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Role of embayments in local recruitment and connectivity of the fisheries-important snapper *Chrysophrys auratus*

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ABSTRACT: Understanding the reproductive contribution of different geographic areas to fisheries stocks is crucial for their effective management. This is particularly important for heavily exploited marine resources with large populations and high connectivity. The Australasian snapper *Chrysophrys auratus* is an important fisheries resource that forms major spawning aggregations along its range, especially in embayments, such as Cockburn Sound and Warnbro Sound on the west coast of Australia. Here, we combined population genomic analyses with assessments of reproductive output to evaluate the contribution of embayment spawning aggregations to the adjacent open coast stock. We used 10 438 SNPs for 533 individuals from 19 locations to characterize fine-scale population structure and connectivity. Adults and juveniles sampled over consecutive spawning seasons were used to test whether recruitment within embayments occurs primarily from local spawning events. We found low genetic differentiation and high connectivity, yet strong evidence of local recruitment, including within embayments. Seascape genomics revealed a signal of local genetic differentiation associated with variation in sea surface temperature and primary productivity. While population genomics demonstrates that Cockburn Sound and Warnbro Sound spawning aggregations contribute to recruitment across the species' south-western Australian stock, our assessment of relative reproductive output indicates that the contribution of individuals from embayments may be higher than from the adjacent open coast. Our findings expand our knowledge about fine-scale connectivity and population dynamics in a highly mobile, heavily exploited species and highlight the important role of embayments to regional population recruitment by providing favourable conditions for both spawning aggregations and juveniles.

KEY WORDS: Fisheries genomics · Natal homing · Stock structure · Stock assessment · Fisheries biology · Connectivity

1. INTRODUCTION

Many fisheries worldwide rely on the benefits provided by coastal regions such as embayments, which offer habitat, food, shelter, nursery and spawning grounds for fish species (Nagelkerken et al. 2015, Lefcheck et al. 2019). However, anthropogenic impacts and climatic change often have negative effects on these environments and their associated fisheries (Cheung et al. 2021, Mitchell et al. 2025). Implementing informed management approaches that consider the role of such habitats in fish life cycles can promote healthy stocks and translate into sustainable economic and social benefits for fishing communities (Bernatchez et al. 2017, Hilborn et al. 2020).

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Most species are structured into populations or groups of relatively isolated individuals that differ in demographic and life history traits, which directly influence their resilience to exploitation. Effective fisheries management therefore depends on accurately identifying biological populations, their levels of connectivity and, when applicable, the relative reproductive contribution of fish from different geographic areas (Cadrin 2020, Fontoura et al. 2022). More specifically, determining the spatial scales over which reproductive areas contribute recruits to the adult populations is critical to understand population dynamics, determine the right management spatial scales and prioritize conservation areas (Erisman et al. 2017). Ignoring the relative contribution of specific areas to recruitment, particularly if there are known important areas, could result in the overexploitation of local populations and associated loss of genetic diversity and adaptive potential (Allendorf et al. 2014). Moreover, environmental changes in areas where significant reproductive behaviour occurs, such as spawning aggregations, may also compromise reproductive function and habitat reuse rates (Gokturk et al. 2022).

Estimating the contribution of a region to recruitment is not easy, especially for relatively large and highly connected populations. Genomic data provide exceptional power to identify demographically distinct management units, estimate the levels of connectivity between stocks and determine the relative contribution of each stock to adult recruitment (Bernatchez et al. 2017). Moreover, when combined with environmental information, genomic data can also be used to test for local adaptation of fish spawning in different areas and their recruits (Grummer et al. 2019).

The Australasian snapper *Chrysophrys auratus* is a large (>1 m), long-lived (>40 yr) sparid that matures at 3–7 yr of age (Norriss & Crisafulli 2010, Parsons et al. 2014, Wakefield et al. 2015) and is important for commercial and recreational fisheries across Australia and New Zealand (Rogers et al. 2024). The species is a broadcast spawner with relatively high fecundity and a pelagic egg and larval phase of up to 33 d, preceding recruitment to coastal benthic habitats (Sim-Smith et al. 2012). In addition to spawning in open-ocean waters, it forms a few significant large spawning aggregations in sheltered embayments, where oceanographic conditions are thought to promote the retention of eggs, larvae and juveniles (Wakefield 2010). Such discrete spawning and nursery areas are assumed critical for the recruitment and subsequent fisheries sustainability of the broader stocks. In Western Australia, the species is managed in 3 different bioregions: Gascoyne Coast, West Coast and South Coast (Newman et al. 2023). Most of the Western Australian fishery production currently comes from the West Coast Bioregion (Rogers et al. 2024), where 2 genetic stocks have been identified: a mid-west and a south-western stock (Bertram et al. 2022).

Within the south-western stock, spawning aggregations are reported to occur only in Owen Anchorage and the adjacent embayments of Cockburn Sound and Warnbro Sound (Wakefield 2010, Crisafulli et al. 2019; see Fig. 1). Adult Australasian snappers migrate into these coastal habitats each year to spawn, with the largest aggregations occurring in Cockburn Sound (Wakefield 2010, Crisafulli et al. 2019). These protected habitats are subsequently used as a nursery by juveniles, which remain for 1–2 yr, before emigrating to coastal and deeper reef environments from which they can disperse widely (Wakefield et al. 2011). Adults return to spawn in multiple years, but not necessarily consecutively. When they leave the sound after spawning, adults can move 10s to 100s of kilometres, with tagged individuals recorded as far as 720 km away; however, the vast majority are recaptured within 20 km, where fishing effort are highest (Crisafulli et al. 2019). The assumed importance of these aggregations to broader stocks led to an annual Australasian snapper fishing closure in Cockburn Sound and Warnbro Sound in the early 2000s to protect both migrating and aggregating fish (Wakefield 2010). As knowledge of spawning dynamics has increased over time, this closure has expanded temporally and spatially (Crisafulli et al. 2019).

Here we used genome-wide single nucleotide polymorphism (SNP) data from adults and juveniles sampled over consecutive breeding seasons to investigate the fine-scale genetic relationship of the Australasian snapper spawning aggregations in the embayments of Cockburn Sound and Warnbro Sound to the broader south-western stock which occurs along ~400 km of coastline. We also integrated biological information on fish size and batch fecundity to determine the relative reproductive output of individuals in these embayment aggregations. More specifically, we evaluated the hypothesis that individuals from the aggregations contribute disproportionately to recruitment along the adjacent open coast. This study contributes to our understanding of the relative importance of embayment spawning aggregations to regional patterns of population recruitment in highly mobile and heavily exploited fisheries resources.

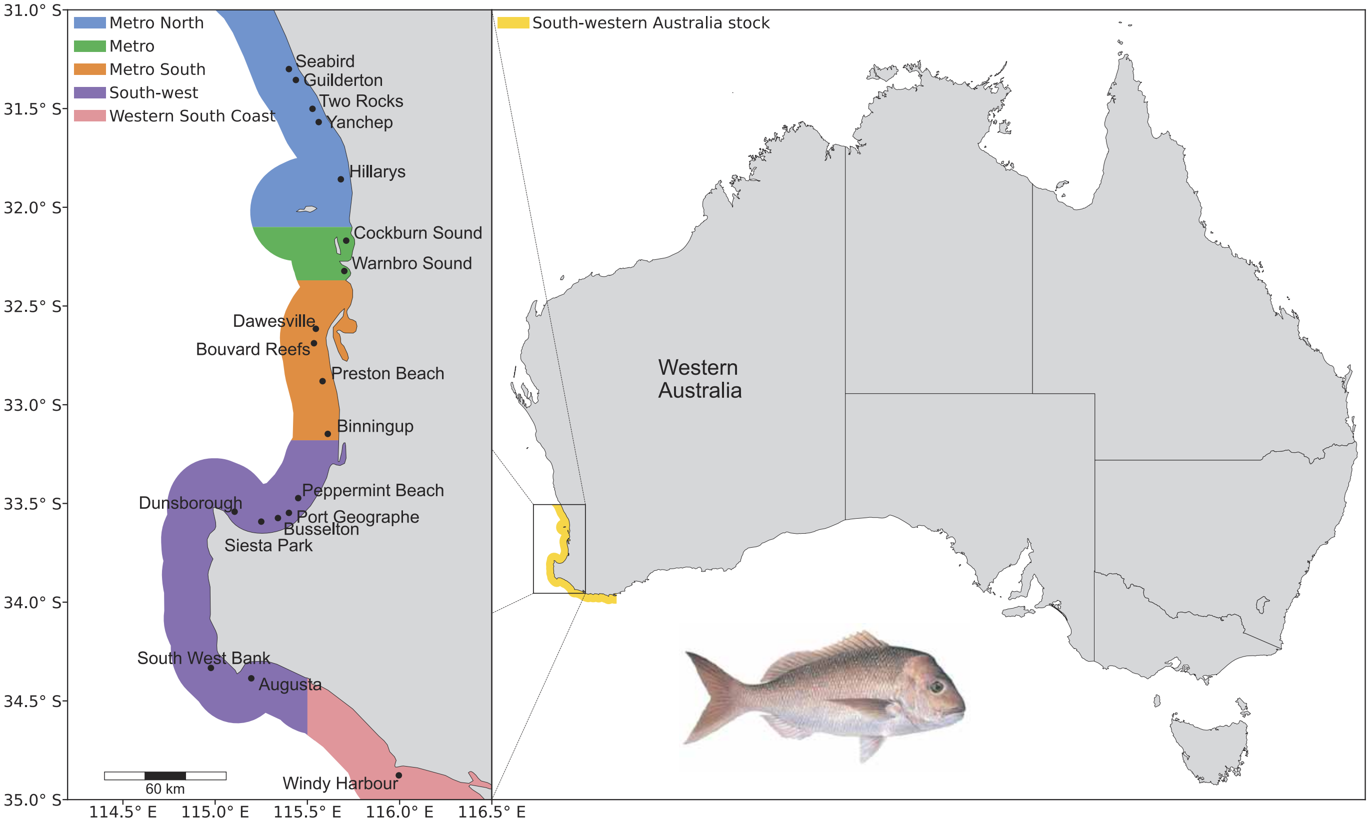

Fig. 1. Sampling locations (black dots; n = 19) in 5 geographic areas (coloured coastlines) of the south-western Australia stock of snapper in Australia. Illustration © R.Swainston/www.anima.net.au

2. MATERIALS AND METHODS

2.1. Tissue sample collection

Samples of fresh muscle from a total of 868 Australasian snapper were preserved in 100% ethanol for DNA extractions. Samples were obtained from fishery-dependent sampling of recreational and commercial landings, as well as fishery-independent sampling. The total includes 407 adult and 394 juvenile Australasian snapper collected during the spawning seasons of 2021/22 and 2022/23 from 19 locations within the south-western Australian stock, between 31° S on the west coast and ~116° E on the western south Australian coast (Fig. 1). These included the embayments Cockburn Sound and Warnbro Sound (32° 08′ – 32° 20′ S, referred to collectively as Metro) and locations within 3 broad geographic areas of the west coast, namely 1 to the north and 2 to the south of Cockburn Sound, i.e. Metro North (northern metropolitan area from Seabird to Hillarys, 31° 16′ – 31° 50′ S), Metro South (southern metropolitan area from Dawesville to Binningup, 32° 36′ – 33° 09′ S) and South-west (from Geographe Bay to Augusta, 33° 25′ – 34° 23′ S). Additionally, 67 adult samples from the Western South Coast (Windy Harbour, ~34° 51′ S, 116° E) were also obtained for comparison (Fig. 1). We kept localities with fewer than 8 samples because the main analyses were performed at the area level (5 broader areas), each of which included 20 or more samples once samples from corresponding localities were pooled.

2.2. DNA extraction, sequencing and SNP calling

DNA was extracted using a salting-out protocol (Sunnucks & Hales 1996). DNA was quantified with Qubit v2.0 (Life Technologies), and its integrity was assessed using gel electrophoresis (2% agarose). High-quality extractions from 541 individuals and 35 replicates were used to produce double-digestion restriction site-associated DNA (ddRAD) libraries following Peterson et al. (2012), with modifications described by Sandoval-Castillo et al. (2018). Samples from this and a different Australasian snapper project were randomly assigned to 9 pools of 96 samples. Five of these pools were sequenced in 5 lanes of an Illumina Hi-seq 4000 (150 bp paired end), and 4 were sequenced in 3 lanes of an Illumina NovaSeq X plus (150 bp paired end), all at Novogene (Hong Kong).

All bioinformatics were done using the DeepThought High Performance Computer at Flinders University, Adelaide, South Australia. Raw reads were first demultiplexed using the 'process_radtags' script from STACKS v2.0 (Catchen et al. 2013). Reads were quality trimmed ($Q < 20$) and residual adapters were removed using ADAPTERREMOVAL v2.3 (Schubert et al. 2016). Trimmed reads were mapped to a high-quality Australasian snapper genome (Catanach et al. 2019) with BOWTIE2 v2.4 (Langmead & Salzberg 2012) before calling SNPs using BCFTOOLS v1.16 (Li 2011). To minimize false variants due to sequencing errors or artifacts, we used VCFTOOLS v1.16 (Danecek et al. 2011) to perform the filtering steps detailed in Table S1 in the Supplement at www.int-res.com/articles/suppl/meps15126_supp.pdf. All scripts used are available at https://github.com/Yuma248/SNPcallingPipe.

2.3. Genomic diversity and population structure

The proportion of polymorphic loci, expected (H_e) and observed heterozygosity (H_o) were estimated at each location and area using the R package 'dartR' v2.9.7 (Mijangos et al. 2022). Pairwise fixation index (F_{ST}) values were calculated using the same package, with 1000 bootstraps to calculate corresponding p-values, which were then corrected for multiple comparisons using a false discovery rate approach (Benjamini & Hochberg 1995) with the R function 'p.adjust' (R Core Team 2024). Population structure was further assessed using 2 complementary approaches with different assumptions. First, principal components analysis (PCA) was performed using the R package 'ade4' v1.7 (Dray & Dufour 2007). For this analysis, missing data (~0.48%) were imputed using the mean allele frequency with the R package 'adegenet' v2.1.10 (Jombart 2008). Second, we implemented the maximum likelihood approach of ADMIXTURE v1.3 (Alexander & Lange 2011). The most likely K value was determined using a 5-fold cross-validation for K values between 1 and 5, and over 10 independent runs of each K.

2.4. Isolation by distance, local recruitment and connectivity

Isolation by spatial distance was tested using the relationship between linearised $F_{ST}(F_{ST}/1 - F_{ST})$ and the shortest coastal distance between sampling locations. Pairwise oceanic distances were calculated using the R function 'viamaris' from 'melfuR' (https://github.com/pygmyperch/melfuR). Spatial autocorrelation at the geographic area level was assessed using GENEALEX v6.5 (Peakall & Smouse 2006) to test if recruitment occurs mostly within each area. Correlation coefficients (r) were calculated, and their significance was determined using 1000 bootstrap iterations, while 95% CIs around the null hypothesis of randomly distributed genotypes were determined with 1000 permutations. To determine the level of connectivity between areas, we estimated the relative migration rates (Nm, normalized by the largest value estimated) with the 'divMigrate' function implemented in the R package 'diveRsity' (Sundqvist et al. 2016). Briefly, this method models a hypothetical pool of migrants between pairs of populations and then estimates the genetic differentiation between the pool of migrants and each of the populations. The direction of gene flow can be estimated based on these levels of differentiation (Sundqvist et al. 2016). We tested for significant asymmetric gene flow among areas using 1000 bootstrap iterations.

2.5. Seascape genomics

We used a seascape genomics framework (Grummer et al. 2019) to test if environmental variation in the study region is associated with patterns of genetic diversity and population differentiation. We selected 5 key oceanographic variables known to impact adaptive genetic diversity and connectivity in coastal organisms from this region (Sandoval-Castillo et al. 2018): sea surface temperature (°C), pH, salinity (practical salinity units), oxygen concentration (mmol m^{-3}), and primary productivity (expressed as carbon in seawater, g m^{-3} d^{-1}). For each variable, layers of the annual minimum, maximum, mean, and range between the years 2000 and 2014 were used, except pH, for which only the annual mean was available, resulting in a total of 17 variables. The layers of these variables were downloaded from the BioOracle database (Assis et al. 2018) using the R package 'sdmpredictors' (Bosch et al. 2017) at a spatial resolution of 0.25 degrees. After removing correlated variables (variance inflation factor >3) or those without variation in the region, 2 variables were selected: mean sea surface temperature and primary productivity range. Using standard geographic coordinates for seascape analysis could distort biological spatial patterns because the effect of land masses is not considered. Consequently, to control for spatial autocorrelation, pairwise oceanic distances between sampling localities were transformed into synthetic coordinates using the R package 'MASS' (Ripley et al. 2013), and then used as conditional factor. These variables were used to perform a partial redundancy analysis (RDA) controlled by geographic distance using the R package 'vegan', function 'rda' (Oksanen et al. 2024). Significance of the whole model, each axis and each explanatory variable was calculated via 1000 permutations. We calculated the Mahalanobis distance of SNPs projected on the significant RDA axes using the R package 'robusst' (Wang et al. 2014). This distance reflects the strength of association between loci and environmental variables, accounting for correlation among RDA axes. Loci were identified as candidates being under selection if their Mahalanobis distance significantly exceeded the null distribution, with a false discovery rate ≤0.1 (Capblancq et al. 2018). In addition, we used SnpEff (Cingolani et al. 2012) to explore the genomic position of candidate loci relative to genes and to predict their functional impact.

2.6. Relative contribution to reproductive output

Length-frequency distributions and estimated batch fecundity were used to evaluate the relative contribution of Cockburn Sound and Warnbro Sound Australasian snapper individuals to the reproductive output across the south-western stock. Biological data for Australasian snapper were obtained from Western Australian Department of Primary Industries and Regional Development data sets derived from sampling of commercial and recreational catches across the south-western stock between 2000 and 2024, and from research sampling over the same period (Fisher et al. 2025). In both cases, fish were caught by baited hook and line. In the laboratory, total lengths (TL) or, if caudal fins were incomplete, fork lengths (FL), were measured to the nearest 1 mm. The sex and gonadal development stage of each fish was then determined according to standard methods (Wakefield et al. 2015). FLs were converted to TLs using the equation TL = (FL + 23.058) / 0.897 (Wakefield 2006) to compare length frequency distributions.

Comparisons of relative reproductive output were conducted between adult female Australasian snapper collected in Cockburn and Warnbro Sounds, as adults move between these locations (Crisafulli et al. 2019), and those from the coastal waters of the other geographic areas of the south-western stock combined, i.e. Metro North, Metro South and South-west, as their length data were similar (Fig. S1). Data were limited to fish collected in the main spawning months (October, November, December) in this region (Wakefield et al. 2015). Comparisons between embayments and coastal waters were made with 2 subsets of length data: (1) for females assumed to be sexually mature based on whether their TL was ≥585 mm, i.e. the estimated TL at which 50% of females reach maturity (TL_{50}) in the south-western stock and (2) for all female Australasian snapper that were in spawning condition (i.e. ovaries contained hydrated oocytes; Wakefield et al. 2015).

For each subset, relative reproductive output was compared between embayments and coastal waters in 2 ways. Firstly, individual batch fecundity (F) was calculated from FL using the equation for Australasian snapper $F = 0.00009436 \times FL^{3.359}$, where FL = (TL × 0.897) − 23.058 (Jackson et al. 2012) to produce box and whisker plots of batch fecundity distributions. Secondly, the batch fecundity of each 50 mm length class (using its midpoint) was calculated and then weighted by the female percentage frequency in that class to account for differences in sample sizes. Weighted batch fecundities for each length class were summed to estimate and compare the relative reproductive output of fish in embayments and coastal waters.

3. RESULTS

3.1. SNP genotyping and genetic diversity

After completing all filter steps and removing 8 samples due to having >20% missing data, our final data set contained 533 Australasian snapper genotyped at 10 438 SNPs (Table S1). These samples have an average of 0.69% missing data (range 0–19.03%) and an average coverage depth of 109.86 (range 4.16–368.45).

Genetic diversity was very similar across sampling areas (Table 1). Across locations, observed heterozygosity ranged from 0.2559 at South West Bank to 0.2915 at Seabird, while expected heterozygosity ranged from 0.1981 at Binningup to 0.2678 at Cockburn Sound. Values of population inbreeding coefficient (F_{IS}) were negligible, being close to 0 for all locations and ranging from −0.0531 at Seabird to 0.0349 at Bouvard Reef, with higher values observed at locations with smaller sample sizes.

Table 1. Genomic diversity of Australasian snapper in south-western Australia. The embayment samples come from Cockburn Sound and Warnbro Sound (referred to collectively as Metro). nInd: number of individuals; polyLoc: number of polymorphic loci; H_o: observed heterozygosity; H_e: expected heterozygosity; F_{IS}: population coefficient of inbreeding. All indices calculated by locality and by area

Locality	Area	Adults	Juveniles	nInd	polyLoc	H_o	H_e	F_{IS}
Seabird	Metro North	6	0	6	8241	0.2915	0.2535	−0.0531
Guilderton	Metro North	22	0	22	9905	0.2607	0.2621	0.0281
Two Rocks	Metro North	41	40	81	10387	0.2613	0.2667	0.0261
Yanchep	Metro North	5	0	5	7543	0.2720	0.2399	−0.0182
Hillarys	Metro North	5	0	5	7699	0.2719	0.2429	−0.0072
	Metro North	**79**	**40**	**119**	**10420**	**0.2636**	**0.2676**	**0.0189**
Cockburn Sound	Metro	80	87	167	10423	0.2620	0.2678	0.0244
Warnbro Sound	Metro	18	31	49	10309	0.2625	0.2661	0.0235
	Metro	**98**	**118**	**216**	**10430**	**0.2621**	**0.2681**	**0.0245**
Dawesville	Metro South	6	0	6	8088	0.2727	0.2472	−0.0110
Bouvard Reef	Metro South	8	0	8	8590	0.2576	0.2501	0.0349
Preston Beach	Metro South	6	0	6	8062	0.2638	0.2449	0.0128
Binningup	Metro South	2	0	2	5030	0.2613	0.1981	0.0111
	Metro South	**22**	**0**	**22**	**9930**	**0.2637**	**0.2619**	**0.0159**
Peppermint Beach	South-west	13	0	13	9427	0.2600	0.2576	0.0295
Port Geographe	South-west	51	38	89	10394	0.2593	0.2650	0.0271
Busselton	South-west	12	0	12	9250	0.2574	0.2542	0.0302
Geographe Bay	South-west	20	0	20	9853	0.2601	0.2604	0.0260
Dunsborough	South-west	7	0	7	8343	0.2591	0.2471	0.0270
South West Bank	South-west	6	0	6	7960	0.2559	0.2427	0.0348
Augusta	South-west	9	0	9	8970	0.2744	0.2572	−0.0072
	South-west	**118**	**38**	**156**	**10426**	**0.2601**	**0.2662**	**0.0260**
Windy Harbour	Western South Coast	20	0	20	9773	0.2576	0.2580	0.0268

3.2. Genetic differentiation and population structure

Pairwise F_{ST} values between locations were nil or low, ranging from 0 to 0.009 (Fig. S2). Similarly, nil or low values were found when samples were grouped by geographic area, separated by life stage (adults vs. juveniles), and by year of collection (2021/2022 and 2022/2023) (Fig. S3). However, when arranged by life stage and year of collection, a few pairs of samples from different geographic areas showed significant F_{ST} (e.g. Metro North adults from the first season and Metro adults from the second season). Since there was no evidence for significant differences between locations in the same area, all further analyses used samples grouped by their broader geographic areas (i.e. Metro North, Metro, Metro South, South-west and Western South Coast).

Consistent with the findings of nil or low F_{ST} values and the assumption of a single genetic stock, the PCA showed a single cluster with marked overlap between samples from different areas (Fig. 2A). Likewise, there was no evident clustering in the PCA when separating samples by life stage or by year of collection (Fig. S4). As expected, admixture cross-validation indicated that $K = 1$ is the most likely number of population clusters in our study region (CV error = 0.485; Fig. S5).

3.3. Fine-scale connectivity and local recruitment

Concordant with the overall pattern of low genetic differentiation, high rates of migration (>77%) were detected between most pairs of geographic areas, and there was no evidence of asymmetric migration, consistent with the hypothesis of high fine-scale population connectivity (Fig. 3; Table S2). However, we found lower rates of migration to and from the Western South Coast area. Moderate migration was also evident between Metro South and other areas, but these estimates are likely influenced by the small sample size for Metro South locations (n ranged from 2 to 8 individuals) and for the total Metro South area (n = 22).

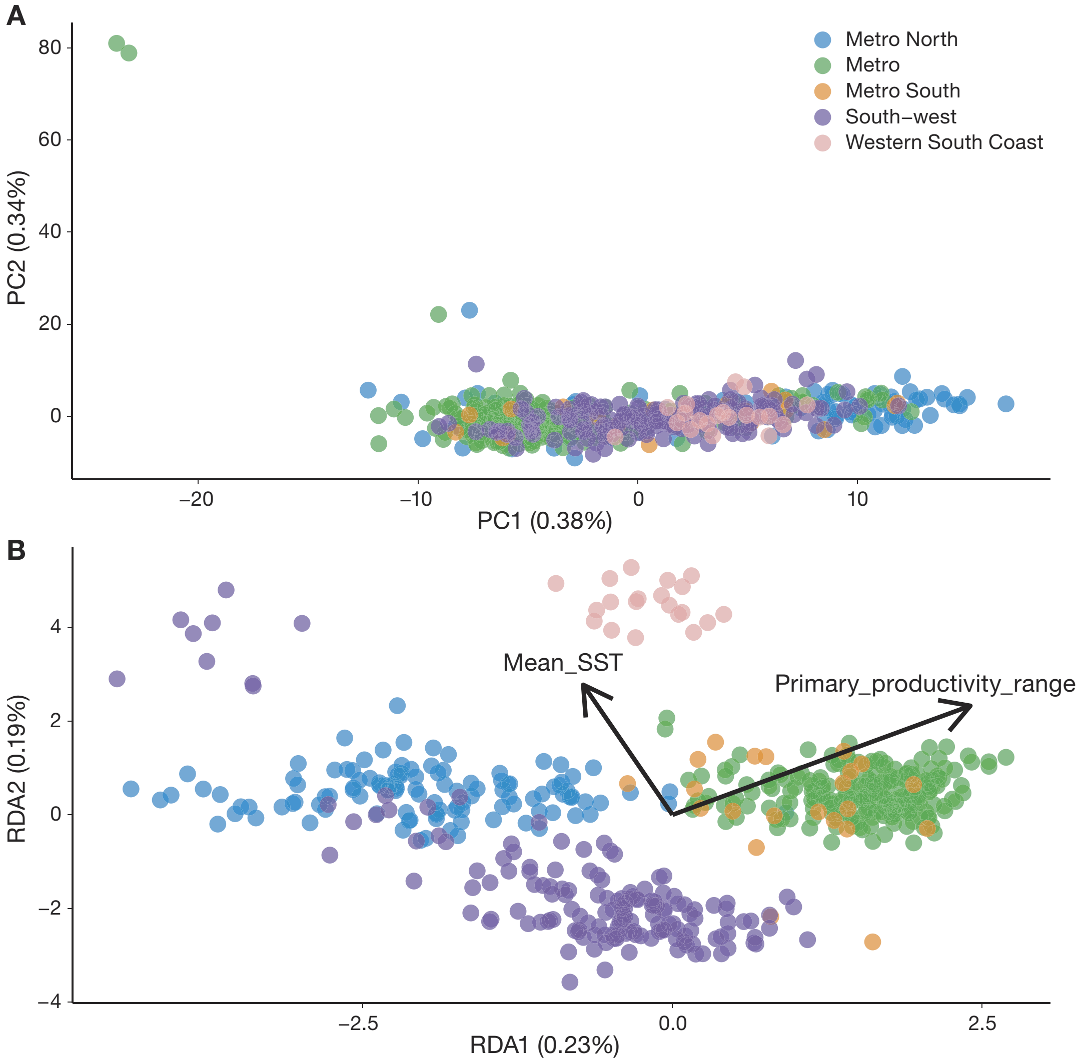

Fig. 2. (A) PCA based on 10 438 single nucleotide polymorphisms (SNPs) and 533 snapper collected across 5 geographic areas of the south-western Australia stock. Metro North (Hillarys to Seabird), Metro (Cockburn and Warnbro Sound), Metro South (Dawesville to Binningup), South-west (Geographe Bay to Augusta), Western South Coast (Windy Harbour). (B) Ordination plot summarising the first 2 axes of partial redundancy analysis (pRDA) with genetic variation based on 10 438 SNPs explained by 2 environmental variables controlling for the oceanic distance between pairs of sampling localities. Mean_SST: mean sea surface temperature

When considering all locations, there was no evidence of isolation by distance (Mantel test $R^2 = 0.001$, $p = 0.67$). However, the same test was significant when only the locations with larger samples ($n > 8$) were considered ($R^2 = 0.29$, $p = 0.03$). The latter is consistent with results of the spatial autocorrelation analysis, which indicated significantly positive autocorrelation for 3 areas (Metro North, $r = 4.8 \times 10^{-4}$; Metro, $r = 3.9 \times 10^{-4}$; South-west, $r = 2.7 \times 10^{-4}$; $p < 0.05$), especially for Metro and Metro North (Fig. 4). These results are indicative of substantial local recruitment within each area.

3.4. Seascape genomics

The overall RDA model was significant (df = 2; $p = 0.001$) after controlling for oceanic distance. Of the genomic variance in the data, 0.42% was explained by the retained environmental variables, while 0.21% was explained by the oceanic distance (Fig. 2B; Table S3). Both the primary productivity range and the mean sea surface temperature were statistically significant (df = 1; $p = 0.001$), with the former explaining slightly more variance. The first 2 RDA axes explained 0.41% of the genetic variation and split

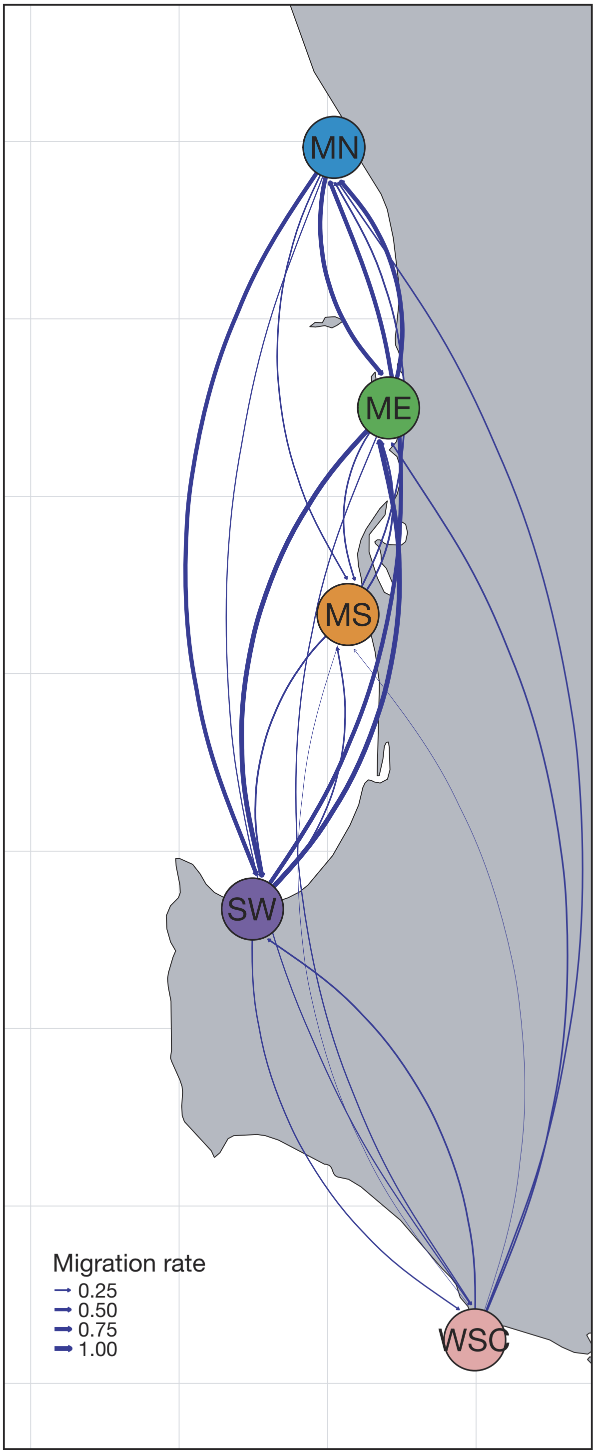

Fig. 3. Relative migration rates per generation (Nm) among areas, calculated based on 10 438 SNPs and 533 snapper collected across 5 geographic areas of the south-western Australia stock. MN: Metro North (Hillarys to Seabird); ME: Metro (Cockburn and Warnbro Sound); MS: Metro South (Dawesville to Binningup); SW: South-west (Geographe Bay to Augusta); WSC: Western South Coast (Windy Harbour). Blue arrows represent direction of migration, and their thickness represents the relative migration rate

samples by areas, except Metro South and Metro (Fig. 2B). Variation at 223 SNPs showed significant associations with environmental variables, identifying them as candidate adaptive DNA markers, or candidate loci (Fig. S6A). These loci were evenly distributed along all 24 chromosomes of the genome (Fig. S6B), with the majority located within intragenic regions (Fig. S7A), but a few have at least moderate predicted impact over gene function (Fig. S7B). Most candidate SNPs (156 out of 223) were located in non-coding transcripts and were classified as having modifier effects, which may influence gene regulation and therefore, adaptation.

3.5. Reproductive capacity

During the main Australasian snapper spawning period (October to December), females ≥TL_{50} at maturity (585 mm) in Cockburn/Warnbro Sounds were mostly much larger than fish sampled from the combined coastal waters (Metro north, Metro South and South-west), with almost all fish in the embayments being >700 mm (Fig. 5A). Large females were also collected in coastal waters, but ~50% were <700 mm. A similar pattern was evident from length distributions of female Australasian snapper in spawning condition from each location, except that spawning females collected in coastal waters were as small as 404 mm (Fig. 5B).

The median batch fecundities of female Australasian snapper greater than the TL_{50} at maturity and females that were spawning were greater in Cockburn/Warnbro Sounds (~427 200 and 405 300 oocytes, respectively) than in coastal waters (~208 100 and 229 900 oocytes) (Fig. 5B). The relative contribution of Cockburn/Warnbro Sounds female Australasian snapper, in terms of batch fecundity and based on the percentage frequency of individuals in each length class, was ~1.8 and 1.6 times that of females in coastal waters, for females above the TL_{50} and females that were in spawning condition, respectively.

4. DISCUSSION

Embayments, sounds, estuaries and other semi-enclosed geomorphological features are important in the ecology and life history of coastal marine biodiversity, providing essential habitat and acting as nurseries for a variety of fishes, including species of high recreational and commercial value (Wakefield et al. 2013). This study evaluated population genomics and repro-

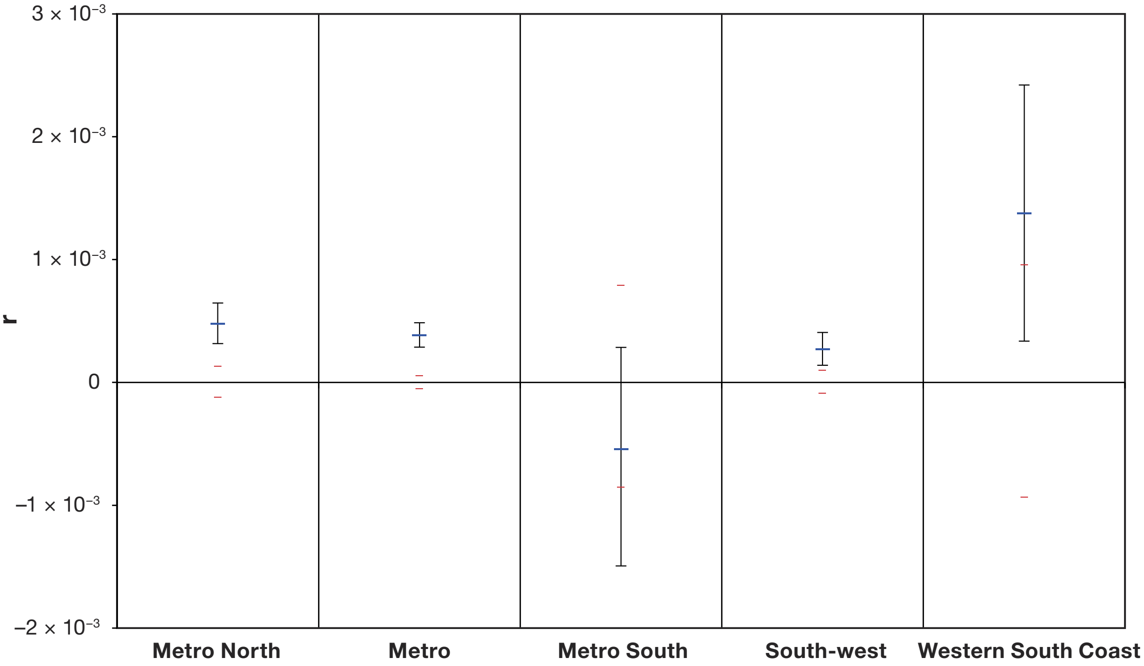

Fig. 4. Spatial autocorrelation analysis using 10 438 SNPs for 533 snapper collected across 5 geographic areas of the south-western Australia stock. Metro North (Hillarys to Seabird), Metro (Cockburn and Warnbro Sounds), Metro South (Dawesville to Binningup), South-west (Geographe Bay to Augusta), Western South Coast (Windy Harbour). Blue bars are the autocorrelation estimates. Red dots indicate the upper and lower bounds of the 95% confidence interval for the null hypothesis of randomly distributed genotypes, as determined by 1000 permutations. Bars represent the 95% confidence intervals of the error determined by 1000 bootstrapping iterations

ductive capacity of a heavily exploited teleost, the Australasian snapper. Our aim was to assess the relative contribution of embayment spawning aggregations to fishery areas in adjacent coastal waters across the species' south-western Australian stock. By implementing an original sampling design that included adults and juveniles over consecutive spawning seasons, we also tested if population recruitment along the open coast and embayments occurs primarily from local spawning events within each area. The results show that all 5 sampled areas are highly connected and confirm a single genetic stock. However, there was evidence of isolation by distance and local recruitment in some of these areas (including in embayments), consistent with a previous study done on a broader spatial scale (Bertram et al. 2022). We also found that differences in sea surface temperature and primary productivity between the embayments and open coast are key environmental variables that may influence adaptive genetic diversity of Australasian snapper. These represent potential environmental proxies promoting local adaptation to different habitats in the study region. While the genomic results establish that local recruits from spawning aggregations in Cockburn Sound and Warnbro Sound contribute to the broader South-west stock, the relative contribution to overall reproductive output is likely higher for individuals in the embayments than along the adjacent open coast. Our findings generate knowledge about fine-scale patterns of connectivity and recruitment for the south-western Australian stock of Australasian snapper and clarify the relative importance of the reproductive output from embayment spawning aggregations to the broader population.

4.1. One stock with high connectivity

The finding of a single genetic population on the south-west coast of Australia (the south-western Australian stock) is consistent with 2 recent studies carried out at a broader geographic scale and with coarser sampling resolution than the one described here. Using microsatellite DNA markers, Gardner et al. (2022) showed genetic homogeneity of Australasian snapper collected along 1350 km of the west Australian coast, from the sub-tropics (~26° S) to the temperate south coast (~35° S). Using a SNP dataset from samples covering most of the range of Australasian snapper in Western Australia, Bertram et al.

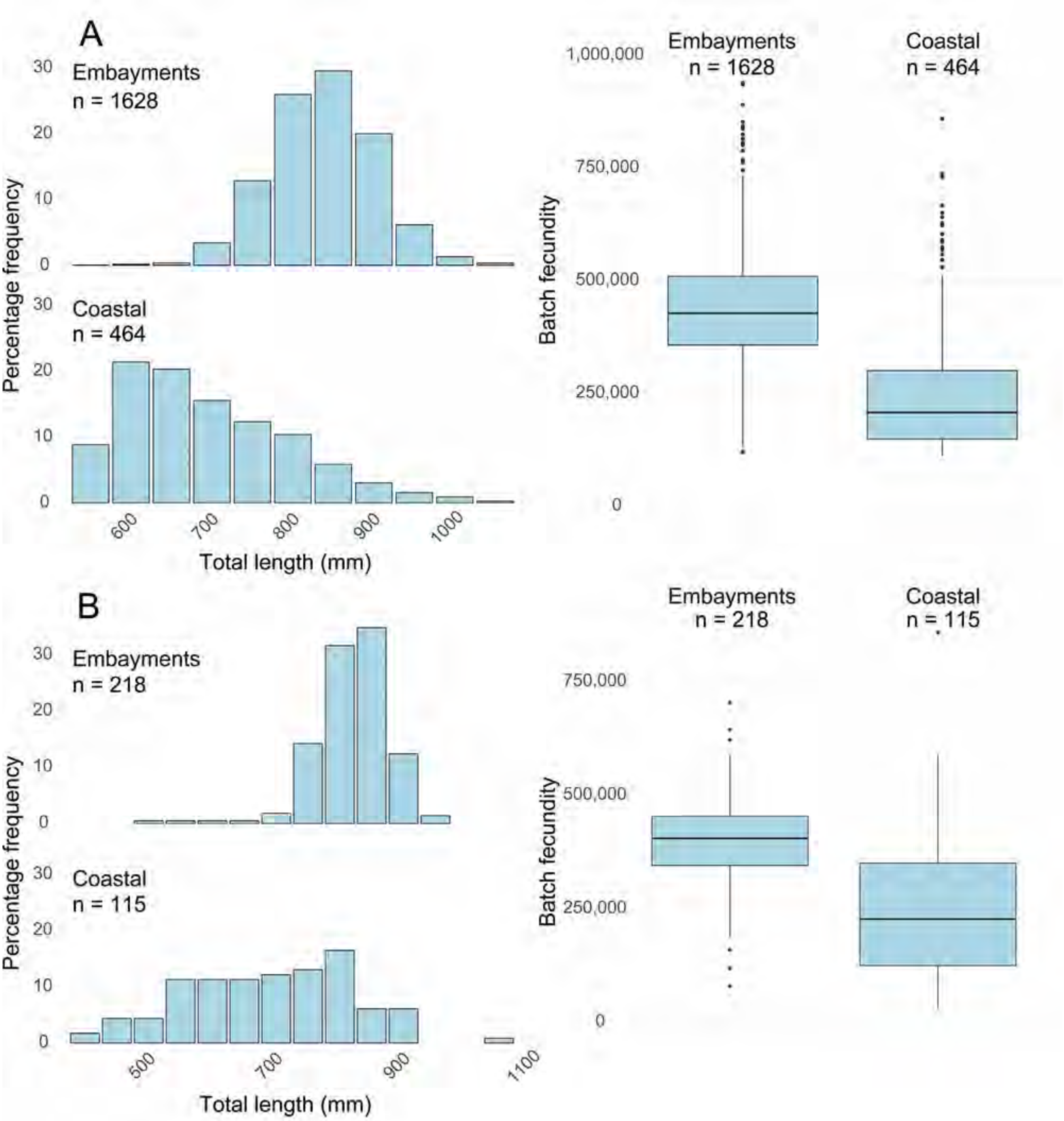

Fig. 5. Length-frequency distributions of female snapper from embayments (Cockburn/Warnbro Sounds) and coastal waters (Metro North, Metro South, South-west) of the south-western Australia stock during the main spawning period (left column) and estimated batch fecundities (right column). (A) Data for females ≥585 mm (the estimated length at which 50% of females reach sexual maturity); (B) data for females that were spawning. Boxes represent the 25th–75th percentiles, the horizontal line inside the box represents the median, the whiskers represent the minimum and maximum values within 1.5× the interquartile range, and the points beyond the whiskers represent outliers

(2022) demonstrated that individuals from Cockburn Sound to Albany (~35° S, 117.9° E) on the south coast of Australia were genetically similar, but distinguishable from those along the mid-west coast (northwards from Lancelin at ~31° S). Here, using a larger, fine-scale and temporally replicated sample that includes both juveniles and adults collected from ~470 km of the south-western coast of Australia, we established relative genetic homogeneity of Australasian snapper from the northern metropolitan area, Cockburn Sound and Warnbro Sound, the southern metropolitan area and the south-west area. Our results also validate the proposal that the genetic break between the mid-west and the south-western Australian stock is further north than Cockburn Sound (Bertram et al. 2022). Although our sampling scheme is not fully balanced, our sample sizes both in number of markers and individuals are much larger than the minimum required to obtain sufficient statistical power to estimate genetic differentiation (Willing et al. 2012). We therefore consider our results to be robust, especially at the area level, which relates to the main spatial scale explored in this study.

Since Australasian snapper has a pelagic larval stage that can last up to 33 d (Sim-Smith et al. 2012), the genetic homogeneity reported here could perhaps be attributed to the advection dispersal of larvae by oceanographic currents in the region. Using particle tracking models, Coleman et al. (2013) reported high advection connectivity associated with the Leeuwin Current along the Western Australia coast. This connectivity is asymmetric, with the current mostly transporting particles polewards along the west coast and eastward along the south coast of Western Australia. Thus, it contrasts to the pattern of symmetric connectivity that we detected among all management areas (Fig. 4). However, the Leeuwin Current is weaker through spring—summer (Feng et al. 2010) when the spawning peak of Australasian snapper occurs (Wakefield et al. 2015), and when northward wind-driven shelf currents dominate the region (Feng et al. 2010). Hence, the combination of shelf currents with some influence of the Leeuwin Current could promote symmetric advection connectivity of Australasian snapper populations. In addition, Australasian snapper juveniles and adults are not sedentary, and some travel 100s of km and sporadically more than 1000 km (Wakefield et al. 2011, Crisafulli et al. 2019, Stewart et al. 2020). Such movements can also promote symmetric gene flow and help to maintain genetic homogeneity along the south-western coast of Australia. Our results demonstrate that spawning aggregations in Cockburn Sound and Warnbro Sound, and the coastal spawning all contribute recruits to the broader, genetically connected, south-western stock. They also reflect the presence of spawning along the open coastline and numerous nursery environments between the northern metropolitan and south-west coasts, such as Geographe Bay, consistent with biological data collections in this and previous studies (see e.g. Fairclough et al. 2013). Our results may also indicate the movement of individuals of this species at both sub-adult and adult stages and possible changes in where individuals spawn during their lifecycle that lead to a more homogeneous genomic signature across the lower west coast (see Wakefield et al. 2011, Crisafulli et al. 2019).

4.2. High connectivity but spatial autocorrelation supporting local recruitment

Despite the high genetic connectivity and low genetic differentiation, our results also indicate that Australasian snappers are recruiting locally into their subpopulations, including within embayments such as Cockburn Sound. This is consistent with the findings of Bertram et al. (2022), as well as with patterns of Australasian snapper recruitment from other coastal regions and stocks in Australia (Bertram et al. 2023, Brauer et al. 2026). The signal of local recruitment might at first appear contradictory to our inference of high connectivity and a single genetic population. However, this conundrum can be explained by several processes. While the combination of the Leeuwin Current with the inshore shelf currents can promote symmetrical dispersal of larvae, the presence of eddies and the geographic characteristics of the region can promote local retention of a higher proportion of eggs and larvae (Feng et al. 2010, Wakefield 2010). Indeed, our results reflect those of previous biological studies that demonstrated that within Cockburn Sound, eggs and larvae produced by spawning aggregations are entrained in wind-driven counterclockwise currents driving settlement within the embayment and the occurrence of juveniles in this nursery environment for around the first 18 mo of life (Wakefield 2010, Wakefield et al. 2011).

Moreover, the dichotomy of high connectivity with significant spatial autocorrelation can be explained by the presence of both migratory and resident individuals in the population. This dimorphism is known as partial migration, which is ubiquitous among many taxonomic groups (Chapman et al. 2012), and has been reported in Australasian snapper (Parsons et al. 2014, Stewart et al. 2020). While the spatial autocorrelation is consistent with the fact that some Australasian snapper adults become residents and/or philopatric to the area where they recruit (Fairclough et al. 2013, Crisafulli et al. 2019), the high connectivity can be explained by the presence of a few nomadic individuals who travel 100s of km (Crisafulli et al. 2019) and potentially reproduce in different areas. This variation in resident and potentially nomadic behaviors within the population could provide resilience to spatial or temporal fluctuations of conditions influencing survival (Apgar et al. 2021). Therefore, management strategies that protect both life history traits should be considered for Australasian snapper when responding to environmental change and loss of spawning or nursery habitats.

4.3. Environmentally associated genetic differentiation

The oceanography of the western coast of Australia is dominated by the Leeuwin Current, which moves warm waters from north to south, contributing to the latitudinal gradient of temperature and to complex patterns of primary productivity in the region (Waite et al. 2007, Huang & Feng 2015). Our results indicate that variation in these oceanographic variables has a relatively small, albeit significant, impact on adaptive diversity of Australasian snapper throughout the south-western stock. The second axis of the RDA was manly driven by temperature, clustering the metro areas (Metro North, Metro and Metro South) and differentiating them from others (South-west and Western South Coast). The pattern is consistent with the significant difference in temperature among the management areas in the West Coast Bioregion (Fairclough et al. 2013). Temperature is often invoked as an important driver of local adaptation in marine organisms (Sandoval-Castillo et al. 2018, Teske et al. 2019, Barceló et al. 2022, Antoniou et al. 2023) and is especially critical for ectotherms during early life stages (Schulte 2015, Moyano et al. 2017). In Australasian snapper, temperature affects larval physiology and is correlated with growth and survival (Fielder et al. 2005, Murphy et al. 2013, McMahon et al. 2020), with strong evidence for a genetic basis to this relationship (Sandoval-Castillo et al. 2022). Australasian snapper larvae from different geographic areas could have different optimal temperatures promoting low genetic differentiation, as observed with other fishes. For example, the western and eastern North Pacific sardine subpopulations have different thermal preferences and are adapted to different water temperatures during larval stages (Sakamoto et al. 2022). Moreover, Australasian snapper spawning is strongly associated with temperature and occurs in a narrow range (19–21°C) and at different times in different regions (Wakefield et al. 2015). Thus, differences in spawning times could produce some level of allochronic isolation between management areas (Hendry & Day 2005).

Primary productivity is not known to directly affect Australasian snapper physiology; however, it significantly influences food availability. The recruitment of Australasian snapper is variable and highly dependent on the quality and availability of food for the larvae (Murphy et al. 2012, 2013). Variations in primary productivity can translate to different plankton community compositions among areas. Thus, larvae from different areas can be adapted to different prey items. Although there is no evidence for population-specific prey in Australasian snapper larvae, there is strong evidence that plankton composition influences larval survival and juvenile recruitment (Black et al. 2016). Different patterns of temperature and primary productivity might impose selective pressures that could restrict dispersal among areas and promote local genetic differentiation. These selective pressures can potentially reinforce migratory and reproductive behaviours that are genetically determined, as demonstrated in salmonids (Waples & Lindley 2018). If the aggregative spawning behaviour and philopatry of Australasian snapper to embayments also have a genetic basis, then replenishing local populations from adjacent areas may be difficult, despite high overall genetic connectivity.

4.4. Relative contribution of embayment spawning aggregations to the other localities

The homogeneous genetic signature, driven by high symmetric connectivity and migration rates, demonstrates the ongoing contribution that Australasian snapper in embayments (Cockburn Sound and Warnbro Sound) make to subpopulations along the lower west coast and vice versa. Given that there is a strong positive relationship between length and batch fecundity in this species (Saunders et al. 2012), and there is a greater relative proportion of large females in the embayments, those individuals could contribute disproportionately to total egg production in the whole stock. This contribution will be enhanced if fish in the embayment spawn more frequently and/or for longer periods than in coastal waters, consistent with large individuals of other species, such as the West Australian dhufish (Evans-Powell et al. 2024). Based on the overall length distribution, the relative contribution of the 2 embayments in terms of total batch fecundity was 1.6–1.8 times that of spawning fish in open coastal waters. Moreover, the higher density observed in the larger embayment aggregations would also increase fertilisation rates (Uguen et al. 2025), while the semiprotected oceanography of these habitats promotes the retention of eggs and larvae (Wakefield 2010), and provides abundant food and shelter for early life stages of Australasian snapper (Whitfield 2020). Collectively, these factors amplify the potential relative contribution of embayments to the regional stock. The higher contribution of embayment spawners to a stock is well documented in several commercially important fish species (Boucek et al. 2017), including Australasian snapper from other regions (Wakefield 2010). While the absolute contribution of embayment spawners to recruitment in the broader stock cannot be determined without comparing the spawning frequency, spawning duration and spawning biomass across both environments, which will require further investigation, it is well established that aggregating to spawn can confer substantial benefits. Although migration and aggregation are energetically expensive and expose adults to predation, the reproductive advantages offered by embayments, such as greater fertilisation success and improved larval and juvenile survival, might outweigh these costs (Molloy et al. 2012, Whitfield 2020).

If Australasian snapper aggregations in the embayments and/or their progeny were impacted by existing or future marine infrastructure development or operation, e.g. disruption of aggregative spawning or impacts on nursery habitats, this could directly affect the contribution that these Australasian snappers make to the broader south-western Australian stock. Although evidence of equivalent connectivity across the south-western stock suggests that embayments could, in principle, be replenished via natural dispersal and migration, the rate of replenishment would depend on the rate of dispersal and migration dynamics along the coast. High genetic connectivity does not necessarily translate into high demographic connectivity, which is determined by the relative contribution of net migration into the total recruitment (Waples & Gaggiotti 2006, Kendrick et al. 2017). Possible replenishment of the aggregation in the embayments assumes that any impacts are not ongoing or long-lasting and that suitable habitat remains available for spawning, larval settlement and juvenile nursery functions. A portion of recruits spawned in embayments such as Cockburn Sound would subsequently be harvested (after reaching the minimum legal length for retention) by recreational and commercial fishers along the lower west coast and therefore any short- or longer-term negative effects of development on their abundance may have temporary or longer-lasting effects on catches in the whole region.

4.5. Conclusions

This study sheds light on the interplay between high connectivity and local recruitment in Australasian snapper along Australia's south-western coast. The results support the idea that partial migration may serve as a mechanism enabling adaptation to local conditions by resident individuals while maintaining high connectivity through migrants, which in turn could enhance resilience to spatial and temporal environmental fluctuations. These findings suggest that effective management strategies should account for this dual behaviour. By integrating population genomics and reproductive capacity analyses, we also provide evidence of the importance of embayments to recruitment within the south-western stock of Australasian snapper. Genetic homogeneity across this stock is facilitated by movement between geographic areas that occurs at egg/larval, sub-adult and adult life cycle stages. Despite this, the relative reproductive contribution to the stock by large individuals that aggregate to spawn in embayments may be greater than that of the typically smaller individuals that spawn in coastal waters. Evaluation of characteristics such as fecundity, spawning frequency and spawning period of individuals would help to understand that contribution further. Aggregating to spawn is a trait of many marine fishes that would confer benefits such as greater fertilisation success and reduced egg predation (Sadovy de Mitcheson 2016). Aggregating in specific environments such as embayments would also enhance local recruitment of early life history stages, provide food and protection from predation to juveniles and enable a disproportionate contribution to stocks. This study highlights the varying importance of coastal environments to the different lifecycle stages of fishes that contribute to recreational and commercial fisheries and therefore the need to maintain the quality of such habitats. Amid growing climatic change and fishing pressures, effective management policies must consider mechanisms that preserve genetic diversity in fisheries stocks, such as partial migration and environmentally associated population differentiation, as well as source populations that could contribute disproportionately to regional stock recruitment. Failing to do so may compromise the long-term sustainability of fisheries resources.

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