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Original Article

Biogeographic provinces and genomically delineated stocks are congruent in snapper (*Chrysophrys auratus*) from southeastern Australia

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Marine species often exhibit genetic discontinuities concordant with biogeographic boundaries, frequently occurring due to changes in ocean circulation, bathymetry, coastline topography, and temperature. Here, we used 10 916 single nucleotide polymorphisms (SNPs) to assess the concordance between population genomic differentiation and coastal biogeography in the fishery-important snapper (*Chrysophrys auratus*) across southeastern Australia. Additionally, we investigated whether spatial scales of assessment and management of snapper align with evidence from population genomics. We detected genomic structure concordant with the region's three biogeographic provinces across snapper from 11 localities ($n = 488$) between the west coast of South Australia and the south coast of New South Wales. We also detected fine-scale genetic structuring relating to spatial variation in spawning and recruitment dynamics, as well as temporal stability in the genomic signal associated with two important spawning areas. The current management boundaries in the region coincided with either the genetic breaks at bioregional boundaries or with local-scale variation. Our study highlights the value of population genomic surveys in species with high dispersal potential for uncovering stock boundaries and demographic variation related to spawning and recruitment. It also illustrates the importance of marine biogeography in shaping population structure in commercial species with high dispersal potential.

Keywords: ddrad, fisheries management, marine biogeography, marine teleost, population genomics, stock delineation.

Introduction

Despite the scarcity of obvious physical barriers in the ocean, marine species are often genetically structured into discrete populations that are connected by various degrees of gene flow, even in species with high dispersal potential (Grummer *et al.*, 2019). In the absence of topographical barriers, genetic structure can form in species with high dispersal potential due to oceanographic features like fronts, eddies, and zones of convergence or divergence of currents, as well as environmental gradients in salinity and temperature (Kelly and Palumbi, 2010; Colgan, 2015; Grummer *et al.*, 2019). Additionally in coastal marine species, patterns of genetic structure often reflect historical vicariance, formed during glaciations when sea levels fell. These patterns can frequently persist after restoration of habitat continuity following inundation of continental shelf regions (Teske *et al.*, 2017). The aforementioned features are often associated with bioregional boundaries, which frequently coincide with genetic breaks across multiple taxa with a range of life histories. For example, along the Pacific coast of North America, several biogeographic barriers associated with upwelling regions and shifts in bathymetry and ocean circulation correspond to genetic structuring in fishes and invertebrates (Kelly and Palumbi, 2010; Briggs and Bowen, 2012).

Understanding how marine species are structured geographically, as well as the levels of connectivity between populations, is vital for effective management. In exploited marine species, differentiated populations not only have different genetic characteristics (genetic diversity and effective population sizes), but are also expected to have unique demographic characteristics (mortality, recruitment, growth rates, and abundances), and therefore have the potential to respond differently to fishing pressures (Cadrin, 2020). Because of this, an objective of fishery assessment and management is to treat differentiated populations as independent units or stocks. However, the characterization of genetic structure and population connectivity in marine species is typically difficult because of their often-great abundances and high dispersal capabilities (Grummer *et al.*, 2019). Recent advances in DNA sequencing technologies now allow for the generation of large datasets of genetic markers, which have greater power to detect the subtle genetic structuring typical of many marine species.

Snapper (*Chrysophrys auratus*) is a coastal sea bream distributed across temperate and sub-tropical Australia and New Zealand (Parsons *et al.*, 2014). The species is a highly fecund, multiple batch broadcast spawner, that forms aggregations to breed when water temperatures are between 15 and 22°C. Snapper's pelagic larval stage lasts for 17–33 days,

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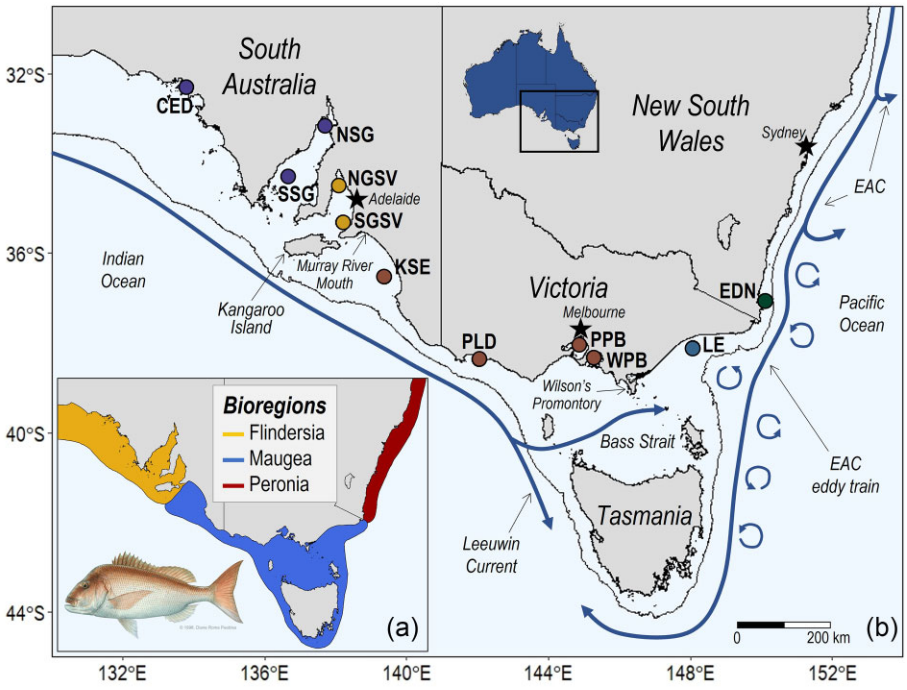

Figure 1. Maps of (a) the sampling sites for snapper (*C. auratus*) across southeastern Australia, with sites coloured by the relevant management area: ● = Spencer Gulf/West Coast, ● = Gulf St Vincent, ● = Western Victoria, ● = Eastern Victoria, ● = East Coast; and (b) the major biogeographic provinces in southeastern Australia: Flindersia, Maugea and Peronia (as in Teske *et al.*, 2017). CED, Ceduna; NSG, Northern Spencer Gulf; SSG, Southern Spencer Gulf; NGSV, Northern Gulf St Vincent; SGSV, Southern Gulf St Vincent; KSE, Kingston SE; PLD, Portland; PPB, Port Phillip Bay; WPB, Western Port Bay; LE, Lakes Entrance; EDN, Eden.

and maturation occurs between 3 and 7 years of age (Parsons *et al.*, 2014; Wakefield *et al.*, 2015). Adult fish can live >60 years of age and reach lengths of ~100 cm. Although snapper is an important commercial and recreational fishery resource across its range, catches in southeastern Australia (Figure 1) have been particularly large (Fowler *et al.*, 2021). Between 2010 and 2019, South Australia (SA) generally provided the largest state-based commercial catches of snapper in Australia, although these catches have recently declined, while Victoria (Vic) dominates the country's recreational snapper catch. In 2011–2012 in SA, ~875 t of snapper were captured commercially, while in Vic in 2006–2007, ~600 t of snapper were captured by recreational fishers (Fowler *et al.*, 2021). Consequently, snapper resources in the southeast are of the most valuable in Australia.

In southeastern Australia, snapper is currently managed as five separate stocks—Spencer Gulf/West Coast, Gulf St Vincent, Western Victoria, Eastern Victoria, and the New South Wales (NSW) component of the East Coast (Figure 1; Fowler *et al.*, 2021). Although Western Victoria and the NSW component of the East Coast are considered sustainable and Eastern Victoria is classified as undefined, the two purely SA snapper stocks have been depleted (Fowler *et al.*, 2021). As a result, the Spencer Gulf/West Coast, and Gulf St Vincent stocks were closed to fishing in 2019. The five southeastern snapper stocks are thought to be mostly sustained by the large spawning aggregations occurring in Spencer Gulf, Gulf St Vincent and Port Phillip Bay (Coutin *et al.*, 2003; Fowler, 2016). However, spawning also occurs in open shelf waters of eastern Vic, as well as farther north in NSW, with eastern Vic inlets serving as nurseries (Hamer and Jenkins, 2004).

The boundaries of the five southeastern Australian snapper stocks are based on knowledge of population structure and connectivity gained primarily from otolith microchemistry (Hamer *et al.*, 2011; Fowler *et al.*, 2017), mark-recapture (Coutin *et al.*, 2003; McGlennon, 2003) and demographic analyses (Fowler, 2016). The most detailed population genetic work done in the region are a mitochondrial DNA study with a Victoria component including Port Phillip Bay only (Donnellan and McGlennon, 1996) and a microsatellite DNA study with Port Phillip Bay as its westernmost sample (Morgan *et al.*, 2018). Additionally, investigations of population structure and connectivity in snapper in southeastern Australia have thus far focused on one state or sub-region, or involved sparse sampling. No population genomic analyses have been done on southeastern Australian snapper.

The marine environment in southeastern Australia is complex (Figure 1). The region possesses islands, variable continental shelf morphology and bathymetry, a topographically complex coastline, temperature fronts, upwellings, boundary currents at the shelf-edge and seasonal inshore wind-driven currents (James and Bone, 2010). It also encompasses three distinct biogeographic provinces (Figure 1)—Flindersia (warm-temperate), Maugea (cold-temperate), and Peronia (warm-temperate; Bennett and Pope, 1953). These bioregions coincide with species distributions as well as phylogenetic and population genetic structure (see the reviews: Colgan, 2015; Teske *et al.*, 2017), particularly in taxa without particularly mobile adult stages, such as seagrass, gastropods, and echinoderms (e.g. Waters *et al.*, 2004; Sinclair *et al.*, 2016; Teske *et al.*, 2017). Consequently, it is not clear how important these marine biogeographic boundaries are for marine fishes that have high dispersal potential across multiple life stages.

Table 1. Numbers of individuals after removing those with >20% missing data, average fork lengths (mm) and ages (years) followed by *SD*s in parentheses (for details on ageing methods see McGlennon, 2003), expected heterozygosity, H_E; observed heterozygosity, H_O; and percentage polymorphic loci, %PL for all snapper samples. Figure 1 shows sample jurisdiction and management area.

	N	Avg. FL	Avg. age	H_E	H_O	%PL
Ceduna (CED)	37	634 (127)	8.7 (4.1)	0.187	0.188	95.0
Northern Spencer Gulf (NSG)	39	477 (134)	3.5 (1.0)	0.187	0.185	95.3
Southern Spencer Gulf (SSG)	40	444 (149)	9.1 (4.7)	0.187	0.188	95.5
Northern Gulf St Vincent (NGSV)	39	488 (184)	7.0 (3.8)	0.191	0.203	95.3
Northern Gulf St Vincent 2010 (NGSV10)	26	653 (75)	9.5 (1.7)	0.186	0.185	91.8
Southern Gulf St Vincent (SGSV)	40	665 (139)	10.3 (3.5)	0.189	0.187	96.7
Kingston SE (KSE)	38	514 (98)	7.9 (2.5)	0.188	0.185	94.8
Portland (PLD)	39	331 (42)	N/A	0.187	0.184	93.6
Port Phillip Bay (PPB)	40	592 (61)	N/A	0.189	0.189	94.4
Port Phillip Bay 2011 (PPB11)	30	504 (69)	8.9 (1.3)	0.187	0.186	91.5
Western Port Bay (WPB)	40	438 (139)	6.5 (3.3)	0.188	0.191	94.4
Lakes Entrance (LE)	40	337 (77)	N/A	0.187	0.187	95.6
Eden (EDN)	40	283 (31)	2.7 (1.5)	0.183	0.181	95.4

Here, we assess population structure in snapper from across 11 locations in southeastern Australia using a dataset of genome-wide SNPs. We test the hypothesis that the population genomic structure of this mobile species corresponds with the major biogeographic provinces of the region. We also investigate whether the current spatial scales of assessment and management adopted in the region are consistent with evidence from population genomics. Our dataset includes fish from all currently recognized snapper stocks in southeastern Australia for assessing the presence of genetic breaks at management boundaries (Figure 1). Last, our dataset comprises two temporally spaced samples from two major spawning sites in southeastern Australia for assessing temporal stability in population genomic structure. Genetically defined stocks have important implications for the management of some of Australia's most important snapper fisheries as well as for understanding drivers of population differentiation in coastal marine environments.

Materials and methods

Sampling

In 2018 and 2019, a total of 435 adult snapper were sampled from 11 sites along the southeastern Australian coast between Ceduna, SA, and Eden, NSW (Figure 1, Table 1). These 11 sites cover all current snapper management areas in southeastern Australia and the vast majority of fishing activity occurring in the region (Fowler *et al.*, 2021). Muscle or fin samples were taken from fish landed by researchers or commercial or recreational fishermen (Supplementary Table S1). Muscle samples were also obtained from snapper used in a microsatellite study (Gardner *et al.*, 2022) landed in NGSV ($n = 26$) and PPB ($n = 30$) in 2010 and 2011, respectively (Table 1). We used these samples to assess temporal stability in population structure. Where possible, age and length data were obtained for each sampled individual (Table 1). All samples were preserved in 100% ethanol and stored at −20°C.

DNA extraction, sequencing and bioinformatics

DNA was extracted from each tissue sample using a modified salting-out protocol (Supplementary Material; Sunnucks and Hales, 1996). Library preparation for double digest restriction-site associated DNA (ddRAD) sequencing was then carried out as in Peterson *et al.* (2012), with modifications as detailed in (Brauer *et al.*, 2016; Supplementary Material). Sequencing was done on six lanes of an Illumina Hi-seq 4000 (150 bp paired end) at Novogene (Hong Kong). Raw sequence reads were put through a bioinformatic pipeline as in Bertram *et al.* (2022) to produce a high-quality SNP dataset (Supplementary Material; Supplementary Table S2). Subsequently, SNP markers potentially under selection were identified and removed to produce a putatively neutral dataset (Supplementary Material; Supplementary Table S2).

Genomic diversity statistics and pairwise genetic differentiation (F_{ST})

Genomic diversity in each snapper sample was assessed with estimates of expected and observed heterozygosity (H_E and H_O) and percentage polymorphic loci (%PL) using the *populations* module in STACKS 2 (Rochette *et al.*, 2019). Genetic differentiation (F_{ST}) between pairs of samples was estimated with ARLEQUIN 3.5 (Excoffier and Lischer, 2010), using 1000 permutations to assess significance. *P*-values were corrected for multiple comparisons with the Benjamini and Hochberg (1995) false discovery rate (FDR) method. Global F_{ST} was determined using HIERFSTAT 0.5–10 (Goudet *et al.*, 2015), with 95% confidence intervals (CIs) calculated using 1000 permutations.

Clustering analyses

The number of genetically distinctive groups was inferred with two approaches. First, principal components analysis (PCA) was performed using VEGAN 2.5–6 (Oksanen *et al.*, 2018). Missing genotypes (0.9% of data matrix) were replaced with the most common one at the locus. We then employed the maximum likelihood approach of ADMIXTURE 1.3 (Alexander *et al.*, 2009; Alexander and Lange, 2011). The software's cross-validation procedure was used to determine the most likely number of *K* genetic clusters in the dataset. A 5-fold cross-validation was conducted for *K* values 1–8. Membership probabilities were illustrated using GGPLOT2 3.3.3 (Wickham, 2016). The analysis was also run with the two temporal samples to investigate temporal variation in membership probabilities to each inferred genetic cluster.

Isolation by coastal distance and its effect size

Isolation by distance (IBD) was tested by comparing matrices of linearized F_{ST} and coastal distance using Mantel tests in GENALEX 6.5 (Peakall and Smouse, 2012). Due to the find-

ing of population differentiation at biogeographic boundaries (see the "Results" section), we also used redundancy analysis (RDA) to estimate the effect size of a distance relationship. This was done using VEGAN by controlling for the effect of population structure using Q values from ADMIXTURE. Coastal distances were estimated as the shortest distance between sampling locations following the coastline using the *vialmaris* function in melfuR 0.9 (https://github.com/pygmyperch/melfuR). The significance of the Mantel tests and RDA were determined with 10 000 and 1000 permutations, respectively.

Spatial autocorrelation

First, we used spatial principal component analysis (sPCA) in ADEGENET 2.1.5 (Jombart, 2008), a method optimized to reveal cryptic spatial genetic differentiation that summarizes both the non-spatial variability and the spatial autocorrelation among genotypes (calculated as Moran's I). We used a connection network based on a spatial weights matrix generated from the inverse of the absolute distances between sampling locations. The analysis was run on the whole 2018–2019 dataset and then separately for the two large groups identified by the clustering analyses using 9999 permutations. Lagged spatial principal component scores were plotted using ADE4 1.7–18 (Dray and Dufour, 2007).

Second, spatial autocorrelation coefficients (r) were calculated for each site separately in GENALEX 6.5 (Smouse and Peakall, 1999; Peakall and Smouse, 2012) to investigate within-location spatial autocorrelation. Significance was calculated using 1000 bootstraps and 95% CIs around the null hypothesis of randomly distributed genotypes were calculated using 1000 permutations. We regarded a value of r to be significant only if it occurred outside of the 95% CIs around the null hypothesis of zero correlation and if its error bars did not overlap the x-axis.

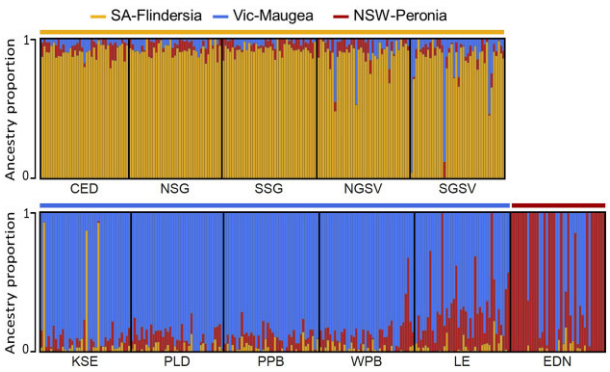

Figure 2. ADMIXTURE results for $K = 3$ based on the 432 snapper from 2018–2019. Biogeographic provinces (Flindersia, Maugea, Peronia) and genetic groupings (SA, Vic, NSW) are marked above the plots. Each vertical bar represents an individual, and its probability of membership to each of the K groups is indicated by its colour makeup.

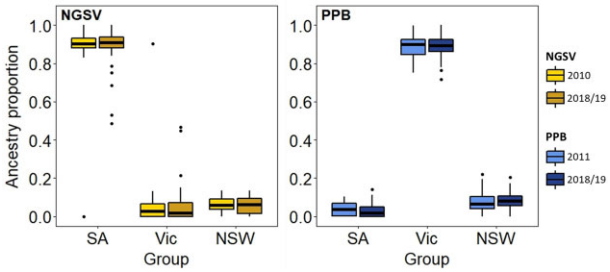

Figure 3. Box and whisker plots illustrating temporal comparisons of snapper membership to the three clusters identified by ADMIXTURE between the two sampling periods at NGSV (gold) and PPB (blue). None of the comparisons at either location were significantly different. Dots are outliers, and whisker extremes represent minimum and maximum scores.

Results

SNP genotyping and genomic diversity

Following alignment of sequence reads to the snapper genome and SNP calling, ~7.3 million raw variants were discovered. Three individuals with >20% missing data were removed from the dataset, leaving 488 for subsequent analyses (432 from 2018–2019 and 56 from 2010–2011; Table 1). After quality filtering and removing 350 outlier SNPs, 10 916 SNPs remained (Supplementary Table S2). Average missing data per sample was 1.0% (0–13.1%) and average coverage depth per locus per sample was 102.6 (6.9–303.5).

Genetic diversity was similar across the 11 snapper localities collected in 2018 and 2019 (Table 1), with expected heterozygosity (H_E) ranging between 0.183 (EDN) and 0.191 (NGSV), observed heterozygosity (H_O) ranging between 0.181 (EDN) and 0.203 (NGSV), and percentage polymorphic loci (%PL) ranging between 93.6% (PLD) and 96.7% (SGSV).

Clustering analyses

Although $K = 2$ was most supported by ADMIXTURE (Supplementary Figure S1), $K = 3$ closely followed (Figure 2), and the PCA indicated the presence of three clusters (Supplementary Figure S2)—the South Australia (CED–SGSV), Victoria (KSE–LE) and New South Wales (EDN) stocks. In the SA stock, two Vic migrants and several individuals with mixed ancestry occurred, but only in Gulf St Vincent, adjacent to the stock's eastern boundary. Only three SA migrants were detected in the Vic stock, adjacent to the stock's western boundary in KSE. While an abrupt genetic break occurred between the SA and Vic stocks, a region of admixture occurred between the Vic and NSW stocks (Figure 2). Even though LE clearly clustered with the Vic stock, our sample contained both NSW migrants and a considerable proportion of individuals with mixed ancestry. Although the EDN sample contained predominantly individuals with NSW ancestry, it also contained fish that were migrants from Vic and that had mixed ancestry.

Temporal analysis

ADMIXTURE ancestry proportions across the temporally spaced samples at NGSV and PPB (separated by approximately nine and eight years respectively) were not significantly different (Figure 3). Additionally, the analysis detected a migrant from the Vic stock into the NGSV sample from 2010 (Vic stock outlier in NGSV10 sample in Figure 3).

Pairwise F_{ST}, and isolation by coastal distance (IBD) and its effect size

Global F_{ST} was small at 0.0116 (95% CIs: 0.0098, 0.0135), and pairwise F_{ST} values were also small, ranging between 0.0002 (CED: SSG) and 0.0223 (NSG: PLD; Figure 4). Of the 55 pairwise F_{ST} values, 42 were significant after FDR correc-

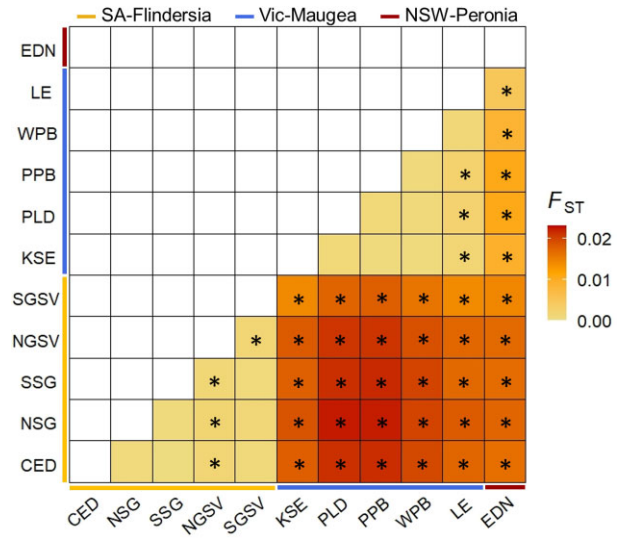

Figure 4. Heatmap of pairwise F_{ST} values (i.e. genetic differentiation) between the 2018–2019 snapper samples, with significant comparisons denoted with an asterisk. F_{ST} values ranged between 0.0002 and 0.0223. Main groupings (SA, Vic, NSW) and biogeographic provinces (Flindersia, Maugea, Peronia) are marked with coloured lines.

tion. The two previously identified broad groupings (SA and Vic stocks) were discernible in the pairwise F_{ST} heatmap, as well as the differentiation of EDN. NGSV and LE were the only samples to show significant differentiation within their respective clusters.

A Mantel test uncovered significant IBD between the west coast of SA and the south coast of NSW ($r = 0.57$, $p = 0.003$; Supplementary Figure S3). However, this trend was largely driven by differentiation at genetic stock boundaries; e.g. no IBD occurred within the SA and Vic stocks (Supplementary Figure S3). This was statistically supported by the RDA results. When both population structure and coastal distance were included as explanatory variables, the RDA model was significant and had more power (3.2% vs. 1.6%) than when only coastal distance was included (Supplementary Figure S5; Table S3).

Spatial autocorrelation

Significant sPCA global spatial structures were detected in the whole dataset ($p = 0.0001$) as well as within the SA and Vic stocks ($p = 0.0109$ and 0.0265). The sPCA including all 2018–2019 samples differentiated the three groups identified with ADMIXTURE and PCA (SA, Vic, and NSW; Supplementary Figure S4). Additionally, it illustrated the nature of the boundaries between the groups, with the SA-Vic boundary occurring abruptly between SGSV and KSE and a region of IBD occurring from WPB to EDN between the Vic and NSW stocks. The sPCA of the SA stock differentiated Gulf St Vincent, especially NGSV, from all other SA sites (Figure 5a), and the sPCA of the Vic group differentiated LE from all other Vic sites (Figure 5b).

Within site, spatial autocorrelation indicated that genotypes were significantly correlated at all sites except SSG, PLD, and WPB. Spatial autocorrelation coefficients were largest for NSG, NGSV, LE, and EDN (Figure 6).

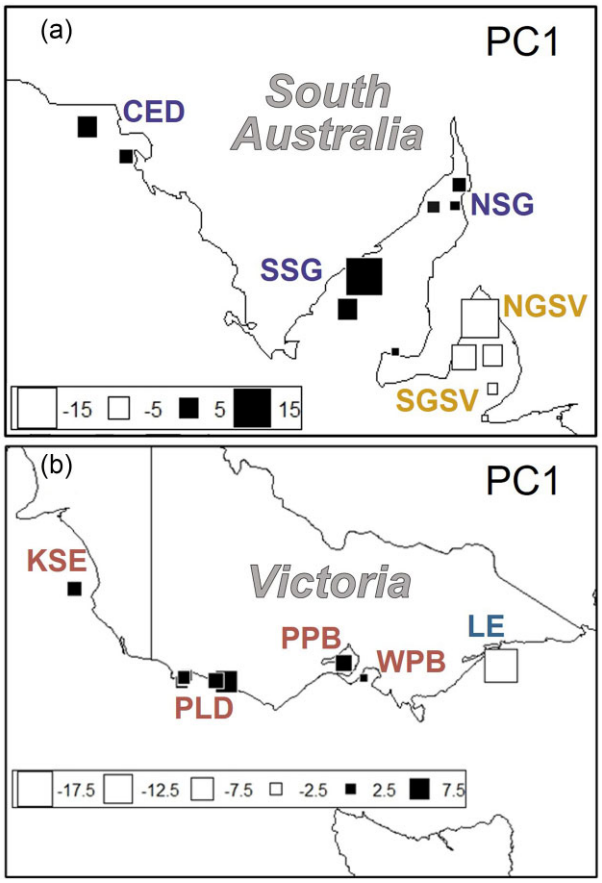

Figure 5. The first global scores of spatial PCA (depicted by squares) of the (a) SA stock and the (b) Vic stock. The colour of squares represents assignment to the main spatial genetic clusters, while square size indicates differentiation magnitude. Site names are coloured according to the management area in which they reside (as in Figure 1): ● = Spencer Gulf/West Coast, ● = Gulf St Vincent, ● = Western Victoria, ● = Eastern Victoria, ● = East Coast.

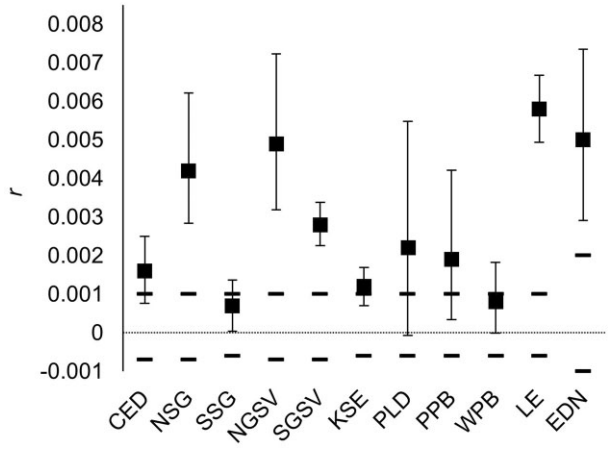

Figure 6. Within site genotypic autocorrelation coefficients (r) for snapper in southeastern Australia with 95% confidence intervals. Individuals are more similar than expected by chance at all sites except for at SSG, PLD, and WPB.

Discussion

Using comprehensive sampling and a genome-wide SNP dataset, we uncovered genetic breaks in the heavily exploited teleost snapper across southeastern Australia concordant with the region's biogeographic barriers. Although these breaks coincide with only two of the four management boundaries used for snapper in the region, we also found evidence for fine-scale genetic structure corresponding with the two other boundaries. This fine-scale structure likely reflects spatial variation in spawning and recruitment dynamics and highlights the power of genome-wide SNP datasets for revealing evolutionary and demographic processes in highly abundant and dispersive species. Our study confirms the importance of marine biogeography in shaping intraspecific genetic structure, even in species with high dispersal potential.

Bioregional divisions and stock structure

Coastal marine species often exhibit distinct breaks within their distributions where movement is limited, frequently aligning with bioregional boundaries (Briggs, 1974; Kelly and Palumbi, 2010; Teske *et al*., 2017). These boundaries may coincide with shifts in features like ocean circulation, bathymetry, temperature, coastline topography, and habitat (Hayden and Dolan, 1976; Gaylord and Gaines, 2000; Colgan, 2015). At a broad scale, the population structure of snapper in southeastern Australia is predominantly shaped by two physical discontinuities that correspond to the boundaries between the three biogeographic provinces in the region—Flindersia, Maugea, and Peronia (Figure 1). Few population genetic studies on finfish in southeastern Australian with high dispersal potential across all life stages have reported structuring corresponding to these biogeographic boundaries. Population genetic work with mulloway (*Argyrosomus japonicus*), gemfish (*Rexea solandri*), and round herring (*Etrumeus sadina*) have reported structuring coinciding only with the boundary between Maugea and Peronia (Colgan and Paxton, 1997; DiBattista *et al*., 2014; Barnes *et al*., 2015).

The relatively strong genetic break detected near the Murray River Mouth in southeast SA corresponds with the boundary between Flindersia and Maugea. This finding agrees with previous work on snapper involving otolith microchemistry (Fowler *et al*., 2017), demographic analyses (Fowler, 2016), mark-recapture (McGlennon, 2003), allozyme and mitochondrial DNA markers (MacDonald, 1980; Donnellan and McGlennon, 1996) and microsatellites (Gardner *et al*., 2022). Otolith microchemical analyses indicate that the region between Wilson's Promontory and the southeast of SA is dominated by fish spawned in Port Phillip Bay, while the area between the southeast and west coast of SA is dominated by fish spawned in the northern gulfs (Fowler *et al*., 2017).

In contrast to the sharp genetic break detected near the Murray River Mouth, a region of admixture occurred at the transition between Maugea and Peronia. This region, between Wilson's Promontory and the south coast of NSW, is a heterogeneous mix between Vic and NSW snapper. Although fewer studies on snapper have included the lower east coast, the inferred admixture was also found in a microsatellite analysis focusing on eastern Australia (Morgan *et al*., 2018). Additionally, otolith microchemistry analyses and recruitment surveys suggest that eastern Victorian snapper originate from several different sources, including local inshore areas off Lakes Entrance, Port Phillip Bay, and areas farther north along the east coast (Hamer and Jenkins, 2004; Hamer *et al*., 2011).

Differentiated populations corresponding with these biogeographic provinces may represent groups that were isolated in different refugia during the glacial maxima when continental shelf habitat was dramatically reduced as well as fragmented (Waters and Roy, 2003; Sinclair *et al*., 2016). When sea levels were ~129 m below their present level during the last glacial maximum (LGM), the Bassian Isthmus, between Tasmania and mainland Australia, and Lacepede Shelf, east of Kangaroo Island in the southeast of SA, were exposed, thereby acting as gene flow barriers between the provinces (James and Bone, 2010; Colgan, 2015). Our results are consistent with the recolonization of the Bass Strait by a proximate Maugean population, instead of Flindersian or Peronian refugia populations. This scenario accounts for the genetic breaks reflecting bioregional provinces and for the formation of the Vic stock despite the area being inhospitable to marine fishes during the LGM. Why genetic differentiation has persisted since the inundation of these regions is uncertain. Many suggest that the vast sandy areas at the bioregion boundaries maintain these genetic discontinuities. However, snapper inhabit both sand and reef, and possess the ability to migrate between these areas. Other studies on species inhabiting sandy areas, including seagrass (*Posidonia australis*), an asteriid sea star (*Coscinasterias muricata*), and cuttlefish (*Sepia apama*), have found population structure coinciding with one or more of the bioregion boundaries (Kassahn *et al*., 2003; Waters and Roy, 2003; Sinclair *et al*., 2016). Alternatively, the maintenance of such historic differentiation may reflect flow patterns and/or competitive or density-dependent interactions (Teske *et al*., 2017). For example, the Maugea–Peronia boundary may be maintained by the convergence of the Leeuwin Current and EAC, and EAC eddies. However, density-dependent interactions are perhaps particularly likely in snapper since it is highly fecund and abundant. Large amounts of immigration would therefore be required to cause genetic changes in a large local population, which may be hindered by local resource monopolization and competitive superiority of locally adapted fish (De Meester *et al*., 2002).

Fine-scale structure within stocks

Spatial autocorrelation analyses can identify the spatial scales over which individuals are more genetically similar than expected at random and therefore, whether local recruitment and/or site fidelity occurs. In the SA stock, our spatial autocorrelation analyses uncovered subpopulation-level structure between Gulf St Vincent and Spencer Gulf and Ceduna, as well as significant local recruitment and site fidelity at the most important spawning and nursery areas for snapper in SA—Northern Spencer Gulf and Northern Gulf St Vincent, (Fowler and Jennings, 2003; Fowler *et al*., 2017). These results may reflect demographic differences between the two gulfs determined with analyses of recruitment history (Fowler, 2016), as well as the limited movement of adults found by mark-recapture work (McGlennon, 2003). The demographic analyses suggest that juveniles that result from periodic strong recruitment events in either of the two gulfs dominate catches across the entire SA stock after recruiting to the fishery. How-

ever, when these infrequent events do not occur, the recruitment dynamics of the two gulfs appear largely independent (Fowler, 2016), potentially leading to the positive spatial autocorrelation uncovered here. The current approach to stock assessment modelling pragmatically treats Spencer Gulf/West Coast and Gulf St Vincent separately, acknowledging the evidence for separation in reproductive and recruitment processes, and the rarity of strong recruitment events. It is possible that the Spencer Gulf and Gulf St Vincent spawning groups originated from a single ancestral population during the LGM when the gulfs were dry (James and Bone, 2010). The intermittent demographic isolation occurring on short time scales between the gulfs is likely not prolonged enough to cause significant genetic differentiation. Additionally, the abundances of snapper in these areas would have to be greatly reduced for a very prolonged period to produce significant genetic differentiation.

Outside the SA stock, we detected positive spatial autocorrelation along the lower east coast between Port Phillip Bay and Eden, indicative of isolation by distance, consistent with allozyme work by Meggs *et al.* (2003). The site-specific spatial autocorrelation analysis indicated that individuals were most similar at the two most eastern locations—Lakes Entrance and Eden—despite them containing individuals with a range of ADMIXTURE ancestry profiles (Figures 2 and 6). This positive spatial autocorrelation may relate to local retention of pelagic life stages by EAC eddies (Mullaney and Suthers, 2013). Another possibility is that the abundances of snapper at Lakes Entrance and Eden are relatively low, increasing the chance of sampling genetically alike individuals. This idea is supported by the lower catches of snapper off Lakes Entrance and Eden (Stewart, 2020; Fowler *et al.*, 2021). The lack of large embayments to support large spawning aggregations and recruits, as well as the scarcity of rocky reef habitat preferred by adults, may prevent populations from becoming very large in these areas.

Temporal analysis supports both broad and fine-scale genetic patterns

The temporal analysis indicated stability in admixture proportions at Northern Gulf St Vincent and Port Phillip Bay over an ~8-year period. This indicates the persistence of the genomic signal of local recruitment and fidelity of adults associated with these two important spawning sites. This result is concordant with similar work in the western part of the range of snapper at the major spawning site Cockburn Sound (Bertram *et al.*, 2022). Both Northern Gulf St Vincent samples captured dispersal from the Vic stock, suggesting that such events are temporally persistent. Demographic analyses suggest that such dispersal results from very strong recruitment events in Port Phillip Bay (Fowler, 2016). The two Port Phillip Bay samples were both devoid of migrants from other stocks as well as admixed individuals. Our temporal analysis therefore also indicates consistency in the patterns of migration between adjacent stocks.

Management implications

Our study allows us to assess the correspondence between current spatial scales of assessment and management in the region and both broad and fine-scale genetic structure. Our results provide strong support for the management boundaries in place at the Murray River mouth and at the Vic-NSW border. Population genomics also supports the spatial scales of the SA fishery closure initiated due to spawning biomass depletions in Gulf St Vincent and Spencer Gulf (Fowler *et al.*, 2021). Our results support the inclusion of the west coast of SA and the exclusion of southeast SA in the ban since they indicate that the former is dependent on spawning in the gulfs, particularly the Spencer Gulf, while the latter depends on spawning in Vic. Additionally, the 2022 SA snapper assessment indicated that the Spencer Gulf/West Coast and Gulf St Vincent stocks were not recovering, while biomass was increasing in southeast SA (Drew *et al.*, 2022), further corroborating our conclusion that the productivity of snapper in southeast SA is independent of the SA gulfs.

The management boundaries currently in place between the two SA gulfs and at Wilson's promontory are not marked by genetic breaks. However, we detected fine-scale genetic structure corresponding to the two boundaries. These boundaries therefore may be suitable depending on the management objectives. Particularly, the unique spawning and recruitment dynamics in each SA gulf and eastern Vic could mean that if depletions occur in these areas, recovery through gene flow from adjacent populations may occur very slowly, particularly because the frequency of strong recruitment events in adjacent populations is highly temporally variable (Hamer and Jenkins, 2004; Fowler, 2016). Although strong recruitment occurred in the Vic stock in 2018 (Fowler *et al.*, 2021), prolonged recruitment failure in the SA gulfs could mean that spawning groups in either the Spencer Gulf or Gulf St Vincent may not be able to recover depleted local snapper resources in a timeframe relevant to fisheries management (Fowler, 2016). Finer-scale sampling and an analysis of local adaptation using seascape genomics (e.g. Sandoval-Castillo *et al.*, 2018) may be beneficial for better understanding patterns of gene flow and recruitment in these areas.

Conclusion

Our study highlights that the well-known southeastern Australian biogeographic provinces can match intraspecific patterns of genetic structure in highly dispersive species like snapper. Traditionally, population differentiation coinciding with these biogeographic provinces was thought to occur due to the vast areas of sandy habitat around the bioregions' boundaries. However, snapper occur in both sandy and reef habitats, and therefore it is possible that other forces may shape intraspecific distribution patterns. Two of the current management boundaries used for snapper in the region coincided with the genetic discontinuities detected at bioregional boundaries. Although the remaining two management boundaries did not coincide with distinct genetic breaks, they were marked by finer-scale genetic structure. Our study highlights the value of population genomic surveys involving exploited marine species with high dispersal potential for uncovering both strong genetic breaks and local-scale structuring associated with spatial variation in spawning and recruitment dynamics.

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Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Conflict of interest statement

The authors have no conflicts of interest to declare.

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Author contributions

LBB, MW, AF, PH and JS conceptualized the study and acquired funding. LBB and AB conceived the idea for the manuscript. AB conducted the laboratory work, with contributions from JS and CB. AB analysed the data, with assistance from JS and CB. AB led the writing of the first version of the manuscript. All authors contributed to the revising of the final manuscript.

Data availability statement

The SNP dataset is available on figshare: https://doi.org/10.6084/m9.figshare.22339921.

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