Rev Fish Biol Fisheries (2023) 33:295–310
https://doi.org/10.1007/s11160-023-09756-9

ORIGINAL RESEARCH

Circumpolar sampling reveals high genetic connectivity of Antarctic toothfish across their spatial distribution

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Received: 16 November 2021 / Accepted: 8 January 2023 / Published online: 20 January 2023
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Abstract Antarctic Toothfish are a circumpolar species which are targeted in multiple fisheries around Antarctica covering nine statistical areas within the Convention for the Conservation of Antarctic Marine Living Resources. Despite this, it is still unclear whether the species forms a single stock across its circumpolar distribution, shows a pattern of isolation by distance, or exhibits discrete stock structure between different regions. Recent genetics studies of Antarctic toothfish have shown connectivity between two areas (Ross Sea and Antarctic Peninsula), but earlier studies with smaller number of markers produced inconsistent results with regards to genetic connectivity between other geographic locations. Here we present a range-wide population genetic study of Antarctic toothfish using > 11,000 nuclear single nucleotide polymorphisms from 715 fish collected. Our results indicate that genetic diversity of the Antarctic toothfish is very low, with only 0.1% of genetic variability associated with geographic location. Multiple clustering methods, both supervised and unsupervised, indicated no distinct breeding populations. These results are consistent with current theories of egg and larval dispersal by the predominant Antarctic currents.

Keywords Fisheries · Antarctica · Close-kin · Population genetics · SNPs

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s11160-023-09756-9.

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Introduction

Understanding population structure of harvested species is an important element of any sustainable resource management strategy, especially where fish stocks and/or the fisheries are spatially structured (Begg and Waldman 1999). Southern Ocean fisheries for the highly valuable Antarctic toothfish (*Dissostichus mawsoni*) have been developed in a number of regions within the area of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR). While suitable habitat for Antarctic toothfish can be found continuously around Antarctica and toothfish have a circumpolar distribution, their fisheries are managed by CCAMLR at the level

of Food and Agriculture Organization Subareas and Divisions (See Fig. 1). However, it is still unclear whether the species forms a single stock across its circumpolar distribution, shows a pattern of isolation by distance, or exhibits discrete stock structure between different regions.

Antarctic toothfish are long-lived (> 30 years old), late maturing (~ 12–16 years old) and highly adapted to cold Antarctic waters through the use of mechanisms such as antifreeze glycoproteins (Hanchet et al. 2015; Nicodemus-Johnson et al. 2011). They utilise a broad range of habitats throughout their lifespan, from the epipelagic as planktonic larvae to benthopelagic slope habitats in excess of 2000 m depth as adults (Hanchet et al. 2010). Stock hypotheses for Antarctic toothfish have been developed for several areas and often include elements of connectivity with adjacent areas due to either continuous habitat or ocean currents.

The first stock hypothesis was developed for the Ross Sea region (Hanchet et al. 2008) and later extended by Parker et al. (2014) to the entire Area 88 (Fig. 1) including the Amundsen Sea (CCAMLR Subarea 88.2) and the Bellinghausen Sea (Subarea

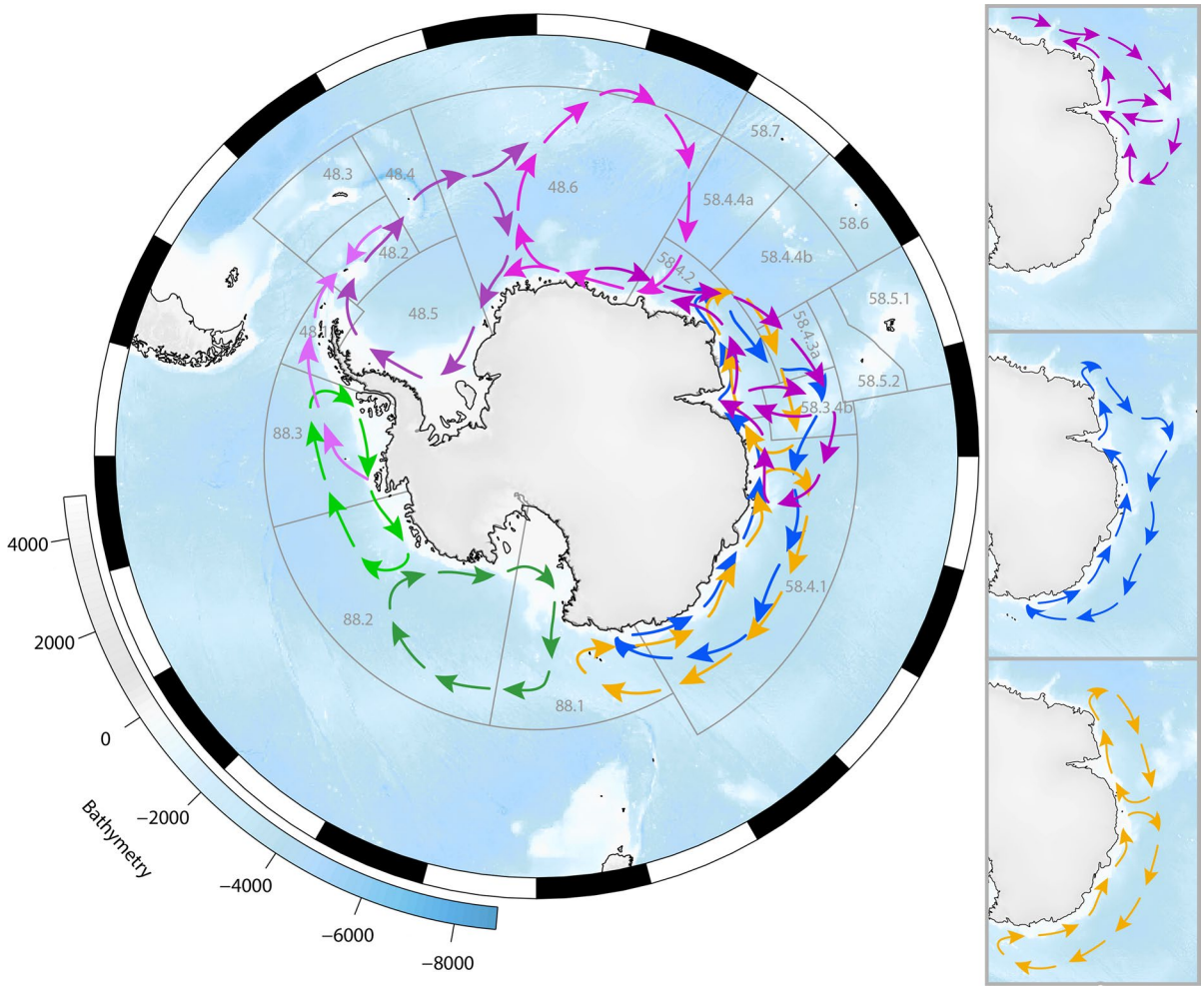

Fig. 1 Amalgamated stock hypotheses for Antarctic toothfish (*Dissostichus mawsoni*) in the Southern Ocean from Agnew et al. (2009; orange arrows), Yates et al. (2017; blue arrows) and Okuda et al. (2018; purple arrows) for East Antarctica (Area 58), Parker et al. (2014; green arrows) for Area 88, and Söffker et al. (2018 – Hypothesis 3; pink arrows) for Area 48. Grey lines indicate CCAMLR management boundaries. Side panels show each layer of overlapping hypotheses in East Antarctica. Different shades indicate differing stocks in the same hypothesis

88.3). Questions still remain around broader connectivity of toothfish to the surrounding areas of the Southern Indian Ocean (CCAMLR Division 58.4.1) and to the north in the region managed by the South Pacific Regional Fisheries Management Organisation (SPRFMO).

For East Antarctica (Area 58) three different stock hypotheses have been developed which differ in the assumptions around the locations of spawning grounds and connectivity to other regions. Agnew et al. (2009) proposed two stocks in the region, one to the west centred on Prydz Bay, the other one stretching to the east towards the Ross Sea (Fig. 1). Yates et al. (2019) analysed catch rates, mean weight, maturity stage and sex ratios of Antarctic toothfish in East Antarctica. The distribution of mean weight and maturity indicated the presence of both spawning and nursery grounds on the continental slope, a conclusion which supported the hypothesis of a spawning migration from the Antarctic continent to BANZARE Bank (CCAMLR Division 58.4.3b) by Taki et al. (2011). Okuda et al. (2018) hypothesised similar distributions of spawning and nursery grounds but expanded the proposed area to include Subareas 48.6 and 48.2.

In 2018, the CCAMLR Workshop for the Development of a *D. mawsoni* Population Hypothesis for Area 48 brought together available information on Antarctic toothfish, resulting in three potential population hypotheses. These hypotheses included between two and four subpopulations contributing to Antarctic toothfish in Area 48 (Söffker et al. 2018). All three hypotheses assumed different levels of connectivity between adjacent CCAMLR areas, e.g. between Subarea 48.6 and Division 58.4.2, and between Subareas 48.2 and 88.3 (Fig. 1).

Genetic studies can be used to evaluate the existence of gene flow between fish populations across regions and therefore provide insights into stock structure (Ward 2000). In early population genetic studies of Antarctic toothfish conflicting results were reported by investigators. These studies focussed on a limited number of genetic markers and the methods to collect genetic data have been inconsistent.

The first genetic study of Antarctic toothfish examined random amplified polymorphic DNA markers and found significant differentiation between McMurdo Sound (Subarea 88.1) and Antarctic Peninsula (Subarea 48.1) populations (Parker et al. 2002). Smith and Gaffney (2005) then investigated mitochondrial DNA (mtDNA) sequences and seven nuclear single-nucleotide polymorphism (SNP) markers and found no population differentiation among samples taken from CCAMLR Subareas 48.1 and 88.1, and Division 58.4.2. Kuhn and Gaffney (2008) expanded on the work of Smith and Gaffney (2005) by examining four mitochondrial regions and 13 nuclear markers in samples from the same three areas and one additional area in the Southern Ocean (Subarea 88.2). Unlike Smith and Gaffney (2005), the results showed genetically distinct populations between all four areas. Mugue et al. (2014) collected samples from seven CCAMLR management units and compared five of the most polymorphic nuclear genes previously analysed by Kuhn and Gaffney (2008). They found no genetic differences between locations, and highlighted discrepancies in allelic frequencies for several marker loci compared to Kuhn and Gaffney (2008).

More recently, a study has expanded mtDNA analysis and added seven nuclear microsatellite markers (Choi et al. 2021). Another study with genome-wide SNP markers was presented in Ceballos et al. (2021). In both instances the studies used two regions of interest, the first using neighbouring regions and the second regions on opposite sides of the Antarctic continent. Neither of these more recent studies which used a range of genetic techniques were able to find convincing evidence of genetic population differences between regions.

Here, we use nuclear SNP markers obtained through genotyping-by-sequencing to investigate the stock structure of Antarctic toothfish in the Southern Ocean around Antarctica. The genetic data generated based on comprehensive circumpolar sampling provides a more detailed view of the Antarctic toothfish genetic population structure compared to previous work. Recently, increased interest has been given to estimating a fisheries biomass through the use of genetic methods such as close-kin mark recapture where traditional biomass estimations have been unreliable (Bravington et al. 2016a,b). Based on our results, we also discuss the possibility of using close-kin mark recapture techniques to estimate the population size of Antarctic toothfish.

Methods

Sample collection

Tissue samples (either muscle or fin clip) from 4,551 Antarctic toothfish were collected during commercial fishing operations in small-scale research units (SSRU) from ten CCAMLR management areas and two areas adjacent to the CCAMLR boundary within SPRFMO waters (Fig. 2). Samples were all collected within an 18 month period and collected by either crew, researchers or scientific observers on board of fishing vessels aiming to maintain an even length across samples, stored in at least 70% ethanol and sent to the Australian Antarctic Division for processing.

Samples were collected from Subareas 48.1, 48.2, 48.4, 48.6, 88.1, 88.2 and 88.3, Divisions 58.4.1, 58.4.2 and 58.5.2, as well as the SPRFMO area north of Subarea 88.1 (Fig. 2, Table 1). While samples from Division 58.4.3b were not available, samples were collected from Division 58.5.2, where Antarctic toothfish are occasionally captured in the fishery dominated by Patagonian toothfish (*D. eleginoides*) and were considered a suitable proxy for Division 58.4.3b immediately to the south where Antarctic toothfish reside all year round.

Where large amounts of samples were available within Subareas or Divisions (Table 1), samples were randomly selected within SSRUs with the aim to provide the greatest spatial coverage possible and to maintain an equal distribution of samples.

DNA Extraction

DNA was extracted from muscle or fin clip samples using a Promega 'Maxwell RSC 48' automated nucleic acid purification platform with the Whole Blood kit. Briefly, 30–100 mg of tissue was incubated in 400 µl Tissue Lysis Buffer and 30 µl proteinase K for 3 h at 56 degrees. Following digestion, 15 µl

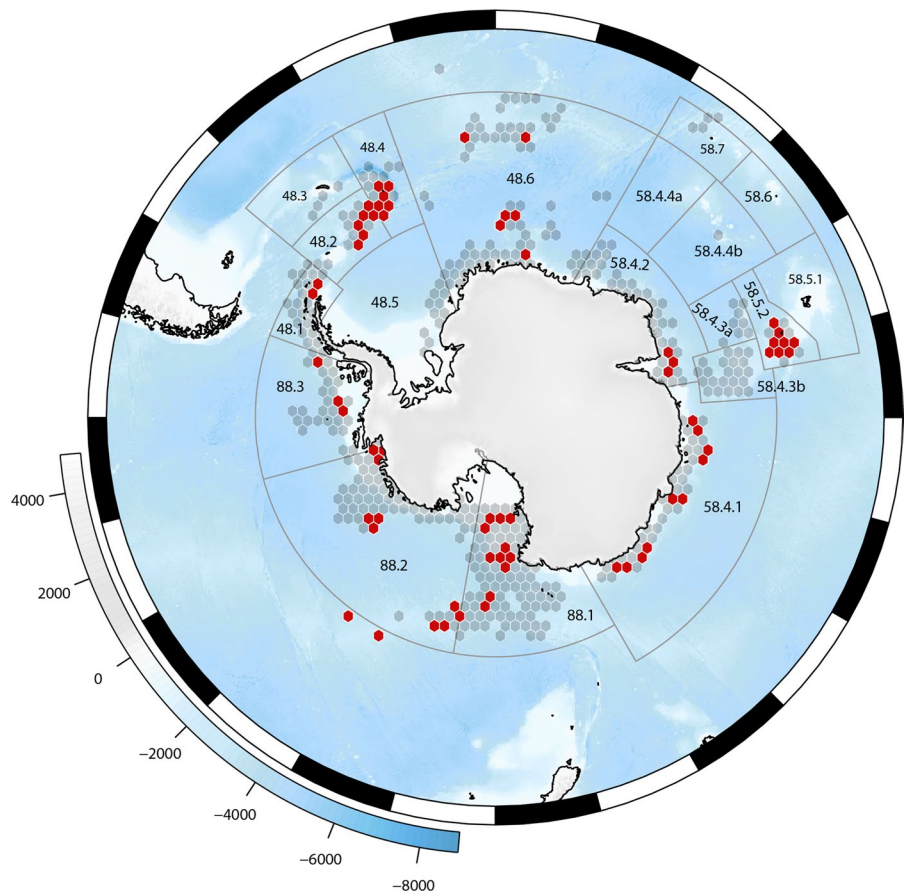

Fig. 2 Locations of Antarctic toothfish (*Dissostichus mawsoni*) tissue samples collected (red) across areas where Antarctic toothfish have been caught (grey hexagons, amalgamated data from Robinson and Reid (2016) and Duhamel et al. (2014))

Table 1 Numbers of available Antarctic toothfish (*Dissostichus mawsoni*) tissue samples and amount that passed quality control and used in subsequent analysis

Area	Available samples	Sequenced samples	Final analysis
48.1	50	50	50
48.2	134	46	42
48.4	239	45	44
48.6	70	41	41
58.4.1	2232	196	191
58.4.2	1033	45	45
58.5.2	117	42	42
88.1	339	104	103
88.2	292	126	126
88.3	30	30	29
SPRFMO	15	3	3
Total	4551	728	715

RNase (4 mg/ml) was added and incubated at room temperature for 5 min. Extracts were eluted in 70 µl of elution buffer and stored at − 20 °C.

DNA was quantified using a Qubit 2.0 fluorometer broad range assay kit (Invitrogen) and quality scored based on an assessment of recovered DNA fragment size using gel electrophoresis. Samples with > 20 ng/µl and containing high molecular weight bands (> 5 Kb) were deemed to be sufficient for sequencing (Table 1). See Maschette et al. (2019a, Appendix 2) for detailed extraction protocol.

Sequencing

To characterise genetic markers from throughout the toothfish genome, sequencing was conducted by Diversity Arrays (https://www.diversityarrays.com/) using the DArTseq™ methodology. DArTseq™ represents a combination of a complexity reduction methods (i.e. selection of a small subset of the genome) and next generation DNA sequencing (Courtois et al. 2013; Cruz et al. 2013; Kilian et al. 2012; Raman et al. 2014; Sansaloni et al. 2011). Similar to DArT methods based on array hybridisations, the technology is optimized for each organism and application by selecting the most appropriate complexity reduction method for both the size of the representation and the fraction of a genome selected for assays. Based on testing several restriction enzyme combinations for complexity reduction, the PstI-SphI combination was selected for *D. mawsoni*. DNA samples were processed in digestion/ligation reactions following Kilian et al. (2012) but with two different adaptors corresponding to the two different restriction enzyme overhangs. The PstI-compatible adapter was designed to include an Illumina flowcell attachment sequence, a sequencing primer sequence and a "staggered", varying length barcode region, similar to the sequence reported by Elshire et al. (2011). The reverse adapter contained a flowcell attachment region and a SphI-compatible overhang sequence.

Only mixed fragments (PstI-SphI) were effectively amplified in 30 rounds of PCR using the following reaction conditions: (1) 94 °C for 1 min, (2) 30 cycles of: 94 °C for 20 s, 58 °C for 30 s, 72 °C for 45 s, and (3) 72 °C for 7 min. PCR duplication was controlled for using large DNA input amounts of high-quality DNA and tested for using replicates of samples.

After PCR, equimolar amounts of amplification products from each sample of the 96-well microtiter plate were bulked and applied to c-Bot (Illumina) bridge PCR, followed by sequencing on Illumina Hiseq2500. The single end sequencing was run for 77 cycles.

Sequences generated from each lane were processed using proprietary DArT analytical pipelines. In the primary pipeline the fastq files were first processed to remove poor quality sequences, applying more stringent selection criteria to the barcode region compared to the rest of the sequence. This resulted in reliable assignments of the sequences to specific samples carried in the "barcode split" step. Approximately 2,500,000 sequences per barcode/sample were identified and used in marker calling. Finally, identical sequences were collapsed into fastqcoll files. The fastqcoll files were groomed using DArT pipelines proprietary algorithm, which corrects low quality base from singleton tag into a correct base using collapsed tags with multiple members as a template.

The groomed fastqcoll files were used in the secondary pipeline for DArT PL's proprietary SNP calling algorithms (DArTsoft14). For SNP calling, tags from all libraries included in the DArTsoft14 analysis were clustered using DArT PL's C + + algorithm at the threshold distance of 3. This was followed by parsing the clusters into separate SNP loci using a range of technical parameters, especially the balance of read counts for the allelic pairs. Additional selection criteria were added to the algorithm based

on analysis of approximately 1,000 controlled cross populations. Testing for Mendelian distribution of alleles in these populations facilitated the selection of technical parameters discriminating true allelic variants from paralogous sequences.

In addition, multiple samples were processed from DNA to allelic calls as technical replicates and scoring consistency was used as the main selection criteria for high quality/low error rate markers. Calling quality was assured by high average read depth per locus, with an average of over 30 reads/locus across all markers. The average number of sequences per sample in this analysis was 2.4 million and the average number of unique sequences per sample was 248,000.

We developed an algorithm to make the genotype calling transparent and to remove genotype calls based on very small number of sequence reads. Calling of SNPs was conducted on raw count data provided by Diversity Arrays using the following calling rules (Fig. 3):

1. Total counts less than 6 and greater than 500 were called as NA.
2. Markers where over 5/6 of counts were reference allele, were called homozygous (0)
3. Markers where over 5/6 of counts were alternate allele, were called homozygous (2)
4. All remaining markers were called heterozygous (1)

Filtering of loci and samples was conducted using the dartR package (Gruber and Georges 2018) in R v3.6.3 (R Core Team 2018). Repeatability of loci was calculated from technical replicates using the count of replicates where each pair of replicates agreed or disagreed at a loci where both can be called for that loci. Monomorphic loci and those with < 80% repeatability were removed. Additionally, both loci and individual fish with > 15% NAs were removed. Finally, data were filtered so only a single biallelic SNP was included at each locus and minor allele count (MAC) was > 8 (see Linck and Battey 2019 for discussion). To test the effect of missing data on the analysis below, the analysis were also run using data sets with loci and individual fish with filtering set to > 5%, > 20% and > 30% NAs as to cover the suggested range of acceptable values discussed in Schmidt et al. (2021).

Analysis

To explore regional genetic variability between locations, individual samples were allocated to prospective geographic sample populations by single linkage agglomerative clustering based on great circle distance. Two samples were allocated to the same sample population if separated by no more than 600 km (Fig. 4). One sample population with less than 10 samples present was joined with the next closest group, resulting in a total of 12 geographic sample populations. A single isolated sample that was not naturally allocated to any cluster was removed from the analysis. Measures of genetic diversity, including observed and expected heterozygosity and inbreeding coefficient, were calculated for all SNPs that passed the quality filtering steps using the dartR package (Table 2). All figures were created using a combination of the R packages: DiagrammeR (Iannone 2020), dplyr (Wickham et al. 2021), ggplot2 (Wickham 2016), grid (R Core Team 2018), hexbin (Carr et al. 2021), sf (Pebesma 2018), SOmap (Maschette et al. 2019a, b), and tidyr (Wickham 2021). Principal coordinate analysis (PCoA) was used to create a low dimensional representation of the genetic data implemented using the dartR package in R (Gruber and Georges 2018; R Core Team 2018). To test for differentiation amongst the geographic sample populations, an analysis of molecular variance (AMOVA; Excoffier et al. 1992) based on Nei's Distance (Nei 1972) was performed with the R packages pegas

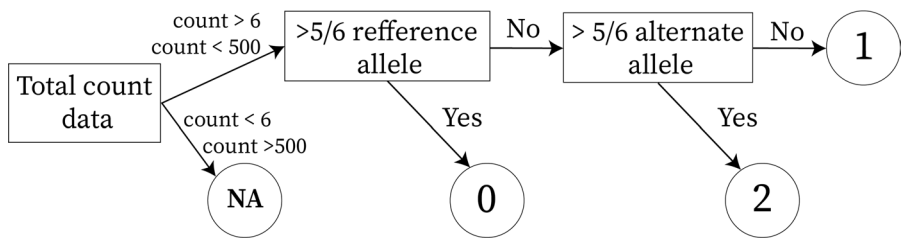

Fig. 3 Single nucleotide polymorphisms (SNP) calling rules used for Antarctic toothfish (*Dissostichus mawsoni*) counts obtained from Diversity Arrays

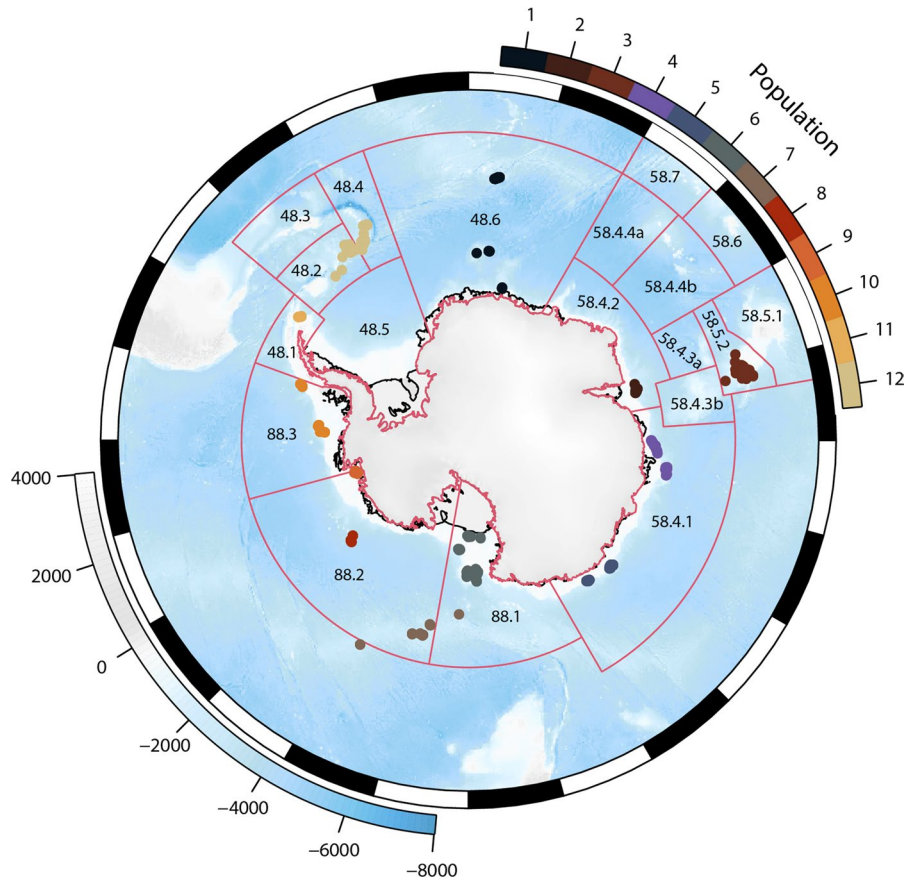

Fig. 4 Geographic sample populations of Antarctic toothfish (*Dissostichus mawsoni*) which were tested for genetic stock differences. Sample populations are numbered eastward from the prime meridian

Table 2 Summary of genetic diversity indices inferred from 11,007 loci. Ho, observed heterozygosity; He, expected heterozygosity; FIS, inbreeding coefficient. Standard deviation in parentheses

Geographic population	Sample numbers	Ho	He	FIS
1	41	0.128 (0.143)	0.141 (0.154)	0.092
2	45	0.128 (0.143)	0.141 (0.153)	0.088
3	42	0.128 (0.143)	0.141 (0.153)	0.095
4	101	0.130 (0.140)	0.142 (0.150)	0.082
5	90	0.129 (0.139)	0.141 (0.151)	0.089
6	101	0.128 (0.139)	0.141 (0.150)	0.089
7	27	0.128 (0.147)	0.141 (0.156)	0.092
8	49	0.128 (0.142)	0.141 (0.152)	0.090
9	54	0.129 (0.142)	0.141 (0.152)	0.088
10	29	0.129 (0.148)	0.141 (0.155)	0.084
11	50	0.128 (0.142)	0.141 (0.152)	0.090
12	86	0.131 (0.141)	0.142 (0.151)	0.080

(Paradis 2010) and StAMPP (Pembleton et al. 2013), using 10,000 permutations to assess significance. Wright's fixation index (FST; Weir and Cockerham 1984) was calculated with StAMPP as a measure of genetic distance between geographic sample populations. Pairwise comparisons of geographic sample populations testing for genetic distances (F_{ST}) greater than zero by bootstrap resampling with 10,000 replicates and subsequently adjusting to control the false discovery rate (Benjamini and Hochberg 1995).

Isolation by distance was tested based on two measures of geographic distance. Genetic distances (F_{ST}) were compared to (1) distance along Rhumb lines (*i.e.* lines of constant bearing), and (2) pairwise differences in longitudinal angle ignoring latitude, using Mantel permutation tests (Mantel 1967) with 10,000 replicates to assess significance. Great circle distances were not considered for the isolation by distance test as the calculated great circle lines connecting many sample locations cross the Antarctic continent and as such are not a realistic representation

of possible fish movement. A distance-based method, the Moran's eigenvector map was also conducted using the memgene package (Peres-Neto and Galpern 2022).

The clustering algorithms StockR (Foster 2018) and snapclust (Beugin et al. 2018) were used to search for latent population structure. These models can be used with two different methods: unsupervised (no initial grouping information given) or semi-supervised (initial grouping information given). Both methods were used, and semi-supervised runs were initialized from several random configurations corresponding to 1–12 sample populations, as well as the initial configuration defined by the geographic clustering. The sample distributions relative to clusters are shown in supplementary material 1. The optimal clustering for both StockR and snapclust were selected using the lowest BIC from the models, with those models within 2 BIC units considered plausible.

Results

Extraction and sequencing

DNA from 952 Antarctic toothfish samples were extracted, and of these 728 were deemed to contain sufficient quantity and quality to be sequenced by Diversity Arrays. Overall quantity of DNA was much higher in extractions from fin clips than from muscle tissue, with the exception of a batch of 30 muscle samples that were frozen first and put into ethanol only later. Whilst unclear why this is the case it is consistent with many fish DNA extractions that fin clips seem to result in higher yields and may simply be epithelial cells contain higher concentration of DNA than muscle cells. Sequencing of the 728 samples by Diversity Arrays resulted in identification of 63,101 variable nucleotide SNP sites. After a rigorous data filtering process (Supplementary material 2), 715 individuals and 11,007 unlinked SNPs remained to be used in the subsequent analysis.

Analysis

Exploring the effects of missing data rates used in the analysis showed consistent results across all four thresholds tested. As such, the results for the > 15% filtering threshold sampling are discussed below as the middle range value of those tested. When attributing samples to populations based on geographic distance (Fig. 4), no discernible structure was revealed by the principal coordinate analysis (PCoA) (Fig. 5). The respective geographic sample populations showed substantial overlap, with principal coordinates 1 and 2 both representing 0.3% of the total variation in the data. An analysis of molecular variance (AMOVA) showed weak evidence ($p = 0.068$) of genetic differentiation amongst these twelve geographic sample populations, with the population differentiation statistic $\Phi = 0.0003$ showing that the differentiation observed amongst the populations is only a small fraction of the total genetic variability. Wright's fixation index F_{ST} for genetic distance suggested that there was limited differentiation between the twelve geographic sample populations (Table 3). Benjamini and Hochberg (1995) adjusted pairwise comparisons of geographic sample populations based on F_{ST} showed weak evidence of some population differences. These weak differences were primarily between sample population 7 (Subarea 88.1 seamounts) with populations 1 (Division 48.6) and 4 (Division 58.4.1), between population 6 (Subarea 88.1 shelf) and 4 (Division 58.4.1), as well as between populations 3 (Division 58.5.2) and 9 (Subarea 88.2). These weak differences however, may also be a result of type one errors.

A Mantel test showed moderate evidence ($p = 0.016$) of correlation in genetic distance (F_{ST}) between geographic sample populations and the absolute difference of longitudes between geographic sample population centroids, with correlation $R = 0.22$ (Fig. 6). A Mantel test of genetic distances and the Rhumb line distances between geographic sample population centroids showed only weak evidence ($p = 0.051$) with a correlation of $R = 0.19$. These results indicate that whilst genetic differences are small, they do appear to increase with increasing longitudinal distance. A distance-based method, the Moran's eigenvector map was also tested and the results were consistent with that of the Mantel test.

For both the stockR and snapclust clustering algorithms, the inferred clusters bore no obvious resemblance to the geographic structure of the samples when initialized from a random configuration, and both preferred models selected by the BIC consisted of the lowest number of clusters (Table 4; Fig. 7).

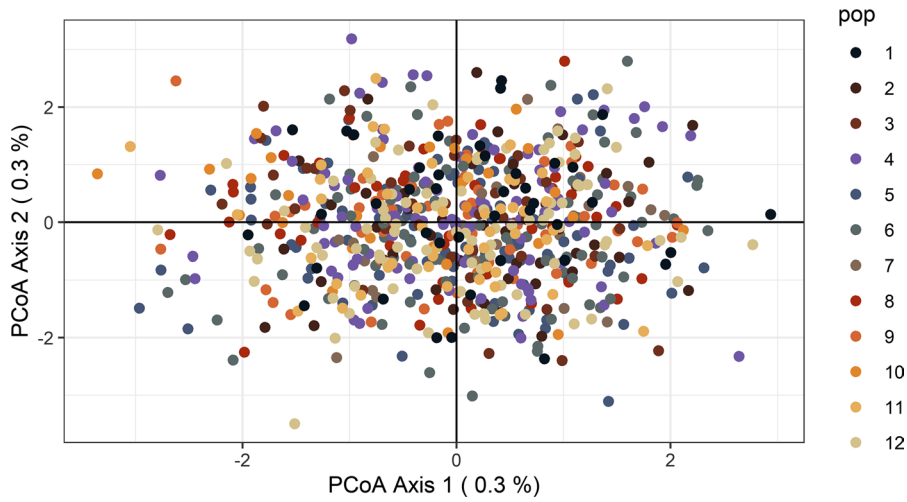

Fig. 5 Principle Coordinate Analysis (PCoA) of Antarctic toothfish (*Dissostichus mawsoni*) from the twelve geographic sample populations (pop 1–12)

Only when the algorithms were initialized from a configuration corresponding to a geographic cluster, the inferred clusters coincided exactly with the initial sample populations. However, these solutions were not favoured by the BIC suggesting the algorithms were converging to local maxima in the likelihood distribution. The sample distributions relative to clusters are shown in supplementary material 1.

Discussion

The results from this study indicate that the genetic structuring of Antarctic toothfish is very weak. The sampled toothfish shared over 99.9% of the observed variation between sites, i.e. less than 0.1% of the genetic variation was attributable to the sampling sites. Implementation of AMOVA was unable to detect differences between the geographical sample populations based on Nei's Distance.

Unsupervised clustering analyses using PCoA, stockR and Snapclust indicated that no genetically distinct breeding populations existed among the sampled Antarctic toothfish in this study. While semi-supervised clustering using geographic sample populations as initialisers favoured the same populations after clustering, the Bayesian Information Criterion indicated unsupervised models performed better than semi-supervised, and both clustering methods preferred models with fewer populations. In addition, there was only weak evidence of a correlation between genetic and geographic distances.

The findings of this study are consistent with other recent population genetic studies conducted on Antarctic toothfish. Whilst both Ceballos et al. (2021) and Choi et al. (2021) only compared samples from two areas, neither found convincing evidence between areas of genetic population differences. This study contained more samples across both the areas covered by Ceballos et al. (2021) and Choi et al. (2021) as well as all the other areas Antarctic toothfish are currently fished within the Southern Ocean. Whilst previous studies have indicated evidence of population structure between areas (Kuhn and Gaffney 2008; Parker et al. 2002; Smith and Gaffney 2005) we agree with Ceballos et al. (2021) that these findings are likely the result of using limited sets of molecular markers. The effects of sample size however should also not be overlooked and may play an important role in findings of population connectivity.

Whilst many biological and ecological aspects of the population dynamics for Antarctic toothfish have been studied, stock structure and linkages at different life stages are still poorly understood. The overall lack of genetic structure we observed mirrors the findings of many other Southern Ocean fish species (Damerau et al. 2012; Van de Putte et al. 2012) although it is increasingly being recognised that subtle population structure, or even relatively strong genetic breaks, can occur in some fish species in this region (Christiansen 2020; Young et al. 2018). The closely related Patagonian toothfish which has a more northerly distribution has shown to consist of several genetically distinct populations (Arkhipkin et al. 2022; Canales-Aguirre

Table 3 Wright's fixation index F_{ST} of Antarctic toothfish (*Dissostichus mawsoni*) amongst twelve geographic sample populations (lower diagonal), with *p* values (upper diagonal)

	1	2	3	4	5	6	7	8	9	10	11	12
1		0.927	0.870	0.522	0.740	0.057	**0.048**	0.352	0.152	0.340	0.301	0.124
2	-3.62×10^{-04}		0.819	0.263	0.264	0.112	0.145	0.848	0.306	0.115	0.310	0.350
3	-2.89×10^{-04}	-2.24×10^{-04}		0.866	0.850	0.098	0.056	0.531	**0.017**	0.237	0.162	0.759
4	-9.62×10^{-06}	1.15×10^{-04}	-1.95×10^{-04}		0.290	**0.026**	**0.016**	0.877	0.525	0.246	0.395	0.523
5	-1.20×10^{-04}	1.17×10^{-04}	-1.95×10^{-04}	6.55×10^{-05}		0.496	0.150	0.275	0.147	0.161	0.516	0.563
6	3.13×10^{-04}	2.32×10^{-04}	2.56×10^{-04}	2.16×10^{-04}	2.50×10^{-06}		0.281	0.320	0.371	0.046	0.086	0.137
7	5.74×10^{-04}	3.56×10^{-04}	5.49×10^{-04}	5.85×10^{-04}	2.83×10^{-04}	1.58×10^{-04}		0.074	0.102	0.066	0.075	0.400
8	9.29×10^{-05}	-2.32×10^{-04}	-1.68×10^{-05}	-1.86×10^{-04}	1.03×10^{-04}	7.55×10^{-05}	4.83×10^{-04}		0.438	0.708	0.248	0.312
9	2.45×10^{-04}	1.16×10^{-04}	5.07×10^{-04}	-7.27×10^{-06}	1.73×10^{-04}	5.44×10^{-05}	3.91×10^{-04}	3.36×10^{-05}		0.631	0.631	0.578
10	1.35×10^{-04}	3.69×10^{-04}	2.32×10^{-04}	1.66×10^{-04}	2.43×10^{-04}	4.03×10^{-04}	6.35×10^{-04}	-1.59×10^{-04}	-9.00×10^{-05}		0.336	0.477
11	1.39×10^{-04}	1.16×10^{-04}	2.39×10^{-04}	4.67×10^{-05}	-5.58×10^{-06}	2.34×10^{-04}	4.66×10^{-04}	1.52×10^{-04}	-7.03×10^{-05}	1.25×10^{-04}		0.160
12	2.33×10^{-04}	6.99×10^{-05}	-1.30×10^{-04}	-5.20×10^{-06}	-1.88×10^{-05}	1.36×10^{-04}	7.03×10^{-05}	8.90×10^{-05}	-3.09×10^{-05}	1.54×10^{-05}	1.82×10^{-04}	

p values lower than 0.05 are shown in bold font

et al. 2018; Shaw et al. 2004; Toomey et al. 2016). Like its congener Patagonian toothfish, Antarctic toothfish are winter spawners with pelagic eggs (Ghigliotti et al. 2018; Parker et al. 2019; Yates et al. 2019). With the majority of the species residing at higher latitudes which is under sea ice during the spawning season, the reproduction strategy and early life history stages of Antarctic toothfish are difficult to study (Ghigliotti et al. 2018).

Large-scale egg and larvae dispersal, together with long-distance fish movement at juvenile and adult stages, are the most likely processes that contribute to the dissolution of the genetic stock structure. This style of dispersal is likely for Antarctic toothfish due to a combination of extended egg and larvae stages before fish larvae settle on or near benthos. Dunn et al. (2012) modelled the likely distribution of eggs and larvae of Antarctic toothfish over a two-year period assuming 15 spawning locations around the Antarctic coast. Their simulations indicated fish larvae from northern spawning grounds such as BANZARE Bank or the northern seamounts in the South–East Atlantic sector (Okuda et al. 2018; Yates et al. 2019) were carried far distances around the continent, often with movements of between 60 and 90° longitude after 2 years (Figs. 8 and 9). Only fish larvae from spawning grounds inside the Ross Sea and Weddell Sea gyres would mostly remain in similar locations, although some could be transported into other areas when the larvae were caught in the Antarctic Circumpolar Current or the Antarctic Slope Fronts.

In addition to expected large transport distances of eggs and larvae, some long-distance movements of adult toothfish have also been reported in mark-recapture tagging studies. Whilst most Antarctic toothfish are recaptured within 200 km of their initial tagging location, ~ 7% of the 3773 recaptures reported between 2001 and 2019 travelled further distances, with a maximum of over 4000 km (greater-circle distance) between release and recapture locations (Grilly et al. 2022).

Population genetic studies provide a robust measure of differentiation when populations have virtually no connectivity. However, even with a low-level exchange or migration between sampled areas, the diversifying effect of isolation is erased, and the actual level of genetic stock exchange becomes difficult to determine. Therefore, the patterns of

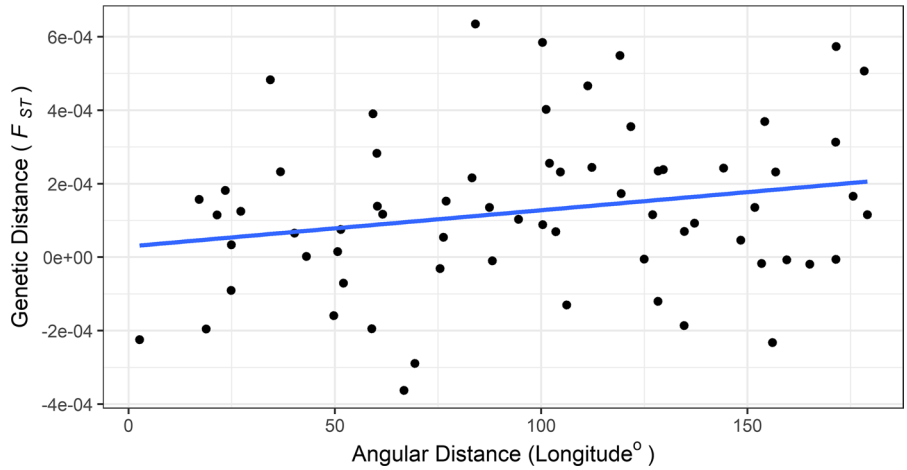

Fig. 6 Angular (longitude°) and genetic distance (F_{ST}) pairwise comparisons of Antarctic toothfish (*Dissostichus mawsoni*) geographic sample population centroids ($R = 0.22$)

Table 4 Bayesian Information Criterion (BIC) for the stockR and Snapclust algorithms fitted to Antarctic toothfish (*Dissostichus mawsoni*) starting from random and geographic initial configurations for 2 to 12 clusters

	stockR		Snapclust	
# Clusters	Random	Geographic	Random	Geographic
2	6,265,641	6,268,635	6,310,734	6,311,863
3	6,323,945	6,329,000	6,370,918	6,373,255
4	6,381,722	6,388,708	6,431,325	6,434,466
5	6,440,025	6,448,271	6,491,762	6,496,035
6	6,498,622	6,508,389	6,552,304	6,557,591
7	6,556,913	6,568,297	6,612,791	6,619,382
8	6,614,918	6,628,263	6,673,404	6,681,202
9	6,672,923	6,687,952	6,734,330	6,742,839
10	6,730,583	6,747,576	6,795,392	6,804,464
11	6,790,431	6,807,451	6,856,080	6,866,289
12	6,848,160	6,867,072	6,916,916	6,927,845

large-scale egg and larvae dispersal and long-distance fish movement found in Antarctic toothfish, even if they resulted only in low levels of population exchanges, would be sufficient to explain the results found in this study. As Ward (2000) stated:

> *"Gene flow rates of 1%, 5%, 20% and 50% will give genetic homogeneity among samples and thus cannot be distinguished, yet each of these cases should have different consequences for stock assessment models. Findings of sample homogeneity are thus of little assistance to fishery managers."*

Based on these findings we draw a number of conclusions relevant to the management of Antarctic toothfish stocks in the Southern Ocean:

Firstly, we consider that CCAMLR's management of toothfish fisheries at the levels of Subareas and

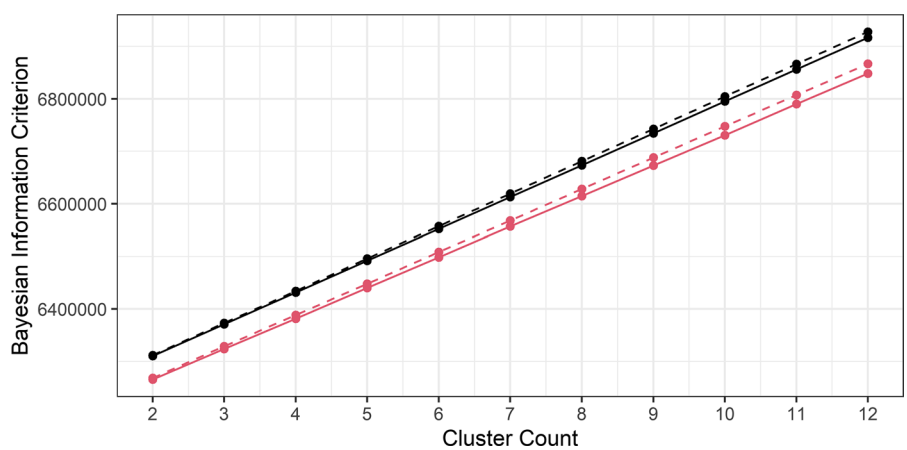

Fig. 7 Bayesian Information Criterion (BIC) for the stockR (red) and Snapclust (black) algorithms assigning samples of Antarctic toothfish (*Dissostichus mawsoni*) , starting from random (solid) and geographic (dashed) initial configurations for 2 to 12 clusters

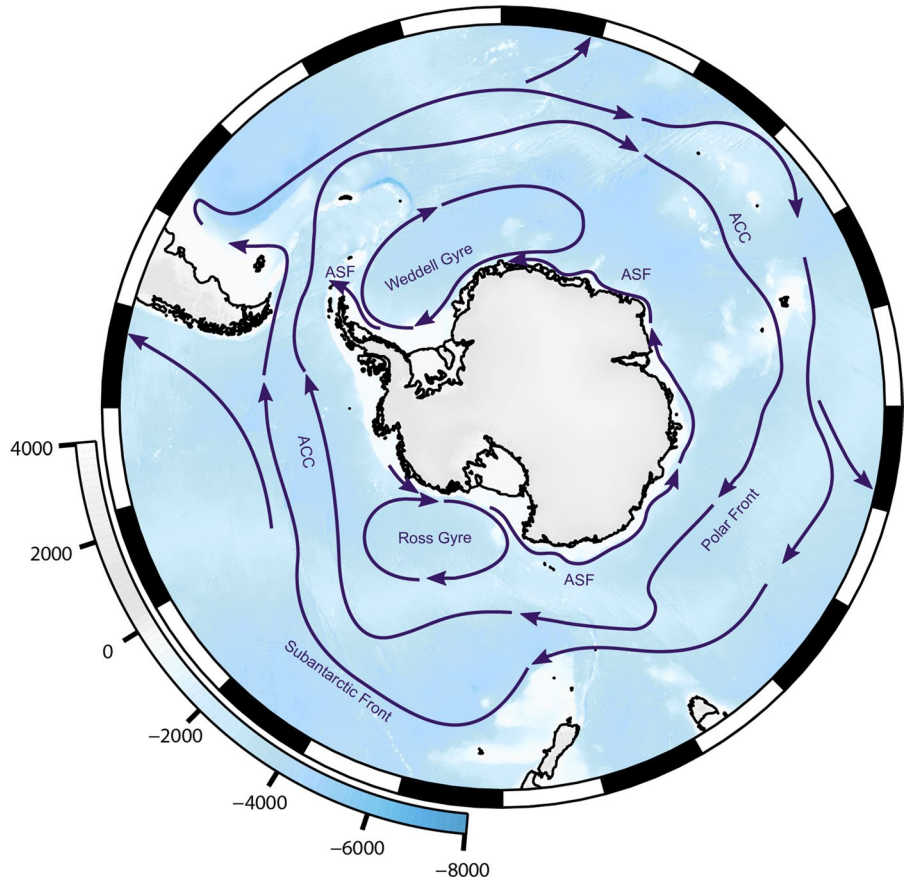

Fig. 8 Major Southern Ocean circulation features (from Post et al. 2014), showing the Polar and Sub-Antarctic Fronts of the Antarctic Circumpolar Current, sub-polar gyres and the Antarctic Slope Front (ASF). Background colours show bathymetry

Divisions does not need to be changed. While this study found only weak genetic structuring of Antarctic toothfish across the Southern Ocean, the level of stock linkages between areas cannot be determined from genetic studies alone. To update stock hypotheses and stock boundaries relevant to fisheries management, studies of fish movement and larval dispersal such as the one by Dunn et al. (2012) to account for new information on the early-life history (Hanchet et al. 2015; Ghigliotti et al. 2018; Parker et al. 2021) or expanding that presented in Mori et al. (2022) to the whole Southern Ocean to gain a better insight into the potential distribution patterns of pre-settlement Antarctic toothfish should be conducted. Whilst genetic methods are consistently showing little to no population structure for Antarctic toothfish (and we question the utility of funding further studies for this species which solely use genetics) other methods such as stable isotopes, or trace element work may prove more insightful, both of these however also come with their own assumptions and difficulties (see Avigliano 2022; Trueman et al. 2012).

Secondly, it is important that Antarctic toothfish stocks are managed sustainably in all fished areas given the potential stock linkages of recruits and adults between different areas. Antarctic toothfish is targeted by fisheries throughout almost their entire species range. For the management of these fisheries within the CCAMLR area, CCAMLR applies decision rules to set catch limits at Subarea or Division level. These rules are based on the objectives of the CAMLR Convention and aim to ensure that the biomass level of each harvested population stays above a target level to maintain sufficient recruitment potential for the long-term sustainability of the fish stocks (CCAMLR 1980). Given the potential stock linkages of recruits and adult toothfish between different areas, it is important that such a management framework is applied to all managed fisheries outside the CCAMLR area as well.

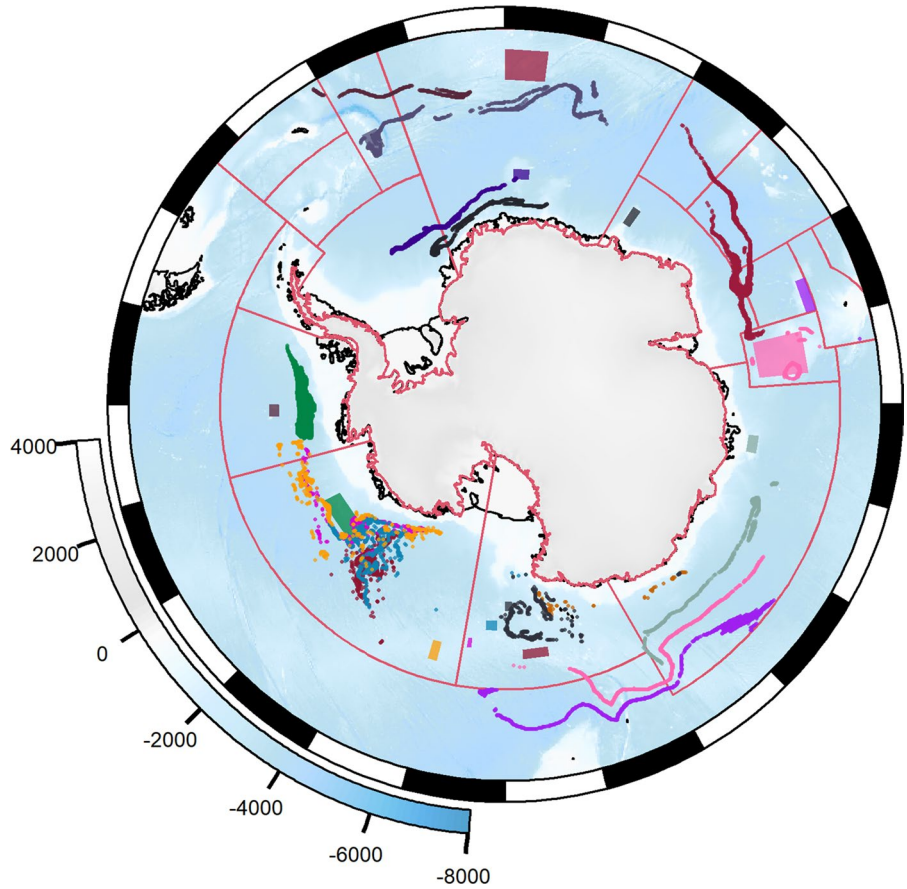

Fig. 9 Simulated larval locations of Antarctic toothfish (*Dissostichus mawsoni*) after 2.0 years around Antarctica at a depth of 150 m using the HadGEM model adapted from Dunn et al. (2012). Coloured boxes indicate the starting locations of same coloured dots

Thirdly, whilst genetic based estimates of population size for fisheries of other species in the world (e.g. *Thunnus maccoyii*) have been shown to provide reliable estimates with traditional biomass estimating methods (Bravington et al. 2016b), methods such as close-kin mark recapture require knowledge of stock boundaries (Bravington et al. 2016a). As such, the inability to define geographic stock boundaries for Antarctic toothfish from genetics limits the ability to perform genetic stock size estimation through methods like close-kin mark recapture. There are a number of reasons for this, mainly (1) the juveniles found in a given location may not be related, (2) they could have originated from different areas, and (3) they may not be related to any of the adults in that area. This would likely lead to a large over-estimation of biomass in the given area. To use such close-kin mark recapture techniques, the genetic stock needs to be sampled. In this case, this would mean sampling Antarctic toothfish from its entire geographical distribution, which is both expensive and operationally difficult. However, if such project was deemed to be feasible, the SNP markers we have identified here could be used in targeted genotyping assays to provide informative and accurate genotypes required for identifying related parent–offspring pairs or half-sibling pairs. The close-kin mark recapture technique may be more suitable for Patagonian toothfish which are found on seamounts and submersed plateaus in the Southern Ocean, and for which genetic differences between locations have been identified (Toomey et al. 2016; Welsford et al. 2011).

Lastly, illegal, unregulated and unreported (IUU) fishing has been prevalent in many parts of the CCAMLR area in the past and are still ongoing, albeit at a lower level. Given the estimated removals of IUU fishing compared to that of the regulated fisheries, we believe they are unlikely to have had any impact on the genetic connectivity between stocks. While genetic methods have been identified as potential tools to identify the region of origin for Patagonian toothfish product sold to international

markets (Toomey et al. 2016), genetic methods are unlikely to be useful for Antarctic toothfish given the low levels of genetic stock discrimination.

Acknowledgements We would like to thank all scientists and scientific observers who collected genetic samples for this project, specifically: Adam Shaw, Alistair Burls, Andy Smith, Brandon Meteyard, Charlotte Chazeau, Chris Engelbrecht, Christophe Baillout, David Luis Rodriguez, Dmitry Marichev, Elcimo Pool, Garry Breedt, Gavin Kewan, Henry Oak, Jake Horton, Jarrad James, John Simons, Juan Agulló García, Juan Manuel Martínez Carmona, Keith Paterson, Lock Nel, Marius Kapp, Mark Belchier, Martin Tucker, Michael Basson, Rudian Baily, Nicolas Gasco, Roberto Sarralde Vizuete, Sam Langholz, Sangdeok Chung, Schalk Visagie, Siya Lumkwana, Stephen Cunliffe, Steve Parker, Sobahle Somhlaba, Tamre Sarhan. We would also like to thank Tim Lamb and Troy Robertson for logistical and data handling support, as well as the Fisheries Research Development Corporation (Project 2017-021) and Australian Longline Pty Ltd for financial and in-kind support.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions.

Data Availability Genetic data for this project will be made available through GenBank during the submission project and be publicly available upon request.

Declarations

Conflict of interest None of the authors of this paper have any direct or indirect conflicts of interest to declare.

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