertebrates were also detected, including heat shock protein 60 (HSP60) and 6-phosphofructo-2-kinase/fructose-2,6-bisphosphatase 2 (PFK-2/Fru-2,6-P2).

Haemocyanins are copper-binding oxygen transport proteins that are found in arthropods and molluscs (van Holde, Miller, and Decker 2001). A previous study examining the blood oxygen binding capacity in the Antarctic octopus *P. charcoti*, a closely related species to *P. turqueti*, suggested haemocyanin in *P. charcoti* is thermally sensitive, and can maintain oxygen supply at warmer water temperatures up to 10°C (Oellermann, Lieb, et al. 2015). Despite the diversity of phylogenetic distance in haemocyanin functional unit G across octopus, there are few sequence differences between *P. charcoti* and *P. turqueti* (Oellermann, Strugnell, et al. 2015), suggesting the physiological functions of haemocyanins observed in *P. charcoti* could be applicable to *P. turqueti*. Considering RDAmodels indicated samples from Shag Rocks and South Georgia exhibited a positive association with temperature and MEM1 (a spatial vector), alongside a correlation between locus containing haemocyanin G-type sequence and bottom water temperature/MEM1, the evidence suggests possible selection for haemocyanin under warmer bottom temperatures around the more northerly sub-Antarctic Scotia Sea (i.e., Shag Rocks and South Georgia).

RNA editing is a strategy to adapt to polar conditions (including *Pareledone*) and cold induction in octopus (Birk et al. 2023; Garrett and Rosenthal 2012). Outlier loci detection analyses across all *P. turqueti* samples uncovered a locus related to RNA-mediated gene expression (Peptidyl-prolyl cis-trans isomerase (PPIases) (Thapar 2015). RDA models also indicated this locus was correlated with bottom water temperature, suggesting a relationship between a warm-to-cold temperature gradient and PPIases. It is also understood that RNA editing alters calcium ions binding in *Octopus bimaculoides* under cold induction (Birk et al. 2023). In this study, voltage-dependent calcium channel type D subunit alpha-1 (CACNA1D; a protein that mediates the entry of calcium ions into excitable cells) was also found to be associated with an outlier locus within the Scotia Sea. The putative selection for RNA-mediated gene expression and CACNA1D likely suggests distinct adaptations possibly linked to colder parts of the Southern Ocean.

5 | Conclusion

Understanding how the genomic patterns and adaptive loci of benthic species are structured across the Southern Ocean seascape offers insights on their potential for adapting to future environmental changes. The genomic structure of circum-Antarctic *P. turqueti* is complex and differs across spatial scales. From a circumpolar perspective, the genomic structure of *P. turqueti* is generally regional, as expected for a benthic direct developer, and while some long-distance dispersal appears likely, the specific mechanism of dispersal remains elusive. However, within the Scotia Sea, strong fine-scale genetic differentiation coupled with migrations is observed throughout the region, which could simultaneously be linked to the influence of local oceanic regimes, association with water depth and other biological and historical demographic processes. Outlier loci detection analyses also highlight possible local physiological adaptation to warmer temperatures in the sub-Antarctic, as well as signatures of adaptation to colder polar temperatures near the continental shelf. These findings indicate that the genomic features of *P. turqueti* are highly differentiated across spatial scales and seascape features, and its current adaptive potential to change, such as warming, is likely only limited to *P. turqueti* already living in the warmer sub-Antarctic. Future conservation efforts should concentrate on maximising the protection of genetic diversity and connectivity to maintain species' evolutionary resilience across seascape features.

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Author Contributions

N.G.W. and J.M.S. designed the study. P.C.W., A.L.A., F.C.M. and K.L. provided the material. T.J. performed laboratory work. N.G.W., C.N.S.S. and J.M.S. supervised data analyses. I.R.C. and S.C.Y.L. analysed data. S.C.Y.L. lead writing. All authors contributed to the results interpretation and final manuscript editing.

Acknowledgements

We thank the Australian Antarctic Division (AAD), Alfred Wegener Institute for Polar and Marine Research (AWI), British Antarctic Survey (BAS), Museum Victoria (MV), National Institute of Water and Atmospheric Research (NIWA) and George Jackson for assistance and samples for genetic analysis. This work was supported by Australian Research Council (ARC) Discovery grant DP190101347 (to J.M.S., N.G.W); Thomas Davies Research grant (Australian Academy of Science) (to J.M.S.); David Pearse bequest, Antarctic Science Bursary, Antarctic PhD student support grant (Antarctic Science Foundation) (to S.C.Y.L.); CoSyst grant (to J.M.S. and P.C.W.); Research Council of Finland grant 305532 (to P.C.W.); and the Australian Research Council (ARC) SRIEAS Grant SR200100005 Securing Antarctica's Environmental Future.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data Accessibility: The target capture of ddRAD loci data in *Pareledone turqueti* is deposited under the BioProject PRJNA853871, with SRA accessions SRR19892485—SRR19892582. The partial genome sequence of *P. turqueti* is deposited at the Queensland Cyber Infrastructure Foundation's (QCIF) QRIScloud public repository (http://data.qld.edu.au/public/Q5999/PTurqGenome/PT186.fasta). Detailed methods, including scripts and commands used to perform all analyses, are provided at https://github.com/sallycylau/seascape_turqueti.

Benefits Generated Statement

Research collaboration was developed with scientists from the countries providing samples and sequencing data, with all collaborators included as co-authors. Benefits from this research accrue from the sharing of our data and results on public databases as described above.

References

Ahrens, C. W., R. Jordan, J. Bragg, et al. 2021. "Regarding the F-Word: The Effects of Data Filtering on Inferred Genotype-Environment Associations." *Molecular Ecology Resources* 21, no. 5: 1460–1474. https://doi.org/10.1111/1755-0998.13351.

Alcala, N., J. Goudet, and S. Vuilleumier. 2014. "On the Transition of Genetic Differentiation From Isolation to Panmixia: What We Can Learn From GST and D." *Theoretical Population Biology* 93: 75–84. https://doi.org/10.1016/j.tpb.2014.02.003.

Allcock, A. L., I. Barratt, M. Eléaume, et al. 2011. "Cryptic Speciation and the Circumpolarity Debate: A Case Study on Endemic Southern Ocean Octopuses Using the COI Barcode of Life." *Deep-Sea Research Part II: Topical Studies in Oceanography* 58, no. 1–2: 242–249. https://doi.org/10.1016/j.dsr2.2010.05.016.

Allcock, A. L., A. S. Brierley, J. P. Thorpe, and P. G. Rodhouse. 1997. "Restricted Gene Flow and Evolutionary Divergence Between Geographically Separated Populations of the Antarctic Octopus *Pareledone turqueti*." *Marine Biology* 129, no. 1: 97–102. https://doi.org/10.1007/s002270050150.

Altschul, S. F., W. Gish, W. Miller, E. W. Myers, and D. J. Lipman. 1990. "Basic Local Alignment Search Tool." *Journal of Molecular Biology* 215, no. 3: 403–410. https://doi.org/10.1016/S0022-2836(05)80360-2.

Baird, H. P., K. J. Miller, and J. S. Stark. 2011. "Evidence of Hidden Biodiversity, Ongoing Speciation and Diverse Patterns of Genetic Structure in Giant Antarctic Amphipods." *Molecular Ecology* 20, no. 16: 3439–3454. https://doi.org/10.1111/j.1365-294X.2011.05173.x.

Barratt, I. M., M. P. Johnson, M. A. Collins, and A. L. Allcock. 2008. "Female Reproductive Biology of Two Sympatric Incirrate Octopod Species, *Adelieledone polymorpha* (Robson 1930) and *Pareledone turqueti* (Joubin 1905) (Cephalopoda: Octopodidae), from South Georgia." *Polar Biology* 31: 583–594. https://doi.org/10.1007/s00300-007-0392-x.

Bartlett, J. C., P. Convey, K. A. Hughes, S. E. Thorpe, and S. A. L. Hayward. 2021. "Ocean Currents as a Potential Dispersal Pathway for Antarctica's Most Persistent Non-Native Terrestrial Insect." *Polar Biology* 44: 209–216. https://doi.org/10.1007/s00300-020-02792-2.

Bastías, J., D. Chew, C. Villanueva, et al. 2023. "The South Shetland Islands, Antarctica: Lithostratigraphy and Geological Map." *Frontiers in Earth Science* 10: 1002760. https://doi.org/10.3389/feart.2022.1002760.

Belanger, C. L., D. Jablonski, K. Roy, S. K. Berke, A. Z. Krug, and J. W. Valentine. 2012. "Global Environmental Predictors of Benthic Marine Biogeographic Structure." *Proceedings of the National Academy of Sciences of the United States of America* 109, no. 35: 14046–14051. https://doi.org/10.1073/pnas.1212381109.

Belyayev, A. 2014. "Bursts of Transposable Elements as an Evolutionary Driving Force." *Journal of Evolutionary Biology* 27, no. 12: 2573–2584. https://doi.org/10.1111/jeb.12513.

Bernal-Durán, V., D. Donoso, A. Piñones, et al. 2024. "Combining Population Genomics and Biophysical Modelling to Assess Connectivity Patterns in an Antarctic Fish." *Molecular Ecology* 33, no. 11: e17360. https://doi.org/10.1111/mec.17360.

Binns, D., E. Dimmer, R. Huntley, D. Barrell, C. O'Donovan, and R. Apweiler. 2009. "QuickGO: A Web-Based Tool for Gene Ontology Searching." *Bioinformatics* 25, no. 22: 3045–3046. https://doi.org/10.1093/bioinformatics/btp536.

Birk, M. A., N. Liscovitch-Brauer, M. J. Dominguez, et al. 2023. "Temperature-Dependent RNA Editing in Octopus Extensively Recodes the Neural Proteome." *Cell* 186, no. 12: 2544–2555.e13. https://doi.org/10.1016/j.cell.2023.05.004.

Brasier, M. J., D. Barnes, N. Bax, et al. 2021. "Responses of Southern Ocean Seafloor Habitats and Communities to Global and Local Drivers of Change." *Frontiers in Marine Science* 8: 622721. https://doi.org/10.3389/fmars.2021.622721.

Broad Institute. 2019. "Picard Toolkit." Broad Institute, GitHub Repository. https://broadinstitute.github.io/picard/.

Capella, J. E., R. M. Ross, L. B. Quetin, and E. E. Hofmann. 1992. "A Note on the Thermal Structure of the Upper Ocean in the Bransfield Strait-South Shetland Islands Region." *Deep Sea Research Part A, Oceanographic Research Papers* 39, no. 7-8: 1221–1229. https://doi.org/10.1016/0198-0149(92)90065-2.

Catchen, J., P. A. Hohenlohe, S. Bassham, A. Amores, and W. A. Cresko. 2013. "Stacks: An Analysis Tool Set for Population Genomics." *Molecular Ecology* 22, no. 11: 3124–3140. https://doi.org/10.1111/mec.12354.

Chapman, C. C., M. A. Lea, A. Meyer, J. B. Sallée, and M. Hindell. 2020. "Defining Southern Ocean Fronts and Their Influence on Biological and Physical Processes in a Changing Climate." *Nature Climate Change* 10: 209–210. https://doi.org/10.1038/s41558-020-0705-4.

Chen, S., T. Huang, Y. Zhou, Y. Han, M. Xu, and J. Gu. 2017. "AfterQC: Automatic Filtering, Trimming, Error Removing and Quality Control for Fastq Data." *BMC Bioinformatics* 18, no. S3: 80.

13652394, 2025, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.17601 by Alfred Wegener Institut F. Polar- U. Meeresforschung Awi, Wiley Online Library on [10/01/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Chen, S., Y. Zhou, Y. Chen, and J. Gu. 2018. "Fastp: An Ultra-Fast All-In-One FASTQ Preprocessor." *Bioinformatics* 34, no. 17: i884–i890. https://doi.org/10.1093/bioinformatics/bty560.

Clarke, A., H. J. Griffiths, D. K. A. Barnes, M. P. Meredith, and S. M. Grant. 2009. "Spatial Variation in Seabed Temperatures in the Southern Ocean: Implications for Benthic Ecology and Biogeography." *Journal of Geophysical Research: Biogeosciences* 114: G03003. https://doi.org/10.1029/2008JG000886.

Collares, L. L., M. M. Mata, R. Kerr, J. Arigony-Neto, and M. M. Barbat. 2018. "Iceberg Drift and Ocean Circulation in the Northwestern Weddell Sea, Antarctica." *Deep-Sea Research Part II: Topical Studies in Oceanography* 149: 10–24. https://doi.org/10.1016/j.dsr2.2018.02.014.

Collins, E. E., M. P. Galaska, K. M. Halanych, and A. R. Mahon. 2018. "Population Genomics of *Nymphon australe* Hodgson, 1902 (Pycnogonida, Nymphonidae) in the Western Antarctic." *Biological Bulletin* 234: 180–191. https://doi.org/10.1086/698691.

Constable, A. J., J. Melbourne-Thomas, S. P. Corney, et al. 2014. "Climate Change and Southern Ocean Ecosystems I: How Changes in Physical Habitats Directly Affect Marine Biota." *Global Change Biology* 20, no. 10: 3004–3025. https://doi.org/10.1111/gcb.12623.

Danecek, P., A. Auton, G. Abecasis, et al. 2011. "The Variant Call Format and VCFtools." *Bioinformatics* 27, no. 15: 2156–2158. https://doi.org/10.1093/bioinformatics/btr330.

Dauphin, B., C. Rellstab, R. O. Wüest, et al. 2023. "Re-Thinking the Environment in Landscape Genomics." *Trends in Ecology & Evolution* 38, no. 3: 261–274. https://doi.org/10.1016/j.tree.2022.10.010.

De Broyer, C., B. Danis, A. Louise, et al. 2011. "How Many Species in the Southern Ocean? Towards a Dynamic Inventory of the Antarctic Marine Species." *Deep-Sea Research Part II: Topical Studies in Oceanography* 58: 5–17. https://doi.org/10.1016/j.dsr2.2010.10.007.

Demarchi, M., M. B. Chiappero, M. Tatián, and R. Sahade. 2010. "Population Genetic Structure of the Antarctic Ascidian *Aplidium falklandicum* From Scotia Arc and South Shetland Islands." *Polar Biology* 33: 1567–1576. https://doi.org/10.1007/s00300-010-0848-2.

Dormann, C. F., J. Elith, S. Bacher, et al. 2013. "Collinearity: A Review of Methods to Deal With It and a Simulation Study Evaluating Their Performance." *Ecography* 36, no. 1: 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Douglass, L. L., J. Turner, H. S. Grantham, et al. 2014. "A Hierarchical Classification of Benthic Biodiversity and Assessment of Protected Areas in the Southern Ocean." *PLoS One* 9, no. 7: e100551. https://doi.org/10.1371/journal.pone.0100551.

Dray, S., D. Bauman, G. Blanchet, et al. 2023. "adespatial: Multivariate Multiscale Spatial Analysis." R Package Version 0.3-23. https://CRAN.R-project.org/package=adespatial.

Earl, D. A., and B. M. VonHoldt. 2012. "STRUCTURE HARVESTER: A Website and Program for Visualizing STRUCTURE Output and Implementing the Evanno Method." *Conservation Genetics Resources* 4: 359–361. https://doi.org/10.1007/s12686-011-9548-7.

Etchegaray, E., M. Naville, J. N. Volff, and Z. Haftek-Terreau. 2021. "Transposable Element-Derived Sequences in Vertebrate Development." *Mobile DNA* 12: 1. https://doi.org/10.1186/s13100-020-00229-5.

Exposito-Alonso, M., T. R. Booker, L. Czech, et al. 2022. "Genetic Diversity Loss in the Anthropocene." *Science* 377, no. 6613: 1431–1435. https://doi.org/10.1126/science.abn5642.

Fabri-Ruiz, S., B. Danis, N. Navarro, P. Koubbi, R. Laffont, and T. Saucède. 2020. "Benthic Ecoregionalization Based on Echinoid Fauna of the Southern Ocean Supports Current Proposals of Antarctic Marine Protected Areas Under IPCC Scenarios of Climate Change." *Global Change Biology* 26: 2161–2180. https://doi.org/10.1111/gcb.14988.

Foll, M., and O. Gaggiotti. 2008. "A Genome-Scan Method to Identify Selected Loci Appropriate for Both Dominant and Codominant Markers: A Bayesian Perspective." *Genetics* 180: 977–993. https://doi.org/10.1534/genetics.108.092221.

Forester, B. R., J. R. Lasky, H. H. Wagner, and D. L. Urban. 2018. "Comparing Methods for Detecting Multilocus Adaptation With Multivariate Genotype–Environment Associations." *Molecular Ecology* 27, no. 9: 2215–2233. https://doi.org/10.1111/mec.14584.

Galaska, M. P., C. J. Sands, S. R. Santos, A. R. Mahon, and K. M. Halanych. 2017. "Geographic Structure in the Southern Ocean Circumpolar Brittle Star *Ophionotus victoriae* (Ophiuridae) Revealed From mtDNA and Single-Nucleotide Polymorphism Data." *Ecology and Evolution* 7, no. 2: 475–485. https://doi.org/10.1002/ece3.2617.

Garcia, H. E., K. W. Weathers, C. R. Paver, et al. 2013. "World Ocean Atlas 2013. Volume 3: Dissolved Oxygen, Apparent Oxygen Utilization, and Oxygen Saturation." In *NOAA Atlas NESDIS*, edited by S. Levitus and A. Mishonov, vol. 75, 27. Silver Spring, MD: NOAA.

Gargiulo, R., T. Kull, and M. F. Fay. 2020. "Effective Double-Digest RAD Sequencing and Genotyping Despite Large Genome Size." *Molecular Ecology Resources* 21, no. 4: 1037–1055. https://doi.org/10.1111/1755-0998.13314.

Garrett, S., and J. J. C. Rosenthal. 2012. "RNA Editing Underlies Temperature Adaptation in K^+ Channels From Polar Octopuses." *Science* 335, no. 6070: 848–851. https://doi.org/10.1126/science.1212795.

Gissi, E., E. Manea, A. D. Mazaris, et al. 2021. "A Review of the Combined Effects of Climate Change and Other Local Human Stressors on the Marine Environment." *Science of the Total Environment* 755: 142564. https://doi.org/10.1016/j.scitotenv.2020.142564.

González-Wevar, C. A., Y. Poveda, N. I. Segovia, et al. 2024. "Both High and Low Dispersal? Apparently Contradictory Genetic Patterns in the Antarctic Littorinid Gastropod *Laevilacunaria antarctica*." *Frontiers in Ecology and Evolution* 11: 1320649. https://doi.org/10.3389/fevo.2023.1320649.

González-Wevar, C. A., T. Saucède, S. A. Morley, S. L. Chown, and E. Poulin. 2013. "Extinction and Recolonization of Maritime Antarctica in the Limpet *Nacella concinna* (Strebel, 1908) During the Last Glacial Cycle: Toward a Model of Quaternary Biogeography in Shallow Antarctic Invertebrates." *Molecular Ecology* 22, no. 20: 5221–5236. https://doi.org/10.1111/mec.12465.

González-Wevar, C. A., N. I. Segovia, S. Rosenfeld, et al. 2018. "Unexpected Absence of Island Endemics: Long-Distance Dispersal in Higher Latitude Sub-Antarctic *Siphonaria* (Gastropoda: Euthyneura) Species." *Journal of Biogeography* 45: 874–884. https://doi.org/10.1111/jbi.13174.

Goudet, J. 2005. "Hierfstat, a Package for r to Compute and Test Hierarchical F-Statistics." *Molecular Ecology Notes* 5, no. 1: 184–186. https://doi.org/10.1111/j.1471-8286.2004.00828.x.

Goslee, S. C., and D. L. Urban. 2007. "The Ecodist Package for Dissimilarity-Based Analysis of Ecological Data." *Journal of Statistical Software* 22, no. 7: 1–19. https://doi.org/10.18637/jss.v022.i07.

Grummer, J. A., T. R. Booker, R. Matthey-Doret, P. Nietlisbach, A. T. Thomaz, and M. C. Whitlock. 2022. "The Immediate Costs and Long-Term Benefits of Assisted Gene Flow in Large Populations." *Conservation Biology* 36, no. 4: e13911. https://doi.org/10.1111/cobi.13911.

Gutt, J., N. Bertler, T. J. Bracegirdle, et al. 2015. "The Southern Ocean Ecosystem Under Multiple Climate Change Stresses – An Integrated Circumpolar Assessment." *Global Change Biology* 21, no. 4: 1434–1453. https://doi.org/10.1111/gcb.12794.

Gutt, J., E. Isla, A. N. Bertler, et al. 2018. "Cross-Disciplinarity in the Advance of Antarctic Ecosystem Research." *Marine Genomics* 37: 1–17. https://doi.org/10.1016/j.margen.2017.09.006.

13652394, 2025, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.17601 by Alfred Wegener Institut F. Polar- U. Meeresforschung Awi, Wiley Online Library on [10/01/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Hemery, L. G., M. Eléaume, V. Roussel, et al. 2012. "Comprehensive Sampling Reveals Circumpolarity and Sympatry in Seven Mitochondrial Lineages of the Southern Ocean Crinoid Species *Promachocrinus kerguelensis* (Echinodermata)." *Molecular Ecology* 21, no. 10: 2502–2518. https://doi.org/10.1111/j.1365-294X.2012.05512.x.

Hoban, S., J. L. Kelley, K. E. Lotterhos, et al. 2016. "Finding the Genomic Basis of Local Adaptation: Pitfalls, Practical Solutions, and Future Directions." *American Naturalist* 188, no. 4: 379–397. https://doi.org/10.1086/688018.

Hoffman, J. I., A. Clarke, M. S. Clark, P. Fretwell, and L. S. Peck. 2012. "Unexpected Fine-Scale Population Structure in a Broadcast-Spawning Antarctic Marine Mollusc." *PLoS One* 7, no. 3: e32415. https://doi.org/10.1371/journal.pone.0032415.

Hoffman, J. I., A. Clarke, K. Linse, and L. S. Peck. 2011. "Effects of Brooding and Broadcasting Reproductive Modes on the Population Genetic Structure of Two Antarctic Gastropod Molluscs." *Marine Biology* 158: 287–296. https://doi.org/10.1007/s00227-010-1558-6.

Hohenlohe, P. A., S. J. Amish, J. M. Catchen, F. W. Allendorf, and G. Luikart. 2011. "Next-Generation RAD Sequencing Identifies Thousands of SNPs for Assessing Hybridization Between Rainbow and Westslope Cutthroat Trout." *Molecular Ecology Resources* 11: 117–122. https://doi.org/10.1111/j.1755-0998.2010.02967.x.

Ingels, J., A. Vanreusel, A. Brandt, et al. 2012. "Possible Effects of Global Environmental Changes on Antarctic Benthos: A Synthesis Across Five Major Taxa." *Ecology and Evolution* 2, no. 2: 453–485. https://doi.org/10.1002/ece3.96.

Jombart, T., and I. Ahmed. 2011. "Adegenet 1.3-1: New Tools for the Analysis of Genome-Wide SNP Data." *Bioinformatics* 27, no. 21: 3070–3071. https://doi.org/10.1093/bioinformatics/btr521.

Jurka, J., W. Bao, and K. K. Kojima. 2011. "Families of Transposable Elements, Population Structure and the Origin of Species." *Biology Direct* 6: 44. https://doi.org/10.1186/1745-6150-6-44.

Keenan, K., P. Mcginnity, T. F. Cross, W. W. Crozier, and P. A. Prodöhl. 2013. "DiveRsity: An R Package for the Estimation and Exploration of Population Genetics Parameters and Their Associated Errors." *Methods in Ecology and Evolution* 4, no. 8: 782–788. https://doi.org/10.1111/2041-210X.12067.

Kelly, T. B. 2019. "TheSource: It Will Hold Your Beer." *Zenodo*. https://doi.org/10.5281/zenodo.3468524.

Langmead, B., and S. L. Salzberg. 2012. "Fast Gapped-Read Alignment With Bowtie 2." *Nature Methods* 9: 357–359. https://doi.org/10.1038/nmeth.1923.

Lau, S. C. Y., and J. M. Strugnell. 2022. "Is the Southern Ocean Ecosystem Primed for Change or at the Cliff Edge?" *Global Change Biology* 28: 4493–4494. https://doi.org/10.1111/gcb.16224.

Lau, S. C. Y., J. M. Strugnell, C. J. Sands, C. N. S. Silva, and N. G. Wilson. 2021. "Evolutionary Innovations in Antarctic Brittle Stars Linked to Glacial Refugia." *Ecology and Evolution* 11: 17428–17446. https://doi.org/10.1002/ece3.8376.

Lau, S. C. Y., J. M. Strugnell, C. J. Sands, C. N. S. Silva, and N. G. Wilson. 2023. "Genomic Insights of Evolutionary Divergence and Life History Innovations in Antarctic Brittle Stars." *Molecular Ecology* 32: 3382–3402. https://doi.org/10.1111/mec.16951.

Lau, S. C. Y., N. G. Wilson, N. R. Golledge, et al. 2023. "Genomic Evidence for West Antarctic Ice Sheet Collapse During the Last Interglacial." *Science* 382, no. 6677: 1384–1389. https://doi.org/10.1126/science.ade0664.

Leese, F., S. Agrawal, and C. Held. 2010. "Long-Distance Island Hopping Without Dispersal Stages: Transportation Across Major Zoogeographic Barriers in a Southern Ocean Isopod." *Naturwissenschaften* 97: 583–594. https://doi.org/10.1007/s00114-010-0674-y.

Leiva, C., S. Taboada, N. J. Kenny, et al. 2019. "Population Substructure and Signals of Divergent Adaptive Selection Despite Admixture in the Sponge *Dendrilla antarctica* From Shallow Waters Surrounding the Antarctic Peninsula." *Molecular Ecology* 29, no. 13: 3151–3170. https://doi.org/10.1111/mec.15135.

Leiva, C., A. Riesgo, D. Combosch, et al. 2022. "Guiding Marine Protected Area Network Design With Comparative Phylogeography and Population Genomics: An Exemplary Case From the Southern Ocean." *Diversity and Distributions* 28: 1891–1907. https://doi.org/10.1111/ddi.13590.

Levicoy, D., K. Flores, S. Rosenfeld, and L. Cárdenas. 2021. "Phylogeography and Genetic Diversity of the Microbivalve *Kidderia subquadrata*, Reveals New Data From West Antarctic Peninsula." *Scientific Reports* 11: 5705. https://doi.org/10.1038/s41598-021-85042-7.

Li, H. 2011. "A Statistical Framework for SNP Calling, Mutation Discovery, Association Mapping and Population Genetical Parameter Estimation From Sequencing Data." *Bioinformatics* 27, no. 21: 2987–2993. https://doi.org/10.1093/bioinformatics/btr509.

Li, H., and R. Durbin. 2009. "Fast and Accurate Short Read Alignment With Burrows-Wheeler Transform." *Bioinformatics* 25, no. 14: 1754–1760. https://doi.org/10.1093/bioinformatics/btp324.

Li, H., B. Handsaker, A. Wysoker, et al. 2009. "The Sequence Alignment/Map Format and SAMtools." *Bioinformatics* 25: 2078–2079. https://doi.org/10.1093/bioinformatics/btp352.

Linse, K., T. Cope, A.-N. Lörz, and C. Sands. 2007. "Is the Scotia Sea a Centre of Antarctic Marine Diversification? Some Evidence of Cryptic Speciation in the Circum-Antarctic Bivalve *Lissarca notorcadensis* (Arcoidea: Philobryidae)." *Polar Biology* 30, no. 8: 1059–1068. https://doi.org/10.1007/s00300-007-0265-3.

Locarnini, R. A., A. V. Mishonov, O. K. Baranova, et al. 2018. "World Ocean Atlas 2018, Volume 1: Temperature." In *NOAA Atlas NESDIS*, edited by A. Mishonov, vol. 81, 52. Silver Spring, MD: NOAA.

Lörz, A. N., P. Smith, K. Linse, and D. Steinke. 2012. "High Genetic Diversity Within *Epimeria georgiana* (Amphipoda) From the Southern Scotia Arc." *Marine Biodiversity* 42: 137–159. https://doi.org/10.1007/s12526-011-0098-8.

Maroni, P. J., and N. G. Wilson. 2022. "Multiple Doris "Kerguelenensis" (Nudibranchia) Species Span the Antarctic Polar Front." *Ecology and Evolution* 12: e9333. https://doi.org/10.1002/ece3.9333.

Matsuoka, K., A. Skoglund, G. Roth, et al. 2021. "Quantarctica, an Integrated Mapping Environment for Antarctica, the Southern Ocean, and Sub-Antarctic Islands." *Environmental Modelling and Software* 140: 105015. https://doi.org/10.1016/j.envsoft.2021.105015.

McLaughlin, E. L., N. G. Wilson, and G. W. Rouse. 2023. "Resolving the Taxonomy of the Antarctic Feather Star Species Complex *Promachocrinus 'Kerguelensis'* (Echinodermata: Crinoidea)." *Invertebrate Systematics* 37, no. 7: 498–527. https://doi.org/10.1071/IS22057.

Meirmans, P. G. 2014. "Nonconvergence in Bayesian Estimation of Migration Rates." *Molecular Ecology Resources* 14, no. 4: 726–733. https://doi.org/10.1111/1755-0998.12216.

Moffat, C., and M. Meredith. 2018. "Shelf-Ocean Exchange and Hydrography West of the Antarctic Peninsula: A Review." *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 376: 20170164. https://doi.org/10.1098/rsta.2017.0164.

Moore, J. M., J. I. Carvajal, G. W. Rouse, and N. G. Wilson. 2018. "The Antarctic Circumpolar Current Isolates and Connects: Structured Circumpolarity in the Sea Star *Glabraster antarctica*." *Ecology and Evolution* 8, no. 21: 10621–10633. https://doi.org/10.1002/ece3.4551.

Moreau, C., B. Danis, Q. Jossart, et al. 2019. "Is Reproductive Strategy a Key Factor in Understanding the Evolutionary History of Southern

1365294x, 2025, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.17601 by Alfred Wegener Institut F. Polar- U. Meeresforschung Awi, Wiley Online Library on [10/01/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Ocean Asteroidea (Echinodermata)?" *Ecology and Evolution* 9, no. 15: 8465–8478. https://doi.org/10.1002/ece3.5280.

Muñoz-Ramírez, C. P., D. K. A. Barnes, L. Cárdenas, et al. 2020. "Gene Flow in the Antarctic Bivalve *Aequiyoldia Eightsii* (Jay, 1839) Suggests a Role for the Antarctic Peninsula Coastal Current in Larval Dispersal." *Royal Society Open Science* 7: 200603. https://doi.org/10.1098/rsos.200603.

Mussmann, S. M., M. R. Douglas, T. K. Chafin, and M. E. Douglas. 2019. "BA3-SNPs: Contemporary Migration Reconfigured in BayesAss for Next-Generation Sequence Data." *Methods in Ecology and Evolution* 10, no. 10: 1808–1813. https://doi.org/10.1111/2041-210X.13252.

Nakayama, Y., D. Menemenlis, H. Zhang, M. Schodlok, and E. Rignot. 2018. "Origin of Circumpolar Deep Water Intruding Onto the Amundsen and Bellingshausen Sea Continental Shelves." *Nature Communications* 9: 3403. https://doi.org/10.1038/s41467-018-05813-1.

Niu, X. M., Y. C. Xu, Z. W. Li, et al. 2019. "Transposable Elements Drive Rapid Phenotypic Variation in *Capsella rubella*." *Proceedings of the National Academy of Sciences of the United States of America* 116: 6908–6913. https://doi.org/10.1073/pnas.1811498116.

Oellermann, M., B. Lieb, H. O. Pörtner, et al. 2015. "Blue Blood on Ice: Modulated Blood Oxygen Transport Facilitates Cold Compensation and Eurythermy in an Antarctic Octopod." *Frontiers in Zoology* 12: 6. https://doi.org/10.1186/s12983-015-0097-x.

Oellermann, M., J. M. Strugnell, B. Lieb, and F. C. Mark. 2015. "Positive Selection in Octopus Haemocyanin Indicates Functional Links to Temperature Adaptation." *BMC Evolutionary Biology* 15: 133. https://doi.org/10.1186/s12862-015-0411-4.

Oksanen, J. 2012. "Constrained Ordination: Tutorial With R and Vegan."

Oksanen, J., F. G. Blanchet, R. Kindt, et al. 2013. "vegan: Community Ecology Package." R Package Version 2.5-6.

Pante, E., and B. Simon-Bouhet. 2013. "Marmap: A Package for Importing, Plotting and Analyzing Bathymetric and Topographic Data in R." *PLoS One* 8, no. 9: e73051. https://doi.org/10.1371/journal.pone.0073051.

Pearson, W. R. 2013. "An Introduction to Sequence Similarity ("Homology") Searching." *Current Protocols in Bioinformatics* 42: 3.1.1–3.1.8. https://doi.org/10.1002/0471250953.bi0301s42.

Peterson, B. K., J. N. Weber, E. H. Kay, H. S. Fisher, and H. E. Hoekstra. 2012. "Double Digest RADseq: An Inexpensive Method for De Novo SNP Discovery and Genotyping in Model and Non-Model Species." *PLoS One* 7, no. 5: e37135. https://doi.org/10.1371/journal.pone.0037135.

Pimpinelli, S., and L. Piacentini. 2020. "Environmental Change and the Evolution of Genomes: Transposable Elements as Translators of Phenotypic Plasticity Into Genotypic Variability." *Functional Ecology* 34: 428–441. https://doi.org/10.1111/1365-2435.13497.

Pina-Martins, F., D. N. Silva, J. Fino, and O. S. Paulo. 2017. "Structure_threader: An Improved Method for Automation and Parallelization of Programs Structure, FastStructure and MavericK on Multicore CPU Systems." *Molecular Ecology Resources* 17, no. 6: e268–e274. https://doi.org/10.1111/1755-0998.12702.

Pittman, S., K. Yates, P. Bouchet, et al. 2021. "Seascape Ecology: Identifying Research Priorities for an Emerging Ocean Sustainability Science." *Marine Ecology Progress Series* 663: 1–29. https://doi.org/10.3354/meps13661.

Post, A. L., A. J. S. Meijers, A. D. Fraser, et al. 2014. "Part 4. Environmental Setting." In *Biogeographic Atlas of the Southern Ocean*, edited by C. De Broyer, P. Koubbi, H. J. Griffiths, et al. Cambridge, UK: Scientific Committee on Antarctic Research.

Poulin, É., and J. P. Féral. 1996. "Why Are There So Many Species of Brooding Antarctic Echinoids?" *Evolution* 50, no. 2: 820–830. https://doi.org/10.1111/j.1558-5646.1996.tb03891.x.

Pritchard, J. K., M. Stephens, and P. Donnelly. 2000. "Inference of Population Structure Using Multilocus Genotype Data." *Genetics* 155: 945–959. https://doi.org/10.1093/genetics/155.2.945.

Privé, F., K. Luu, B. J. Vilhjálmsson, and M. G. B. Blum. 2020. "Performing Highly Efficient Genome Scans for Local Adaptation With R Package Pcadapt Version 4." *Molecular Biology and Evolution* 37: 2153–2154. https://doi.org/10.1093/molbev/msaa053.

QGIS.org. 2024. *QGIS Geographic Information System*. QGIS Association. http://www.qgis.org/.

Rambaut, A., A. J. Drummond, D. Xie, G. Baele, and M. A. Suchard. 2018. "Posterior Summarization in Bayesian Phylogenetics Using Tracer 1.7." *Systematic Biology* 67, no. 5: 901–904. https://doi.org/10.1093/sysbio/syy032.

Raupach, M. J., S. Thatje, J. Dambach, P. Rehm, B. Misof, and F. Leese. 2010. "Genetic Homogeneity and Circum-Antarctic Distribution of Two Benthic Shrimp Species of the Southern Ocean, *Chorismus antarcticus* and *Nematocarcinus lanceopes*." *Marine Biology* 157: 1783–1797. https://doi.org/10.1007/s00227-010-1451-3.

Renner, A. H. H., S. E. Thorpe, K. J. Heywood, E. J. Murphy, J. L. Watkins, and M. P. Meredith. 2012. "Advective Pathways Near the Tip of the Antarctic Peninsula: Trends, Variability and Ecosystem Implications." *Deep-Sea Research Part I: Oceanographic Research Papers* 63: 91–101. https://doi.org/10.1016/j.dsr.2012.01.009.

Revelle, W. 2020. "psych: Procedures for Personality and Psychological Research." https://cran.r-project.org/package=psych.

Rice, W. R. 1989. "Analyzing Tables of Statistical Tests." *Evolution* 43, no. 1: 223. https://doi.org/10.2307/2409177.

Rochette, N. C., and J. M. Catchen. 2017. "Deriving Genotypes From RAD-Seq Short-Read Data Using Stacks." *Nature Protocols* 12, no. 12: 2640–2659. https://doi.org/10.1038/nprot.2017.123.

Serrato-Capuchina, A., and D. R. Matute. 2018. "The Role of Transposable Elements in Speciation." *Genes* 9, no. 5: 254. https://doi.org/10.3390/genes9050254.

Simms, A. R., K. T. Milliken, J. B. Anderson, and J. S. Wellner. 2011. "The Marine Record of Deglaciation of the South Shetland Islands, Antarctica Since the Last Glacial Maximum." *Quaternary Science Reviews* 30, no. 13-14: 1583–1601. https://doi.org/10.1016/j.quascirev.2011.03.018.

Soler-Membrives, A., K. Linse, K. J. Miller, and C. P. Arango. 2017. "Genetic Signature of Last Glacial Maximum Regional Refugia in a Circum-Antarctic Sea Spider." *Royal Society Open Science* 4, no. 10: 170615. https://doi.org/10.1098/rsos.170615.

Strass, V. H., G. Rohardt, T. Kanzow, M. Hoppema, and O. Boebel. 2020. "Multidecadal Warming and Density Loss in the Deep Weddell Sea, Antarctica." *Journal of Climate* 33, no. 22: 9863–9881. https://doi.org/10.1175/JCLI-D-20-0271.1.

Strugnell, J. M., A. L. Allcock, and P. C. Watts. 2017. "Closely Related Octopus Species Show Different Spatial Genetic Structures in Response to the Antarctic Seascape." *Ecology and Evolution* 7, no. 19: 8087–8099. https://doi.org/10.1002/ece3.3327.

Strugnell, J. M., P. C. Watts, P. J. Smith, and A. L. Allcock. 2012. "Persistent Genetic Signatures of Historic Climatic Events in an Antarctic Octopus." *Molecular Ecology* 21, no. 11: 2775–2787. https://doi.org/10.1111/j.1365-294X.2012.05572.x.

Sundqvist, L., K. Keenan, M. Zackrisson, P. Prodöhl, and D. Kleinhans. 2016. "Directional Genetic Differentiation and Relative Migration." *Ecology and Evolution* 6, no. 11: 3461–3475. https://doi.org/10.1002/ece3.2096.

13652394, 2025, 2, Downloaded from https://onlinelibrary.wiley.com/doi/10.1111/mec.17601 by Alfred Wegener Institut F. Polar- U. Meeresforschung Awi, Wiley Online Library on [10/01/2025]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Supek, F., M. Bošnjak, N. Škunca, and T. Šmuc. 2011. "REVIGO Summarizes and Visualizes Long Lists of Gene Ontology Terms." *PLoS One* 6: e21800. https://doi.org/10.1371/journal.pone.0021800.

Tarakanov, R. Y. 2010. "Circumpolar Bottom Water in the Scotia Sea and the Drake Passage." *Oceanology* 50, no. 1: 1–17. https://doi.org/10.1134/S0001437010010017.

Teschke, K., H. Pehlke, V. Siegel, H. Bornemann, R. Knust, and T. Brey. 2020. "An Integrated Compilation of Data Sources for the Development of a Marine Protected Area in the Weddell Sea." *Earth System Science Data* 12, no. 2: 1003–1023. https://doi.org/10.5194/essd-12-1003-2020.

Thapar, R. 2015. "Roles of Prolyl Isomerases in RNA-Mediated Gene Expression." *Biomolecules* 5, no. 2: 974–999. https://doi.org/10.3390/biom5020974.

Thompson, A. F., K. J. Heywood, S. E. Thorpe, A. H. H. Renner, and A. Trasviña. 2009. "Surface Circulation at the Tip of the Antarctic Peninsula From Drifters." *Journal of Physical Oceanography* 39, no. 1: 3–26. https://doi.org/10.1175/2008JPO3995.1.

van Holde, K. E., K. I. Miller, and H. Decker. 2001. "Hemocyanins and Invertebrate Evolution." *Journal of Biological Chemistry* 276, no. 19: 15563–15566. https://doi.org/10.1074/jbc.R100010200.

Vernet, M., W. Geibert, M. Hoppema, et al. 2019. "The Weddell Gyre, Southern Ocean: Present Knowledge and Future Challenges." *Reviews of Geophysics* 57: 623–708. https://doi.org/10.1029/2018RG000604.

Vieira, F. G., F. Lassalle, T. S. Korneliussen, and M. Fumagalli. 2016. "Improving the Estimation of Genetic Distances From Next-Generation Sequencing Data." *Biological Journal of the Linnean Society* 117: 139–149. https://doi.org/10.1111/bij.12511.

Waters, J. M., T. M. King, C. I. Fraser, and C. Garden. 2018. "Rafting Dispersal in a Brooding Southern Sea Star (Asteroidea: *Anasterias*)." *Invertebrate Systematics* 32, no. 2: 253–258. https://doi.org/10.1071/IS17037.

Weir, B. S., and C. C. Cockerham. 1984. "Estimating F-Statistics for the Analysis of Population Structure." *Evolution* 38, no. 6: 1358. https://doi.org/10.2307/2408641.

Wellenreuther, M., and B. Bernatchez. 2018. "Eco-Evolutionary Genomics of Chromosomal Inversions." *Trends in Ecology & Evolution* 33, no. 6: 427–440. https://doi.org/10.1016/j.tree.2018.04.002.

Whitelaw, B. L., I. R. Cooke, J. Finn, et al. 2020. "Adaptive Venom Evolution and Toxicity in Octopods Is Driven by Extensive Novel Gene Formation, Expansion, and Loss." *GigaScience* 9, no. 11: giaa120. https://doi.org/10.1093/gigascience/giaa120.

Whitlock, M. C., and K. E. Lotterhos. 2015. "Reliable Detection of Loci Responsible for Local Adaptation: Inference of a Null Model Through Trimming the Distribution of F_{ST}." *American Naturalist* 186: S24–S36. https://doi.org/10.1086/682949.

Wilson, N. G., M. Schrödl, and K. M. Halanych. 2009. "Ocean Barriers and Glaciation: Evidence for Explosive Radiation of Mitochondrial Lineages in the Antarctic Sea Slug *Doris kerguelenensis* (Mollusca, Nudibranchia)." *Molecular Ecology* 18: 965–984. https://doi.org/10.1111/j.1365-294X.2008.04071.x.

Wood, D. E., and S. L. Salzberg. 2014. "Kraken: Ultrafast Metagenomic Sequence Classification Using Exact Alignments." *Genome Biology* 15: R46. https://doi.org/10.1186/gb-2014-15-3-r46.

Xavier, J. C., A. Brandt, Y. Ropert-Coudert, et al. 2016. "Future Challenges in Southern Ocean Ecology Research." *Frontiers in Marine Science* 3: 94. https://doi.org/10.3389/fmars.2016.00094.

Young, E. F., M. Belchier, L. Hauser, et al. 2015. "Oceanography and Life History Predict Contrasting Genetic Population Structure in Two Antarctic Fish Species." *Evolutionary Applications* 8, no. 5: 486–509. https://doi.org/10.1111/eva.12259.

Young, E. F., N. Tysklind, M. P. Meredith, et al. 2018. "Stepping Stones to Isolation: Impacts of a Changing Climate on the Connectivity of Fragmented Fish Populations." *Evolutionary Applications* 11, no. 6: 978–994. https://doi.org/10.1111/eva.12613.

Zweng, M. M., J. R. Reagan, D. Seidov, et al. 2019. "World Ocean Atlas 2018, Volume 2: Salinity." In *World Ocean Atlas 2018*, edited by A. Mishonov, 82. Silver Spring, MD: NOAA Atlas NESDIS.

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