Molecular Ecology

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MOLECULAR ECOLOGY

ORIGINAL ARTICLE OPEN ACCESS

Environmental Gradients Decouple Demographic and Adaptive Connectivity in a Highly Mobile Coastal Marine Species

Chris J. Brauer[1] | Andrea Bertram[1] | Jonathan Sandoval-Castillo[1] | Anthony Fowler[2] | Justin D. Bell[3] | Paul Hamer[3,4] | Maren Wellenreuther[5,6] | Luciano B. Beheregaray[1]

[1]Molecular Ecology Laboratory, College of Science and Engineering, Flinders University, Bedford Park, South Australia, Australia | [2]Aquatic Sciences, South Australian Research and Development Institute, Henley Beach, South Australia, Australia | [3]Victorian Fisheries Authority, Queenscliff, Victoria, Australia | [4]Pacific Community, Noumea, New Caledonia | [5]New Zealand Institute for Bioeconomy Science Limited, Nelson, New Zealand | [6]The School of Biological Sciences, University of Auckland, Auckland, New Zealand

Correspondence: Luciano B. Beheregaray (luciano.beheregaray@flinders.edu.au)

Received: 16 July 2025 | **Revised:** 3 February 2026 | **Accepted:** 9 February 2026

Keywords: ecological genomics | fisheries genomics | fisheries management | marine biogeography | recruitment dynamics

ABSTRACT

Understanding how eco-evolutionary processes shape genetic variation and persistence in marine species with highly variable recruitment dynamics and dispersal potential remains a fundamental challenge, particularly when considering the interplay between gene flow and local adaptation. Here, we employed a seascape genomics approach to investigate population connectivity and local adaptation in Australasian snapper (*Chrysophrys auratus*, Sparidae) along 1500 km of the environmentally heterogeneous southern Australian coastline. Using genome-wide SNPs, we identified distinct eastern and western regional populations aligned with known biogeographical regions. Genotype-environment association analyses revealed 855 candidate adaptive loci associated with environmental variation, including temperature, salinity and primary productivity. Connectivity analyses using neutral markers indicated high gene flow within both eastern and western regions, while candidate adaptive loci revealed substantially reduced connectivity, especially for Northern Spencer Gulf and West Coast populations. This contrast implies a decoupling of demographic and adaptive connectivity, in which strong environmental gradients appear to reduce the effective exchange of adaptive variation despite high overall connectivity. Our results support contingent migration as a potential mechanism modulating the balance between local adaptation and gene flow in this economically and ecologically important marine species. These findings might also have implications for regional management of other coastal fisheries that are experiencing substantial declines. As climate change alters coastal marine environments around the world, the dynamics of local recruitment, site fidelity and local adaptation are expected to change. This highlights the importance of integrating knowledge about eco-evolutionary processes into marine resource management, fisheries stock assessment, and restocking and stock enhancement activities.

1 | Introduction

Understanding how evolutionary processes such as gene flow and local adaptation shape the distribution of marine populations are enduring challenges in evolutionary biology and for fisheries management (Bernatchez et al. 2017; Grummer et al. 2019). This is particularly true for many marine species characterised by large population sizes, high fecundity and high connectivity (Gagnaire et al. 2015), including those where recruitment dynamics are influenced by sweepstakes reproductive

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https://doi.org/10.1111/mec.70273

success (Árnason et al. 2023). In these cases, extensive gene flow could limit local adaptation, even across vast geographical ranges (Lenormand 2002; Nielsen et al. 2009). Despite these challenges, growing evidence indicates that locally adapted genetic variation can be maintained in species with high gene flow (Han et al. 2020).

Marine fishes provide ideal natural systems to examine the genomic basis of local adaptation with gene flow, particularly in the context of fisheries resources. The management consequences of local adaptation for widespread fisheries stocks are, however, relatively unexplored (Andersson et al. 2024; Grummer et al. 2019). Highly dispersive marine species often span extremely heterogeneous environments, yet conventional stock assessments may fail to capture this complexity. Additionally, fisheries management and stock assessments are often constrained by government jurisdictional boundaries that reflect political or administrative divisions rather than biologically- or ecologically-relevant population structure (Andersson et al. 2024). This potential disparity between management units and biological populations can lead to localised overfishing, inadequate protection of important spawning or nursery areas or failure to account for source–sink dynamics occurring at larger spatial scales (Berger et al. 2021).

Seascape genomics offers a powerful approach to disentangle demographic and ecological evolutionary processes in these systems (Gagnaire et al. 2015). This interdisciplinary field can clarify ecological and evolutionary factors shaping population structure and connectivity of widespread fisheries species (Xuereb et al. 2021). By examining how the environment influences genetic variation and gene flow, seascape genomics can reveal subtle population structure that may be overlooked by previous genetic methods or stock assessment approaches (Sandoval-Castillo et al. 2018). Atlantic herring (*Clupea harengus*) provide a clear example where, despite limited evidence for population structure at neutral loci, seascape genomics revealed fine-scale differentiation associated with ecological adaptation that helped to resolve mismatches between biological populations and fisheries stock management (Han et al. 2020). Similarly, temperature-associated adaptive variation was identified in the commercially important yellow croaker (*Larimichthys crocea*) along the Chinese coast, challenging the existing stock assessment and highlighting the need for more nuanced management strategies (Chen et al. 2023).

Coastal marine species often exhibit limited population structure across continental-scale distributions even if they encompass a wide range of environments. If patterns of dispersal are locally restricted or temporally variable within these large populations, environmental heterogeneity can, however, create opportunities for natural selection to drive local adaptation. For these reasons, spatially and temporally heterogeneous coastal habitats, such as the zonal coastal boundary of southern Australia, provide ideal opportunities to test for the role of ecologically divergent natural selection in driving adaptation in marine species (Ruzzante et al. 2006; Sandoval-Castillo and Beheregaray 2020).

Here we examine the roles of regional and fine-scale connectivity linked to variable recruitment dynamics in shaping population connectivity and adaptation in the Australasian snapper (*Chrysophrys auratus*), a highly mobile coastal marine species. The focal region of our study spans a range of heterogeneous embayment and open coastal environments along more than 1500 km of the southern Australian coast (Ridgway and Condie 2004). Snapper plays a pivotal role in the commercial and recreational fisheries sector of southern Australia, as well as holding considerable ecological and cultural value across its Indo-Pacific distribution (Parsons et al. 2014). Recent declines in the productivity and status of some snapper stocks have prompted significant shifts in management practices, including an ongoing moratorium, now in its sixth year, on commercial and recreational fishing in much of South Australia (Drew et al. 2022; Fowler et al. 2020). To inform and assess management of the species it is critically important to understand how connectivity and environmental variation shape snapper stocks subject to both fishing pressure and climate change. Several genetic studies have revealed evidence for fine-scale population structure and provide a basis for the hypothesis that selection, imposed by steep environmental gradients, could counteract high gene flow and lead to local adaptation of snapper populations (Bernal-Ramírez et al. 2003; Bertram et al. 2023; Gardner et al. 2017). Spawning aggregations and nursery areas across southern Australia concentrate in three major embayments: northern Spencer Gulf, northern Gulf St. Vincent, and Port Phillip Bay. Previous genetic analyses suggest that these and nearby populations exhibit local recruitment and site fidelity (Bertram et al. 2023; Sandoval-Castillo et al. 2026), traits that favour the evolution of local adaptation. This is supported by early molecular evidence for local adaptation in other embayment populations, including Shark Bay, Western Australia (Johnson et al. 1986) and New Zealand (Smith 1979; Smith and Francis 1983). Adaptive traits such as larval survival, growth and metabolism have been strongly linked to temperature and salinity in snapper (Fielder et al. 2005; McMahon et al. 2020; Wellenreuther et al. 2019) and genomic variation is known to underpin these traits (Ashton, Hilario, et al. 2019; Ashton, Ritchie, and Wellenreuther 2019; Sandoval-Castillo et al. 2022).

In this study, we predicted that genomic variation should not only reflect demographic factors such as large population sizes and high gene flow, but also natural selection in response to environmental heterogeneity. To test these predictions, we built on recent evaluations of snapper stock structure and population size estimates (Bertram et al. 2022, 2023, 2024) and examined how environmental parameters may influence patterns of genomic variation and connectivity in snapper populations along the southern Australian coast. Considering the social, economic, and commercial importance of southern Australian snapper stocks, we also aimed to assess the findings in the context of informing and refining regional fisheries management strategies which are fundamental for sustainable harvesting and species persistence.

2 | Methods

2.1 | Southern Australian Coastal Environment

The focal region of this study, southern Australia, comprises a wide range of coastal and near-shore marine habitats and includes three major embayments. Spencer Gulf and the adjacent Gulf St.

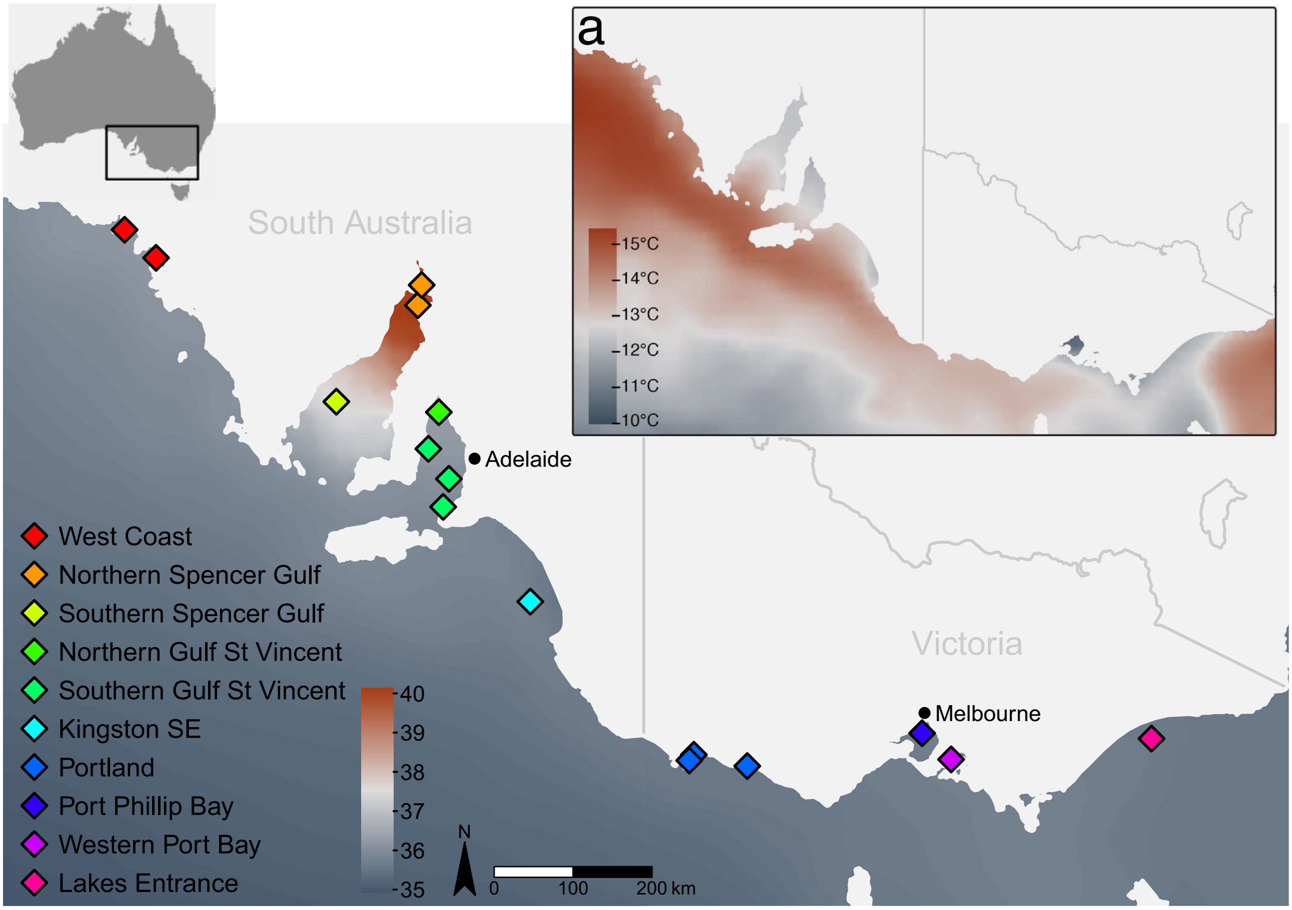

FIGURE 1 | Sampling sites across southern Australia and spatial heterogeneity in mean sea surface salinity (main panel; PSS), and (a) minimum sea surface temperature (°C).

Vincent are large inverse estuaries in South Australia, and Port Phillip Bay is a shallow, enclosed bay just south of Melbourne, Victoria (Figure 1). Broadly, environmental conditions within these embayments differ greatly from open coastal habitats, with cooler minimum sea surface temperature (SST), warmer maximum SST, and reduced current velocities. A west-to-east temperature gradient characterises the region, with the warmest waters along the west coast and coolest in the eastern embayments. Regional variation in climate, topography and oceanography create unique local environments within each embayment. Climate in the east is wetter and cooler than the more arid South Australia. As a result, Port Phillip Bay and Western Port Bay exhibit the coolest SST and receive greater freshwater inputs from rivers, leading to the highest primary productivity in the region and consistently lower salinity. In South Australia, Spencer Gulf is characterised by extreme salinity gradients, particularly in the north where values exceed 45 ppt in summer, combined with large seasonal variation in SST (~12°C–24°C) (Nunes and Lennon 1986). Gulf St. Vincent experiences intermediate conditions that are less saline than Spencer Gulf but saltier than coastal waters. Coastal current circulation outside the Gulfs is dominated by the Leeuwin current system that transports tropical water poleward along the west coast of Australia and eastward along the southern continental shelf, before joining the South Australian Current and eventually heading south along Tasmania's west coast as the Zeehan Current (Richardson et al. 2019; Ridgway and Condie 2004). The strength and impact of this current system is highly variable and shapes seasonal patterns of temperature, salinity and primary productivity across the region. Stronger currents during winter transport warm, low-salinity water to the east, while reduced Leeuwin current flows and coastal upwellings incorporate cooler, more saline and nutrient-rich water during summer (Richardson et al. 2019; Ridgway and Condie 2004; Shute et al. 2022).

2.2 | Sampling and Genomic Data Collection

Our sampling design builds on previous studies that clarified neutral population genetic structure and stock boundaries of snapper along the western (Bertram et al. 2022) and the southeastern (Bertram et al. 2023, 2024) coasts of Australia. A total of 448 snapper (*Chrysophrys auratus*) collected from 23 individual sampling sites along the southern Australian coast were used. These sites were grouped into 10 regional locations based on proximity and similarity of environmental profiles. To ensure adequate sample sizes for allele-frequency estimation, individual sites containing fewer than six samples were merged with the nearest neighbour. This resulted in 16 pooled sites representing the 10 regional locations (Figure 1; Figure S1; Table S1). All the research complies with applicable laws on sampling from natural populations. We extracted DNA from fin clips using a salting-out method (Sunnucks and Hales 1996) and used double-digest restriction site-associated DNA (ddRAD) sequencing to generate genomic data using the enzymes SbfI and MseI. We generated ddRAD libraries of 96 multiplexed samples, following the protocol outlined in Peterson et al. (2012) with modifications described in our previous work (Brauer et al. 2016). Paired-end 150 bp sequencing was conducted over 15 lanes (this included samples not related to this study) of an Illumina HiSeq 4000 at Novogene (Hong Kong). Raw sequence data quality was assessed using FastQC (Andrews 2010). Reads were demultiplexed with the process_radtags module from STACKS 2.0 (Catchen et al. 2013) and trimmed to remove low-quality bases and adapters using TRIMMOMATIC (Bolger et al. 2014). Reads were then mapped to a chromosome-level genome assembly (Catanach et al. 2019) using BOWTIE 2 (Langmead and Salzberg 2012), and SNPs were called using BCFTOOLS (Narasimhan et al. 2016). We filtered the resulting SNP genotypes for quality, missing data per individual and retained one SNP per 500 bp. We also applied further filtering to generate putatively neutral and candidate adaptive datasets. Candidate adaptive loci identified by the genotype–environment association analysis (described below) were separated, and the remaining putatively neutral loci were filtered to remove SNPs out of Hardy–Weinberg equilibrium (FDR of 0.05) in any sampling site, using the gl.filter.hwe function in the *dartR* package. Filtering parameters and the number of SNPs retained following each step are described in Table S2.

2.3 | Genetic Diversity, Population Structure and Connectivity

We estimated population genetic diversity parameters, including the percentage of polymorphic loci, heterozygosity and inbreeding coefficient, using the *hierfstat* R package (Goudet 2005). We examined patterns of neutral population structure and admixture using *hierfstat* to estimate pairwise F_{ST} and ADMIXTURE (Alexander et al. 2009). An analysis of molecular variance (AMOVA) was performed to further assess hierarchical population structure among major sampled regions, among sites within regions, among individuals within sites and within individuals. The poppr.amova function in the *poppr* R package (Kamvar et al. 2014) was used for the molecular variance estimates and significance values were estimated using the *ade4* randtest function (Dray and Dufour 2007) with 1000 permutations. We further examined relative connectivity, both among the eastern and western regional populations, and among sites within each region, using the directional relative-migration (Nm) approach of Sundqvist et al. (2016), as implemented by the divMigrate function in the *diveRsity* R package (Keenan et al. 2013). This approach first calculates pairwise differentiation (G_{ST}), then converts these values into unit-less, normalised (0–1) estimates of relative migration. The method also detects asymmetrical migration for each pairwise comparison by contrasting each population's allele frequencies with those of a hypothetical mixed migrant pool. Analyses were run separately for the neutral and putatively adaptive SNP datasets, and statistical support for asymmetrical migration was evaluated with 1000 bootstrap resamples.

2.4 | Local Adaptation

Environmental heterogeneity across the study area was summarised with 31 raster layers at 5-arc-min resolution (~9 km at the equator) obtained from BioORACLE v2.2 (Assis et al. 2018; Tyberghein et al. 2012), supplemented by bathymetry from BioORACLE v1.0 (Table S3). Each layer represents long-term summary statistics (e.g., mean, minimum, maximum or range), calculated over a baseline period of 2000–2014 and derived either from the ECMWF ORAP5.0 ocean reanalysis (physical variables), or the PISCES biogeochemical hind-cast (nutrients and productivity). Two variables rely on different archives and time periods, pH (1910–2007 observations, World Ocean Database) and calcite (2002–2009 MODIS-Aqua). We performed preliminary analyses using the vifcor and vifstep functions in the *usdm* R package (Naimi et al. 2014) to remove correlated (Pearson $r > 0.7$) and colinear ($\mathrm{VIF} > 10$) variables. The retained environmental variables were finally converted to *z*-scores to standardise across different measurement scales and ensure comparable contributions to downstream analyses.

To detect a genetic signal of local adaptation, we performed genotype-environment association analyses using redundancy analysis (RDA) implemented with the *rda* function in the vegan R package (Oksanen et al. 2018). To examine relationships between SNP allele frequencies and environmental data, we ran an initial partial RDA where we controlled for spatial population structure using a matrix of allele frequency covariance (Ω) estimated with Baypass (Gautier 2015). Candidate adaptive loci associated with environmental variation were identified using the Mahalanobis-distance approach of Capblancq et al. (2018), in which Mahalanobis distances are calculated from SNP loadings, converted to per-locus *p* values and then adjusted for multiple testing by controlling the false discovery rate (FDR). We report FDR-adjusted *q* values and defined candidate loci as those exceeding the FDR threshold ($q < 0.01$). A second RDA was then performed using the candidate adaptive loci and individual SNP genotypes (allele counts) to visualise the distribution of genotype-environment associations within sampling sites. This individual-based ordination is intended to highlight among-individual variation in the multivariate adaptive signal, and provides a qualitative assessment of whether adaptive-associated genotypes are relatively homogeneous within sites or show substantial within-population structure.

Functional annotations of candidate loci were performed using SnpEff to assess genomic position and predicted effects (Cingolani et al. 2012). Variants predicted to have disruptive effects likely to cause protein truncation, loss of function or nonsense-mediated decay were classified as high impact. Variants predicted to be non-disruptive but potentially affecting protein effectiveness were classified as moderate impact, whereas variants assumed to be mostly harmless or unlikely to change protein behaviour were classified as low impact. We then extracted open reading frames (ORFs) from 600 bp flanking sequences around each SNP and searched these against the SwissProt teleost database using DIAMOND BLASTx (Buchfink et al. 2015), applying an e-value threshold of 1×10^{-10} and retaining up to five hits per query. Top-scoring matches were queried through the UniProt REST API to retrieve Gene Ontology (GO) terms and KEGG pathways, retaining only those with experimental or curated evidence codes (EXP, IDA, IPI, IMP, IGI, IEP, TAS, IC) or high-confidence computational inference (ISS, IEA). To identify enriched functional categories, we performed over-representation analysis using the *clusterprofiler* R package (Yu et al. 2012). Annotated candidate loci were compared against all annotated loci using hypergeometric tests, with false discovery rate controlled by the Benjamini–Hochberg procedure (FDR <0.1). Categories containing fewer than five or more than 500 genes were excluded to avoid unstable or overly general terms. The genomic distribution of candidate loci and enriched functional categories was visualised using the ggmanh R package (Lee 2022).

3 | Results

3.1 | Sampling and Genomic Data Collection

The Illumina HiSeq 4000 sequencing generated 5.05 billion raw sequences, and 3.36 billion (mean per sample = 7.51 M, min = 0.87 M, max = 21.38 M) were retained. After filtering, we retained 448 individuals genotyped at 14,699 single nucleotide polymorphisms (SNPs). Filtering for Hardy–Weinberg equilibrium (HWE) retained 14,206 SNPs, and exclusion of candidate adaptive loci resulted in a putatively neutral dataset of 13,453 SNPs.

3.2 | Genetic Diversity, Population Structure and Connectivity

Estimates of genetic diversity were based on the 13,453 neutral loci, with observed heterozygosity (H_o) ranging from 0.124 in southern Gulf St. Vincent to 0.138 in southern Spencer Gulf, while expected heterozygosity (H_e) varied from 0.128 to 0.133. Inbreeding coefficient (F_{IS}) values were generally low, ranging from −0.036 in southern Spencer Gulf to 0.036 in northern Gulf St. Vincent, indicating minimal inbreeding within populations. Percentages of polymorphic loci ranged from 79.1% in Kingston–South East to 87.0% in Port Phillip Bay (Table 1).

ADMIXTURE results indicated that the optimal number of genetic clusters was $K=2$ (Figure 2), corresponding to an eastern and a western cluster with the genetic break situated between southern Gulf St. Vincent and Kingston–South East. Despite this main division, a few migrants (three from the eastern and two from the western cluster) are evident in the ADMIXTURE plot. Pairwise F_{ST} values based on the 13,453 neutral loci were generally low among sites within regions but higher between eastern and western regions (mean = 0.009, range = 0–0.018). Based on the candidate adaptive loci, F_{ST} estimates were elevated, both among sites within each region, and among sites across regions (mean = 0.013, range = 0–0.25; Figure S2). The AMOVA analyses supported the ADMIXTURE results, attributing a significant proportion of genetic variation to differences between regions (2.1%, $\Phi=0.021$, $p<0.01$), while variation among sites within regions was minimal (0.1%, $\Phi=0.001$, $p<0.001$). The AMOVA based on candidate adaptive loci assigned a higher proportion of variation between sites within regions (0.4%, $\Phi=0.004$, $p<0.001$), and among regions (5.9%, $\Phi=0.059$, $p<0.01$), indicating stronger differentiation at loci potentially under selection (Table 2).

TABLE 1 | Genetic diversity indices based on 13,453 neutral loci.

Site	*N*	%poly	H_O	H_E	F_{IS}	LCI	UCI
West Coast (WC)	38	83.5	0.125	0.129	0.033	0.028	0.036
Northern Spencer Gulf (NSG)	40	83.3	0.125	0.128	0.019	0.016	0.023
Southern Spencer Gulf (SSG)	36	84.2	0.138	0.133	−0.036	−0.040	−0.032
Northern Gulf St Vincent (NGSV)	34	83.4	0.127	0.131	0.036	0.032	0.041
Southern Gulf St Vincent (SGSV)	39	80.7	0.124	0.128	0.030	0.027	0.034
Kingston SE (KSE)	70	79.1	0.128	0.130	0.013	0.009	0.016
Portland (PLD)	69	85.6	0.129	0.132	0.022	0.019	0.026
Port Phillip Bay (PPB)	45	87.0	0.129	0.131	0.013	0.008	0.017
Western Port Bay (WPB)	37	85.1	0.131	0.132	0.010	0.006	0.014
Lakes Entrance (LE)	40	81.8	0.129	0.129	0.000	−0.004	0.005

Abbreviations: %PL, percentage polymorphic loci; F_{IS}, inbreeding coefficient (including 95% confidence intervals, LCI and UCI); H_E, expected heterozygosity; H_O, observed heterozygosity; *N*, number of individuals.

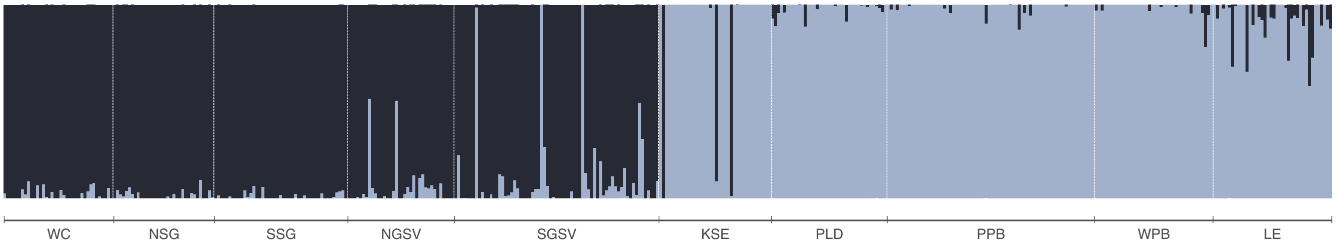

FIGURE 2 | ADMIXTURE results for $K=2$, indicating distinct western (dark) and eastern (light) genetic clusters. Site codes refer to the locations listed in Table 1.

TABLE 2 | Hierarchical analysis of molecular variance (AMOVA) based on 13,453 neutral and 855 candidate loci, illustrating the distribution of genetic variation among regions (eastern, western), sites within each region and individuals within sites, and within individuals.

SNPs	Source of variation	df	Sum of squares	Sigma (σ)	% variance	Phi (Φ)	*p*
13,453	Among regions	1	10590.788	21.112	2.1	0.021	0.009
	Among sites within regions	8	8988.927	1.184	0.1	0.001	0.001
	Among individuals within sites	438	446601.017	13.373	1.3	0.013	0.035
	Within individuals	448	444815.000	992.891	96.5	0.035	0.001
855	Among regions	1	4689.312	9.958	5.9	0.059	0.008
	Among sites within regions	8	1785.722	0.630	0.4	0.004	0.001
	Among individuals within sites	438	73553.296	9.993	5.9	0.063	0.001
	Within individuals	448	66279.000	147.944	87.8	0.122	0.001

Migration (Nm) estimates based on neutral and adaptive loci indicated relatively low connectivity among eastern and western regional populations (mean neutral Nm = 0.32, mean adaptive Nm = 0.13), compared to much higher relative migration among sites within regions (mean neutral Nm = 0.77; mean adaptive Nm = 0.66; Tables S4 and S5). Within each region, estimates based on neutral loci (Figure 3a,c, Table S4) showed particularly high connectivity between the southern areas of the two South Australian gulfs, Spencer Gulf and Gulf St. Vincent (mean Nm = 0.97) and between Port Phillip Bay and all other eastern sites (mean Nm = 0.90). Using the candidate loci (Figure 3b,d, Table S5), relative migration estimates again suggested the southern areas of both South Australian gulfs are highly connected (mean Nm = 0.98) but indicated much lower connectivity for all pairwise estimates involving West Coast (mean Nm = 0.54) and, particularly, northern Spencer Gulf (mean Nm = 0.45). We found no evidence for asymmetrical migration with the bootstrapped 95% confidence intervals for each population's estimate relative to the shared migrant pool overlapping for all pairs.

Filtering correlated (Pearson $r > 0.7$) and colinear (VIF > 10) variables resulted in a final set of five environmental variables describing environmental heterogeneity across the study region (minimum sea surface temperature, mean sea surface salinity, minimum sea surface net primary productivity, pH and calcite concentration; Figure S3, Table S6). These variables capture critical factors known to influence snapper physiology and life history, including thermal tolerance during winter months, osmoregulatory stress in hypersaline embayments, food availability during low-productivity periods and carbonate chemistry affecting calcification processes. The partial RDA identified 855 candidate adaptive loci (5.8% of the total SNPs) significantly associated with the environment (Figure 4a). The individual-level RDA based on those 855 candidate loci (Figure 4b) revealed divergent genotype-environment associations between regions, with western populations showing strong associations with salinity and calcite (reflecting the hypersaline Spencer Gulf environment), while eastern populations were more strongly associated with temperature minima and productivity gradients.

Functional annotation of these loci revealed a substantial proportion located in genic regions, with many predicted to have moderate to high impacts on gene function (Figure 5a,b). We recovered 1188 BLAST hits covering 730 unique loci (85.4% of candidates). These matches corresponded to 562 unique proteins with 5115 GO terms (2640 biological process, 1263 cellular component, and 1212 molecular function terms) and 488 KEGG pathway annotations (Table S7). Based on these annotations, over-representation analysis identified two enriched biological process GO terms. Post-anal tail morphogenesis (GO:0036342; $p = 0.0022$, FDR = 0.062) was represented by three genes involved in FGF-BMP-Wnt signalling (*fgfr1a*, LG10; *tll1*, LG15; *bcl9l*, LG18), a conserved growth-factor network that regulates skeletal and muscle growth and mediates plastic responses to environmental cues, such as temperature and salinity (Johnston 2006). Hemopoiesis (GO:0030097) was also significantly enriched ($p = 0.0043$, FDR = 0.062), with three genes affecting red blood cell production or membrane composition (*rnf145*, LG16; *zfpm1*, LG4; *smarcal1*, LG8). No significant enrichment was detected for molecular function or cellular component categories, or for KEGG pathways. The functionally annotated candidate loci were distributed across the genome, with enriched genes found on multiple linkage groups (Figure 5c).

4 | Discussion

Understanding how environmental heterogeneity shapes population structure and connectivity remains a central challenge in ecology and evolution, particularly for marine species with highly variable recruitment dynamics and dispersal potential. The relationship between gene flow and local adaptation is especially complex in marine environments where oceanographic connectivity can span vast distances while environmental gradients create strong selective pressures. Along the southern Australian coast, our findings reveal that broad environmental gradients influence patterns of dispersal and local adaptation in snapper, despite substantial gene flow among populations. We identified two distinct regional populations with minimal genetic differentiation at neutral loci among sites within each region, consistent with high demographic connectivity. However, genotype-environment association analyses identified 855 candidate adaptive loci linked to five key environmental variables that shape snapper ecology. Minimum temperature that affects spawning, growth and survival, salinity extremes challenging osmoregulation, primary productivity determining prey availability, and carbonate chemistry (pH and calcite) potentially influencing sensory systems and otolith formation (Cook et al. 2021; Fielder et al. 2005). A substantial

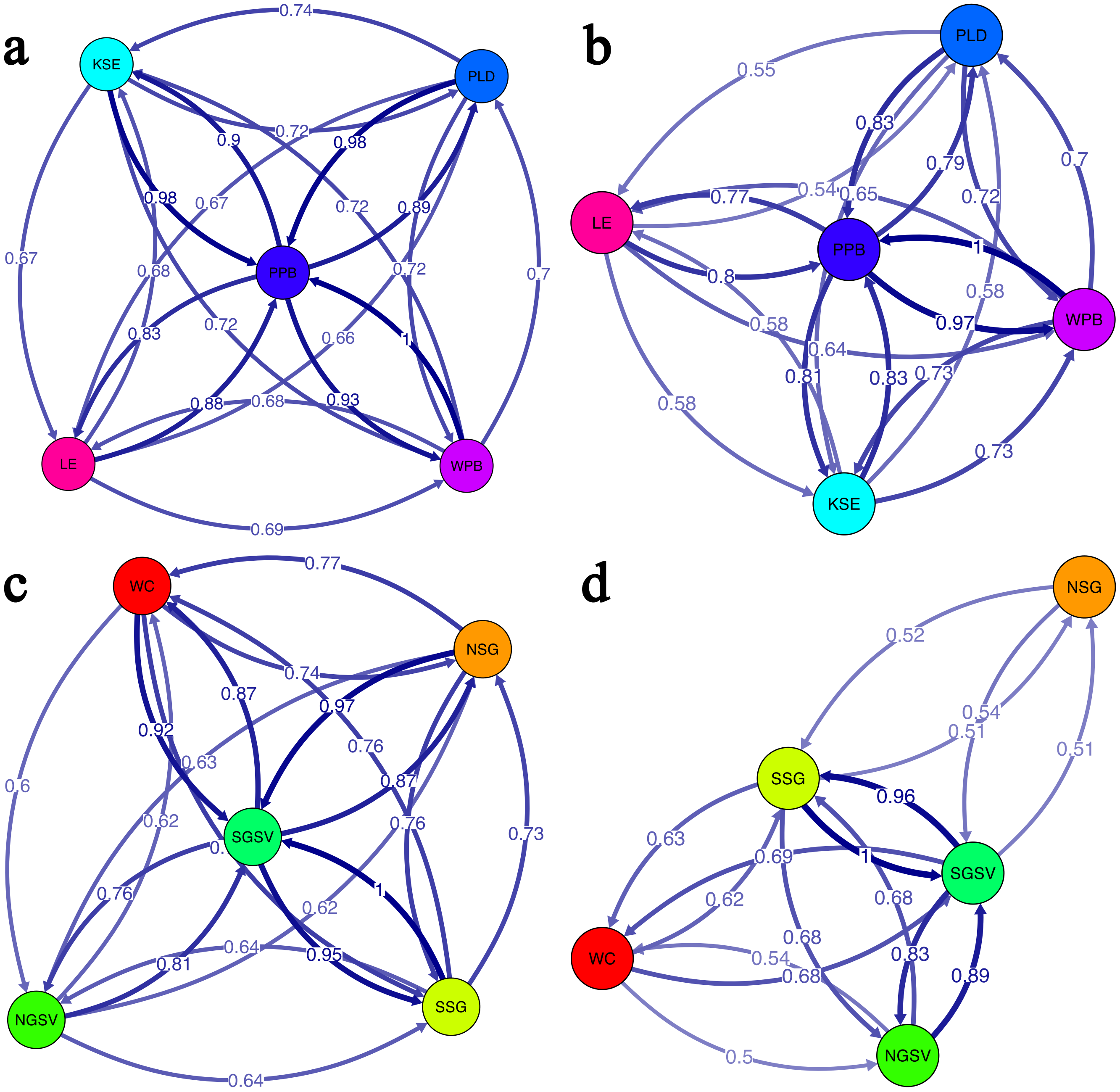

FIGURE 3 | Relative migration networks for the eastern stock estimated using (a) 13,453 neutral and (b) 855 candidate adaptive SNPs, and for the western stock using (c) 13,453 neutral and (d) 855 candidate SNPs, following the method of Sundqvist et al. (2016). Darker arrows signify higher relative migration. Estimates < 0.5 are not shown.

proportion of these putatively adaptive SNPs are located in genic regions with potential moderate to high impacts on gene function. Functional over-representation analyses identified six candidate SNPs that mapped to two enriched GO biological process terms (post-anal tail morphogenesis; hemopoiesis), suggesting hydrodynamic niche and salinity tolerance as potential targets of selection. While relative migration estimates using neutral loci suggested high connectivity among sites within each population, using candidate loci revealed lower connectivity, particularly for West Coast and northern Spencer Gulf populations. This decoupling of demographic and adaptive connectivity highlights that substantial gene flow does not preclude local adaptation, with specific environmental stressors contributing to adaptive genetic divergence of local snapper populations.

4.1 | Strong Environmental Gradients Influence Connectivity and Local Adaptation

Current knowledge of snapper population dynamics across southern Australia, based on size structure, mark-recapture and otolith studies, indicates that spatial and temporal patterns in regional connectivity mainly reflect interannual variation in recruitment to three main nursery areas: Port Phillip Bay in the east, and northern Spencer Gulf and northern Gulf St. Vincent in the west (Drew et al. 2022; Fowler et al. 2020; Hamer et al. 2003; Hamer et al. 2011). We detected evidence for occasional long-distance migration from the eastern stock into southern Gulf St. Vincent, along with more subtle, fine-scale differentiation between sub-populations within, and adjacent

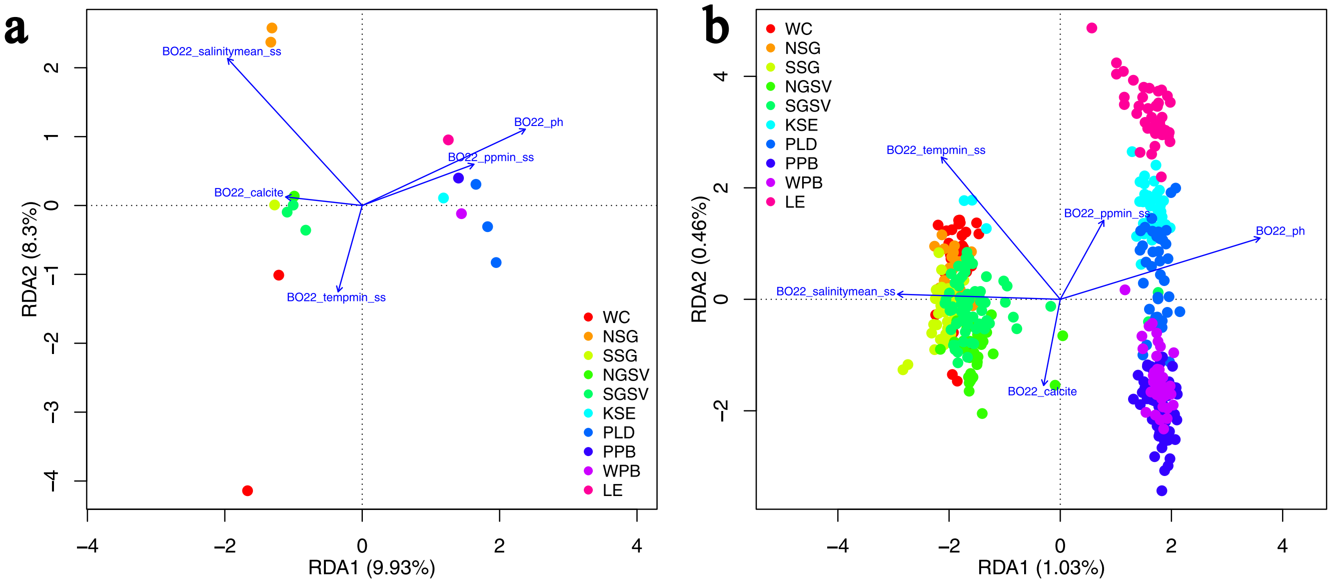

FIGURE 4 | Redundancy analysis (RDA) plots summarising genotype–environment associations in Australasian snapper: (a) RDA biplot showing ordination of sampling locations based on 14,699 genome-wide SNPs after controlling for spatial structure using a population allele frequency covariance matrix. Arrows indicate the direction and strength of environmental gradients, including minimum sea surface temperature, mean sea surface salinity, minimum sea surface net primary productivity, pH, and calcite concentration; (b) Individual-level RDA biplot based on 855 putative adaptive candidate loci, illustrating the distribution of individual genotypes across sites in relation to environmental variables.

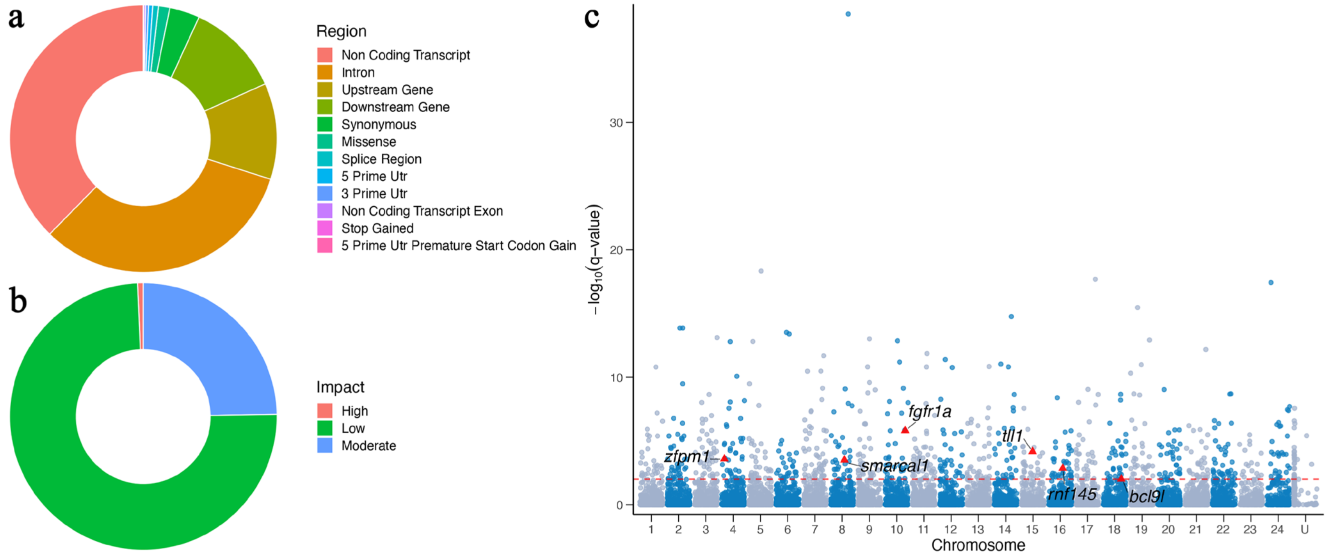

FIGURE 5 | (a) Proportion of 855 candidate adaptive SNPs by genomic region; (b) Proportion of candidate SNPs in genic regions by impact on gene function; (c) Manhattan plot indicating the RDA q-values ($-\log_{10}[q]$) and distribution of 855 candidate adaptive SNPs associated with environmental variation (FDR 0.01; above dashed line). Red triangles highlight loci linked to six genes representing two functional gene ontology terms enriched in the candidate adaptive SNPs (FDR < 0.1), GO:0036342, post-anal tail morphogenesis (*fgfr1a*, *tll1*, *bcl9l*), and GO:0030097, hemopoiesis (*rnf145*, *zfpm1*, *smarcal1*).

to the South Australian gulfs. The major genetic break we observed between the eastern and western populations aligns with the boundary between the well-described Flindersian and Maugean marine biogeographic provinces, suggesting that broad-scale climatic and oceanographic processes are important drivers of stock structure across the region (Teske et al. 2017; Waters et al. 2010). These findings are consistent with previous genetic studies (Bertram et al. 2023), and with the view that strong recruitment events drive dispersal of juvenile snapper among populations at both local and regional spatial scales (Fowler 2016).

Although the coast of southern Australia is relatively well-studied from a biogeographic perspective (Teske et al. 2017; Waters 2008), less is known about how its heterogeneous seascape and strong environmental gradients influence connectivity and local adaptation, particularly for teleosts. Seasonal variation in the intensity and direction of prevailing oceanographic currents can shape local environmental conditions including temperature, salinity and dissolved oxygen (Richardson et al. 2019). Such variation is also known to mediate evolutionary processes, such as dispersal, recruitment and local adaptation for a range of coastal marine species including macroalgae, sea urchins, silversides, sardines and cetaceans (Banks et al. 2007; Barceló et al. 2022; Beheregaray and Sunnucks 2001; Coleman et al. 2011; Teske et al. 2016, 2021; Ward et al. 2006). For snapper, strong recruitment events can enhance demographic connectivity at both regional and local scales, from long-distance westward dispersal originating from the eastern nursery area (Fowler 2016; Hamer and Jenkins 2004; Hamer et al. 2011) to more localised exchange among subpopulations within regions (Sandoval-Castillo et al. 2026). However, environmental heterogeneity among nursery areas and between embayments and adjacent coastal waters likely imposes strong selection on migrants that may favour survival of local recruits (Rankin and Sponaugle 2011). These patterns are consistent with a migration-selection balance, where exceptional recruitment pulses are offset by selection against maladapted immigrants, maintaining local adaptation across environmental gradients (Yeaman and Whitlock 2011).

Supporting this hypothesis, steep environmental gradients between upper gulf and open coastal environments corresponded with allele frequency differences at candidate adaptive loci. This included strong associations with temperature and salinity that are known to impact growth and survival of snapper (Fielder et al. 2005; McMahon et al. 2020; Samuels et al. 2026). Previous snapper studies have demonstrated that adaptive traits, such as growth and survival are strongly linked to these environmental variables (Wellenreuther et al. 2019), and have identified genomic variation underpinning these traits (Ashton, Hilario, et al. 2019; Ashton, Ritchie, and Wellenreuther 2019; Sandoval-Castillo et al. 2022). We found post-anal tail morphogenesis genes (*fgfr1a*, *tll1*, *bcl9l*) and haemopoietic regulators (*zfpm1*, *rnf145*, *smarcal1*) were significantly over-represented in our candidate adaptive loci. These functional modules align with growth-factor and oxygen-transport pathways that Wellenreuther et al. (2019) showed were sensitive to temperature in snapper, and have also been implicated in osmotic-stress responses in other fishes (Fiol and Kültz 2007). This suggests that the same canonical signalling networks could mediate adaptation to the joint temperature-salinity gradients that span the embayment-coastal habitats. More broadly, the distribution of candidate adaptive loci across many regions of the genome is consistent with a signal of polygenic adaptation (Stephan 2016). While similar polygenic signals of selection have been observed in many marine species (Bernatchez 2016), it is important to note that alternative genomic architectures have also been observed in high-gene-flow marine fishes. In Atlantic silversides, strong divergent selection was shown to concentrate adaptive alleles into large genomic haploblocks (or 'supergenes') maintained by suppressed recombination, despite an overall low level of genome-wide differentiation (Wilder et al. 2020). Structural variants can contribute to complex trait variation and can also create localised peaks of differentiation, and recent whole-genome analyses in snapper revealed substantial structural variation (Blommaert et al. 2024). This suggests that future whole-genome studies may not only help to resolve whether our ddRAD candidate SNPs and associated functions are themselves targets of selection, or instead (and more likely) reflect linkage to the causal adaptive variants, but may also yield additional adaptive features.

The role of natural selection in structuring marine populations across environmental gradients is gaining appreciation and this understanding is crucial for predicting climate-driven changes in fisheries sustainability (Teske et al. 2021). Local adaptation to temperature has been documented in economically important species such as the large yellow croaker (*Larimichthys crocea*), where genetic differentiation tracks minimum temperatures despite high connectivity, resulting in climate-induced shifts in stock boundaries (Chen et al. 2023). Similarly, salinity gradients were found to drive adaptive divergence in osmoregulation and reproductive traits among sand goby (*Pomatoschistus minutus*) populations across the North and Baltic Seas (Leder et al. 2021). Within Spencer Gulf and Gulf St. Vincent, where both temperature and salinity increase to the north, these environmental gradients influence multiple species. King George whiting (*Sillaginodes punctatus*) maintain genetic homogeneity across the South Australian region, yet comprise ecologically independent populations supplied by separate spawning grounds (Rogers et al. 2019). Despite their much longer pelagic larval phase (~100 days, compared with 3–4 weeks in snapper), whiting exhibit the same fine-scale genetic structure linked to environmental variation at spawning grounds and to distinct larval dispersal routes. The recurrence of this pattern in taxa with contrasting life-history traits suggests a general pattern of environmental heterogeneity shaping fine-scale connectivity and population structure in marine fish populations across the region.

4.2 | Contingent Migration Can Reinforce Local Adaptation With Gene Flow

Local adaptation across environmental gradients despite high gene flow has been documented in numerous marine species, including Atlantic cod (*Gadus morhua*), Pacific herring (*Clupea harengus*) and sardines (*Sardinops sagax*) (Bradbury et al. 2010; Limborg et al. 2012; Teske et al. 2021). These studies suggest that the balance between selection and gene flow in marine environments may be more nuanced than often assumed. Contingent migration, where populations contain both migratory and resident individuals, provides a potential general mechanism to explain the observed balance between connectivity and local adaptation (Hansson and Åkesson 2014; Secor 1999). Contingent migration strategies have been described for several marine fishes, including southern flounder (*Paralichthys lethostigma*) in the Gulf of Mexico (Steffen et al. 2023) and mulloway (*Argyrosomus japonicus*) and southern garfish (*Hyporhamphus melanochir*) in Australia (Hughes et al. 2022; Steer and Fowler 2015). For snapper, tagging studies of the same population have revealed complex movement patterns with some individuals showing high site fidelity while others undertake extensive migrations (Fowler 2016; Parsons et al. 2003; Stewart et al. 2019). This is supported by evidence for three distinct behavioural groups in Port Phillip Bay snapper: fish that depart immediately after spawning, summer residents that remain until autumn and individuals that overwinter in the bay (Hamer and Mills 2017). Such behavioural variation is consistent with contingent migration where migratory individuals facilitate gene flow, while resident contingents maintain locally adapted genetic variation.

This balance between gene flow and selection is, however, unlikely to be temporally stable. The relative proportions of resident versus migratory contingents can shift in response to environmental variability and recruitment pulses, as documented in white perch (*Morone americana*) and striped bass (*M. saxatilis*) where contingent behaviour varied with river flow, productivity, and climatic conditions (Gahagan et al. 2015; Gallagher et al. 2018). For snapper, strong year classes might disperse more widely to reduce intra-specific competition, while weaker year classes may reinforce local residency (Drew et al. 2022). Previous genomic studies have detected temporal shifts in genetic composition, reflecting these variable recruitment and connectivity dynamics (Bertram et al. 2023). Complex patterns of snapper stock structure observed in Shark Bay, Western Australia, further illustrate this temporal variation. Early tagging, otolith and allozyme studies detected strong isolation between gulf and coastal populations (Jackson and Moran 2012; Johnson et al. 1986), however, subsequent microsatellite work revealed more subtle differentiation linked to salinity and timing of spawning (Gardner et al. 2017). These dynamics may also change under climate warming, potentially altering the timing and intensity of episodic recruitment or shifting the strength of environmental selection across heterogeneous spawning habitats. This highlights the importance of integrating knowledge about ecological and evolutionary processes into fisheries stock assessment and management, and into restocking and stock enhancement programs aimed at improving the abundance and resilience of wild stocks (e.g., Harrisson et al. 2025).

Our study provides novel insights into the complex relationship between gene flow and local adaptation in snapper populations along southern Australia's environmentally heterogeneous coastline. Contrasting relative migration inferred from neutral loci with estimates based on candidate adaptive loci indicates a decoupling of demographic and adaptive connectivity in snapper, consistent with environmental selection reducing the effective exchange of adaptive variation despite high genome-wide connectivity. The potential role of contingent migration, where migratory and resident individuals coexist within populations, appears to be a key mechanism facilitating the balance between connectivity and local adaptation. This has direct implications for fisheries management in the region, particularly given the recent decline of some stocks. While current management necessarily operates within practical jurisdictional frameworks, our findings reveal biologically and ecologically relevant population structure that could enhance existing frameworks by incorporating both the demographic connectivity between regions and the adaptive distinctiveness of local populations. For instance, the Spencer Gulf and West Coast populations, currently managed as a single stock, show distinct adaptive signatures associated with strong environmental gradients (e.g., elevated temperature and salinity toward the head of Spencer Gulf) that may warrant consideration in refining future management strategies. Preserving these locally adapted populations that contribute to regional recruitment may prove crucial for persistence of snapper and other coastal species under climate change. While temporal variability in recruitment is already understood, longitudinal genomic monitoring could enhance assessment frameworks by revealing how this variability affects connectivity patterns and adaptive potential. Furthermore, strengthening collaboration between management jurisdictions would help ensure that population dynamics operating at large spatial scales are captured within local management strategies. As fisheries continue to experience unprecedented environmental changes, management strategies that integrate knowledge of both neutral and adaptive genetic variation, as well as of adaptive capacity, will be essential for ensuring long-term sustainability. Our study shows that demographic and adaptive connectivity can be decoupled in highly connected marine species and highlights that cryptic adaptive variation may prove crucial for population persistence in changing oceans.

Author Contributions

C.J.B. and L.B.B. conceived the study with assistance from J.S.-C. L.B.B., A.F., J.D.B., P.H. and M.W. secured funding and resources. A.F., A.B., P.H. and J.D.B. secured samples. A.B. generated the data. C.J.B. performed data analysis with assistance from A.B. and J.S.-C. All authors contributed to the interpretation of results. L.B.B. supervised the study. C.J.B. drafted the manuscript with assistance from L.B.B.; co-authors revised the manuscript and approved its final version.

Acknowledgements

This study was financially supported by the Australian Research Council (grant LP180100756 to L.B.B.), by Flinders University and by the AJ and IM Naylon and the Playford Trust. We thank everyone who contributed toward sampling, including staff from the South Australian Research and Development Institute and the Victorian Fisheries Authority. We also thank Diana-Elena Vornicu for laboratory assistance. We acknowledge the traditional custodians of the land and sea throughout the regions where this research was done. Open access publishing facilitated by Flinders University, as part of the Wiley - Flinders University agreement via the Council of Australasian University Librarians.

Funding

This work was supported by Australian Research Council, LP180100756.

Disclosure

Benefit-Sharing: Benefits from this research accrue from the sharing of our data and results on public databases as described above.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The study datasets are available in *Figshare*: https://figshare.com/s/034cb8ca31701cf9b687.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Figure S1:** Sampling sites across the study area showing the 16 pooled sites (main panel) representing. **Figure S2:** Pairwise F_{ST} based on (a) 13,453 neutral loci and (b) 855 candidate adaptive loci. **Figure S3:** Environmental variation across the 16 pooled sites for snapper across southern Australia. **Table S1:** Sampling locations for 448 snapper from across southern Australia. Region: describes major genetic break between the east and west of the study area, Regional location: indicates the ten regional locations based on proximity and similar environmental profiles, Pooled sites: indicates the groups of samples pooled due to low sample sizes (16 groups) and Sites: indicates the exact sampling location of each fish (23 distinct sampling sites). **Table S2:** Number of SNPs retained after each bioinformatics filtering step. **Table S3:** Environmental variables used to characterise conditions across the study area. Most layers were sourced from BioORACLE v2.2 and summarise long-term oceanographic conditions from 2000 to 2014. pH and calcite were derived from alternative datasets with different temporal coverage. **Table S4:** Relative migration estimates (Nm) based on 13,453 neutral loci. Shaded sections highlight. **Table S5:** Relative migration estimates (Nm) based on 855 candidate loci. Shaded sections highlight. **Table S6:** Raw environmental data for the 16 pooled snapper locations. **Table S7:** Summary of functional annotations for candidate adaptive loci, including BLAST hits, associated protein identities, GO terms (biological process, molecular function, cellular component) and KEGG pathway assignments. Over-representation analysis identified two enriched biological process GO terms: post-anal tail morphogenesis and hemopoiesis.