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Continent-wide stock structure and connectivity of silver trevally (*Pseudocaranx georgianus*) based on population genomics and otolith shape and chemistry

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ABSTRACT

The high dispersal ability, strong population connectivity, and broad geographic ranges of many exploited marine species present significant challenges for identification, assessment and management of stocks that straddle jurisdictions. Multi-disciplinary approaches are increasingly used to provide a more comprehensive understanding of biological stock structure. Here, we used analyses of population genomics and otolith shape and chemistry to clarify the population structure and connectivity of the socially and economically important silver trevally (*Pseudocaranx georgianus*). Muscle and fin-clipped tissues (n = 835) and otoliths (n = 940) were sampled from 32 locations across five jurisdictions around Australia. The genomic analysis also included three locations in Aotearoa New Zealand to provide broader spatial context for interpreting biological stock structure. Our results identified three populations, or biological stocks, encompassing extensive distances along coastlines and across jurisdictions. Based on the boundaries between populations, we suggest two stocks to be defined for Australia – a 'western' stock spanning Western Australia, South Australia and western Victoria, and an 'eastern' stock spanning eastern Victoria, New South Wales and northern Tasmania, and one biological stock for New Zealand. The boundary between Australian stocks appears to have originated from the historical barrier of the Bassian Isthmus, with contemporary oceanographic processes likely maintaining the separation of the two broad populations and promoting high connectivity within each population. Our findings suggest that current management units may not adequately represent the true biological stock structure of the species. Cross-jurisdictional collaboration is recommended to clarify rates of recruitment within and among jurisdictions and to revise the current assessment framework to ensure effective fisheries management can be achieved for silver trevally in Australia.

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1. Introduction

Effective fishery management based on scientific stock assessments is crucial for maintaining exploitation levels and fish biomass at sustainable levels (Cooke and Cowx, 2006; Ye et al., 2013). Failure to reduce unsustainable levels of fishing mortality exacerbates biomass decline and inhibits stock recovery (Merino et al., 2012). Beyond ecological consequences, declining fishery production also threatens economic benefits and food security (Cheung et al., 2013). Stock assessment models should connect data from fisheries-dependent catch and effort and biological parameters with management units relevant to population dynamics (Cadrin et al., 2014; Berger et al., 2021). Missing biological variables or incorrect assumptions about spatial population dynamics can amplify uncertainty in model outputs, undermining both confidence in stock assessment accuracy and the appropriateness of management recommendations (Chen, 2003; Maunder and Piner, 2015; Ducharme-Barth et al., 2022).

Accurate stock identification and implementation of management strategies at biologically relevant spatial scales are essential for sustainable fisheries management. Misalignments between management units and biological stocks can undermine recovery efforts, increase overfishing risk, and reduce opportunities for improved economic or biological yield (Reiss et al., 2009; Kerr et al., 2017). To refine stock delineation, fisheries scientists have adopted advanced analytical tools, including the use of natural individual markers (Pita et al., 2016). Otoliths, for example, may function as a natural unique identifier of environmentally influenced phenotypic traits, growing in time-resolved increments throughout a fish's life while recording variations in the chemistry of the surrounding water (Tuset et al., 2016; Reis-Santos et al., 2023). Otolith shape and chemical composition may reflect patterns of change in ontogenetic habitat use and environmental gradients, making them valuable indicators of intraspecific variation and potential population or stock separation over ecological timescales (Stransky, 2014; Izzo et al., 2017; Reis-Santos et al., 2023). Genetic markers are also highly informative natural tags; they provide insights into individual movement and population delineation over both ecological and evolutionary timescales, enabling detection of demographic and evolutionary processes shaping connectivity and structure (Bernatchez et al., 2017; Grummer et al., 2019). These markers are particularly useful for revealing regional-scale connectivity patterns that may be driven by ocean currents, dispersal behaviours, and environmental gradients (Harvey et al., 2013; Sandoval-Castillo et al., 2018; Bertram et al., 2022).

Studies of stock structure often rely on a single method to assess population differentiation, boundaries, and range, which can limit resolution and discriminatory power while introducing biases specific to the individual method (Cadrin et al., 2014; Tanner et al., 2016). Integrating multiple approaches increases the likelihood of correctly identifying biological stocks and improves understanding of stock structure (Welch et al., 2015; Izzo et al., 2017; Sarakinis et al., 2024). Abaunza et al. (2008) reviewed various techniques for identifying horse mackerel (*Trachurus trachurus*) stocks, highlighting the benefits of methodological integration, particularly in reducing type I errors in stock structure analysis (i.e., incorrectly reject panmixia). Recent research emphasizes the value of combining otolith and genetic-based approaches, as these methods capture complementary information across different temporal and spatial scales (Brophy et al., 2020; Green et al., 2015; Harrisson et al., 2025; Reis-Santos et al., 2018). These combined methods provide complementary insights that ultimately improve stock delineation accuracy and support more effective, evidence-based fisheries management. For example, an integrative approach redefined the stock structure of beaked redfish (*Sebastes mentella*), leading to management boundaries that better reflect biological realities (Cadrin et al., 2010).

Silver trevally (*Pseudocaranx georgianus* (Cuvier, 1833), family Carangidae) is a medium-to-large-bodied fish distributed along the coastlines of southern Australia and New Zealand (NZ; Smith-Vaniz and Jelks, 2006). In Australia, recreational and commercial fisheries for silver trevally in coastal waters are managed separately by each state jurisdiction encompassed by the species' distribution (Fig. 1), whereas commercial catches beyond three nautical miles off the coast of New South Wales mostly fall under Commonwealth Australian Government authority. Multiple management methods are used in Australian jurisdictions and NZ, including quota, effort, bag and size limits. However, management regulations have largely been established without detailed information on stock structure, population status, or demographic parameters (Emery et al., 2023; Butler et al., 2024). Research supporting breeding programs in NZ has explored growth responses to environmental conditions and physiological sensitivity to climate variability (Catanach et al., 2021; Valenza-Troubat et al., 2022a, 2022b, 2022c). Nevertheless, demographic patterns remain poorly understood across the species' full range, particularly given potential differences in connectivity between coastal and oceanic populations across the Tasman Sea (Chiswell et al., 2003; Waters et al., 2005; Mullaney et al., 2014; Thomas et al., 2021). As a species of substantial social and economic value, there is an increasing need to delineate biological stock structure, improve its stock assessment and implement appropriate management practices.

Several life-history traits of silver trevally in eastern Australia suggest a high dispersal potential through the egg and larval life history periods (Rowling and Raines, 2000; Syahailatua et al., 2011b). In that region, silver trevally reach sexual maturity at a small size (approximately 19 cm fork length) and exhibit moderate fecundity (Rowling and Raines, 2000). The species spawns from September to March across most of its range (Rowling and Raines, 2000) and from July to December in Western Australia (Farmer et al., 2005), releasing multiple batches of pelagic eggs throughout the spawning season (Neira and Miskiewicz, 1998; Annala et al., 1999; Farmer et al., 2005). The southerly flowing East Australian Current, which dominates during the spawning period, likely facilitates long-distance dispersal of early life stages, juveniles and adults, potentially contributing to genetic homogeneity across the east coast (Syahailatua et al., 2011a, 2011b). However, on the west coast, silver trevally spawn as waters begin to warm and southerly winds strengthen in spring, potentially causing more localised recruitment by retaining eggs/larvae in coastal shelf waters (Condie et al., 2011). A tag-recapture study on Australia's southeast coast by Fowler et al. (2018) indicated increased movement in spring prior to the summer spawning season. However, adult movements along the east coast generally occur over small spatial scales (<10 km between tagging and recapture locations), with high recapture rates at, or near, the original release sites (Fowler et al., 2018). On the west coast, telemetry studies demonstrated that adults also remain in localised areas (Fairclough et al., 2011). The consequences of these localised movements to the spatial stock structure of the species are largely unknown.

Current assessment and management strategies for silver trevally could be compromised by the lack of information on biological stock structure. Recent model-based stock assessments indicate that the Australian east coast stock has been depleted since the early 2000s and has only recently shown signs of recovery, while elsewhere, stocks are either unassessed or considered sustainable (Burch et al., 2023; Fowler et al., 2023). To address the knowledge gaps, our study examines the spatial population structure and connectivity of silver trevally in Australia and NZ. We employ a continental-scale sampling design combined with an integrative approach that incorporates analyses of otolith shape and chemistry and population genomics. Our primary aim is to clarify the number and potential boundaries of silver trevally stocks across the species distribution in Australia. The genomic analysis further includes samples from NZ to provide context for interpreting genetic stock structure within Australia. This is particularly relevant given the potential for admixture between eastern Australia and NZ, driven by the oceanographic circulation of the Tasman Front (e.g., Thomas et al., 2021). By elucidating spatial stock structure in Australia, we provide recommendations on stock delineation and define appropriate spatial scales to strengthen existing fisheries management frameworks for this valuable but understudied fish species.

2. Material and Methods

2.1. Sampling

Muscle and fin-clipped tissues and sagittal otoliths of silver trevally were collected from 32 locations across Australia (Fig. 1, Table S1). Locations were selected based on the distribution of the focal points for fisheries where the species is harvested, generally defined where major fishing ports are located. Samples were obtained from commercial or recreational fisheries managed by each jurisdiction, including New South Wales (NSW), Victoria (VIC), Tasmania (TAS), South Australia (SA), Western Australia (WA) and Commonwealth waters (COMM). Sagittal otoliths were used as they are the primary otolith for ageing, shape, and chemical analyses in fisheries science, including stock assessment and ageing of trevally (Walsh et al., 2014). Otolith samples were collected from 940 individuals across 23 of the 32 sampling locations to assess patterns of variation in shape and chemical composition; a subset of these was selected for both shape and chemical analysis (aiming for 30 per location). Analysed fish were sampled between February and March 2022. These time periods were chosen to optimise the likelihood of acquiring samples at a similar time across the entire distribution. For genomic analyses, muscle and fin-clipped samples were obtained in 2022, mainly between January and March, from 835 silver trevally across 26 locations in Australia. Additional fin-clipped samples were obtained from NZ in August 2018 and February 2019 on the east (n = 24), and west (n = 27) coasts of the South Island, and from the Bay of Plenty in the North Island (n = 24). No corresponding samples of otoliths were available from NZ. Tissue samples were collected and kept using either an Allflex® Tissue Sampling Unit (TSU) or standard manual fin-clipping methods following 100% ethanol preservation until further processing.

2.2. Otolith shape

Otoliths were cleaned and inspected for damage prior to imaging. Left otoliths were selected, and only whole undamaged otoliths were analysed (i.e., no damaged or vateritic material), with a target of 30 otoliths per location (Table S2). Otoliths were imaged whole using reflected light with an Olympus SZ61 dissection microscope coupled to Teledyne QImaging Micropublishertm 5.0 RTV. Otoliths were positioned with sulcus side (proximal surface) facing up, the sulcal axis aligned horizontally, with rostrum to the left. In a few cases that left otoliths were damaged, right otoliths were selected. Images for right otoliths were mirrored. All images were converted to monochrome and edited to enhance contrast in Adobe Lightroom to maximise the definition of the otolith perimeter.

The *ShapeR* package v0–1.1 (https://gwithub.com/lisalibungan/shapeR) (Libungan and Pálsson, 2015) was used to extract all shape outlines in R v4.1.1 (R Core Team, 2023). Contour smoothing of the outlines was performed to reduce the risk of interaction from pixel noise in the analysis (Libungan and Pálsson, 2015). The digitised outlines were transformed into shape coefficients (n = 63) using discrete wavelet analysis, best-suited for approximating sharp edges (Libungan and Pálsson, 2015). To account for the allometric relationship between otolith shape and fish length, coefficients were standardised using total fish length. The average otolith outline per source group was plotted, along with variations in wavelet coefficients along polar coordinates to evaluate the differences in shape both within and among source group's locations (Libungan and Pálsson, 2015).

2.3. Otolith chemistry

Left otoliths were also selected for chemical analysis, including those

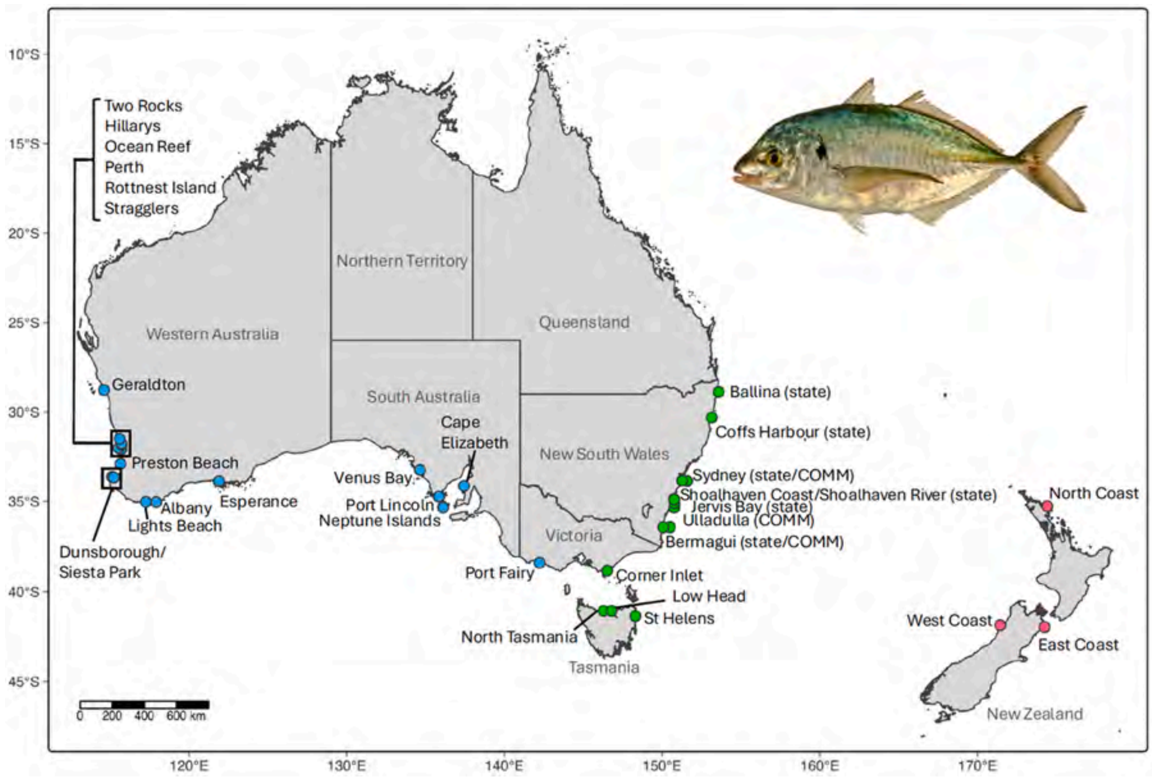

Fig. 1. The 35 sampling locations for silver trevally (*Pseudocaranx georgianus*) in Australia and New Zealand. Locations in New South Wales denoted with State or COMM indicates samples from state-managed and Commonwealth-managed fisheries, respectively. Locations with different colours indicate distinct populations identified via genomic analyses. Silver trevally image by Australian National Fish Collection, CSIRO, licensed under CC BY-NC.

used for shape analysis following imaging. Otoliths were embedded in indium spiked epoxy resin and sectioned transversely through the primordium, using a Gemmasta lapidary saw and diamond blades, then polished (9 and 3 µm lapping film), before mounting on glass slides with thermoplastic glue. Slides were then sonicated, triple rinsed with ultrapure water, and dried in a laminar flow cabinet.

Elemental concentrations of ^{7}Li, ^{11}B, ^{23}Na, ^{24}Mg, ^{55}Mn, ^{60}Ni, ^{63}Cu, ^{66}Zn, ^{88}Sr, ^{138}Ba, ^{208}Pb were ablated and analysed using a RESOlution LR 193 nm Excimer laser ablation system attached to an Agilent 7900x inductively coupled plasma mass spectrometer (LA ICP-MS) (Reis-Santos et al., 2018). Analytes from the laser ablation (at 5 Hz, $\sim$3.5 J/cm^{2}) were transported to the ICP-MS via an argon (Ar) and helium (He) stream. ^{43}Ca was measured as an internal standard to correct for variation in ablation yield. Indium (^{115}In) was measured as a marker of potential contamination from epoxy resin or thermoplastic glue. Spots (38 µm) were used to analyse the marginal edge of the otoliths, and reflect recent time of collection (up to last $\sim$ 6 months of life). Pre-ablations were done to remove any surface contamination. All data reduction, including background corrections and mass count to ppm were conducted using Iolite (Paton et al., 2011), and all data converted to element:Ca ratios (µmol/mol).

Certified reference material NIST 612 (National Institute of Standards and Technology) was analysed at the start and end of each session and repeatedly throughout to correct for mass bias and machine drift. MACS-3 (United States Geological Survey) was also run to check long-term consistency and external precision. Mean recovery for NIST 612 was 100% for all elements (between 99.99% and 100.07%). Precision and coefficient of variation across all samples and sessions (% relative standard deviation, RSD) ranged between 0.3% and 1.0% for NIST612, and 2.8–10.0% for MACS-3.

2.4. Data analysis

Otolith shape coefficients and element:Ca data were compared among individual collection locations to assess spatial variation and potential trends in population structure. To investigate both fine- and broad-scale patterns, and following trends observed in results across locations, proximate locations and jurisdictions that showed consistent misclassification trends were subsequently pooled. This hierarchical approach was used to account for overlapping shape and chemical signatures and to detect broader geographic structuring included the pooling of samples from state and COMM waters in NSW and adjacent jurisdictions across VIC, SA, and WA (Table 1 and Tables S2–S3). To reduce the number of coefficients required to reconstruct otolith outlines and facilitate integration with chemical data, shape coefficients were transformed into principal component (PC) scores. The minimum number of PCs explaining at least 80% of cumulative total variation was retained based on scree plots (Jolliffe, 2002; Sarakinis et al., 2024).

Table 1

Summary of overall correct classification rates (%) of individual silver trevally (*Pseudocaranx georgianus*) to collection location based on canonical analysis of principle coordinates (CAP) of otolith shape and chemistry. Classification analyses were performed among individual locations, and by pooling locations within and among jurisdictions to examine patterns at broader spatial scales. Jurisdictions are Western Australia (WA), South Australia (SA), Victoria (VIC), Tasmania (TAS), New South Wales (NSW) and Commonwealth (COMM).

Overall correct classification	Shape (%)	Chemistry (%)
All locations	20.6	42.3
Jurisdictions	42.3	59.3
Jurisdictions (NSW state and COMM pooled)	53.3	67.2
WA vs (SA – VIC) vs (VIC – TAS) vs (NSW w/COMM)	61.6	67.2
(WA – SA) vs (VIC – AS – NSW w/COMM)	83.2	77.6
(WA – SA – west VIC) vs (east VIC – TAS – NSW w/COMM)	85.9	76.4

Notes: Jurisdictions in (brackets) indicate pooled comparisons.

One-factor permutational multivariate analysis of variance (PERMANOVA, Primer v7) and pairwise tests were used to assess differences in otolith shape PC scores and element:Ca ratios among locations and jurisdictions, following confirmation that assumption of homogeneity of multivariate dispersion was met (, PERMDISP, Primer v7). Both chemistry and shape data were normalised and transformed into Euclidean distance resemblance matrices. Canonical analysis of principal coordinates (CAP, Primer v7) was used to discriminate and assess classification success to sampling location (or higher grouping level in the hierarchy). CAP is a constrained ordination for discriminating among priori groups and provides an objective and unbiased measure of group distinctiveness in multivariate space (Anderson and Willis, 2003; Libungan and Pálsson, 2015). Classification success was estimated using the 'leave one-out' allocation procedure within CAP (Anderson and Willis, 2003; Izzo et al., 2017; Jackson et al., 2023).

To evaluate whether combining otolith shape and chemical data improved discrimination and allocation to sampling locations, an integrated analysis was conducted using both data types. To enable integration, otolith element:Ca data were transformed into PC scores. The Principal Component Analysis (PCA) and scree plots were performed using the *factoextra* (https://CRAN.R-project.org/package=factoextra) (Kassambara and Mundt, 2020) and *ggplot2* (https://ggplot2.tidyverse.org) (Wickham, 2016) packages in R (R Core Team, 2023).

2.5. DNA extractions, genotyping and bioinformatics

A subset of muscle and fin-clipped samples from each location was used to assess DNA quality and quantity before sending for sequencing. The subset was extracted using a modified protocol based on the precipitation in high-salt solution method (i.e., salting-out) (Sunnucks and Hales, 1996), and the quality and quantity of extracted DNA were verified with NanoDrop 1000 spectrophotometer (Thermo Fisher Scientific), gel electrophoresis and fluorescence spectroscopy (Qubit, Thermo Fisher Scientific). After this initial assessment, tissue samples were sent to Diversity Arrays Technology (DArT) (https://www.diversityarrays.com) for extractions, DNA sequencing and genotyping using DArTseq®. This genome complexity reduction procedure generates thousands of Single Nucleotide Polymorphisms (SNPs) by employing a combination of methylation-sensitive restriction enzymes to digest genomic DNA and ligate barcode adaptors. Genotyping was completed using the DArT software pipeline according to Kilian et al. (2012).

The raw SNP dataset was converted into a 'genlight' object using the *dartR* package (https://green-striped-gecko.github.io/dartR/) in R v4.3.1 (Gruber et al., 2018; Mijangos et al., 2022), and filtered *in house* following the Molecular Ecology Lab at Flinders University (MELFU) standard bioinformatics protocols to minimise false SNPs resulting from sequencing errors. Individuals with $>$ 20% missing data were excluded from the dataset. Polymorphic SNPs with a reproducibility $\geq$ 99%, a call rate $\geq$ 80%, and a minor allele frequency (MAF) $\geq$ 3% were retained. Loci with $<$ 5X read depth coverage or that deviated from Hardy-Weinberg Equilibrium (HWE) in more than one population were excluded. One SNP per DArT fragment was randomly selected and retained for the final dataset.

2.6. Genomic diversity, genetic differentiation and migration

Genomic diversity metrics, including the percentage of polymorphic loci, expected heterozygosity (H_E), observed heterozygosity (H_O) and population-level inbreeding coefficient (F_{IS}), were calculated using the *dartR* package (Gruber et al., 2018; Mijangos et al., 2022). The following locations were combined for data analyses due to their close geographical proximity and lack of significant genetic differentiation observed during data exploration (i.e., Shoalhaven Coast/Shoalhaven River (indicated as Shoalhaven), NSW; Port Lincoln/Cape Elizabeth (indicated as Spencer Gulf), SA; Albany-Lights Beach;

Dunsborough-Siesta Park; Stragglers-Rottnest Island; Hillarys-Ocean Reef-Two Rocks, WA) (Fig. 1).

Population genomic structure was inferred using two complementary approaches. First, a PCA was performed with the *ade4* package (https://adeverse.github.io/ade4/) to visualise distinct clusters of silver trevally across all locations (Dray and Dufour, 2007; Dray et al., 2007; Bougeard and Dray, 2018; Thioulouse et al., 2018). The method uses a model-free approach to identify clusters by reducing the dimensionality of genomic datasets. Data were transformed into PCs that capture the greatest proportion of genomic variance, allowing visualisation of genomic similarity among populations (Reich et al., 2008). The genetic clustering was then further tested using ADMIXTURE under a maximum likelihood approach (Alexander et al., 2009; Alexander and Lange, 2011). A 5-fold cross-validation was conducted for *K* values (1−27) to determine the most likely population structure. The ancestry proportions of the most likely *K* were visualised using the *ggplot2* package (Wickham, 2016).

We calculated pairwise F_{ST} based on Weir and Cockerham (1984) to assess genetic differentiation between locations using the *dartR* package with 1000 bootstrap replicates. The p-values were adjusted considering a 5% False Discovery Rate (Benjamini and Yekutieli, 2001). Resulting F_{ST} values were then visualised in a heatmap generated by the *ggplot2* package (Wickham, 2016). Levels of connectivity between the three main study regions (i.e. southern Australia, eastern Australia and NZ) were assessed by estimating relative migration rates (Nm, normalized by the largest value estimated) using the *divMigrate* function of the R package *diveRsity* (https://github.com/kkeenan02/diveRsity) (Sundqvist et al., 2016). *divMigrate* models a hypothetical group of migrants between pairs of populations (i.e. study regions) to estimate genetic differentiation and the direction of gene flow between that group and each population. The significance of asymmetric gene flow between regions was assessed with 1000 bootstrap iterations.

2.7. Isolation by coastline distance

Isolation-by-distance (IBD) was investigated by testing the relationship between geographic and genetic distances ($F_{ST}/(1 - F_{ST})$) across sampling locations using a Mantel test in the *vegan* package (https://github.com/vegandevs/vegan) with 1000 permutations (Mantel, 1967; Oksanen et al., 2012). Coordinates of each location were extracted in Google Earth by calculating the shortest spatial distances following the coastline between locations using the *viamaris* function in the *melfuR* package (https://github.com/pygmyperch/melfuR). After that, a set of synthetic coordinates was projected using the *isoMDS* function in the *MASS* package (https://www.stats.ox.ac.uk/pub/MASS4/) (Venables and Ripley, 2002) for the distance matrix input in the Mantel test. Because population differentiation was strongest at biogeographical boundaries, Mantel tests were further performed separately for samples from each major population group identified from the clustering analysis.

3. Results

3.1. Otolith shape

Wavelet shape reconstructions of whole silver trevally otoliths generated 63 shape coefficients. Average otolith shape variations were significantly different among locations (Pseudo-$F_{(15,\ 567)} = 3.1$, $P < 0.001$) and jurisdictions (Pseudo-$F_{(5,\ 567)} = 6.4$, $P < 0.001$). Shape variations at both spatial scales were more pronounced in the rostrum, excisura, antirostrum and dorsal lobe (Fig. 2, Figure S1). However, overall classification success among locations in the collection range was low (21%), with most locations having classification accuracies below 20%; only Corner Inlet and Port Fairy (VIC) had higher classification accuracy (60% and 40% respectively) (Table 1, Fig. 3, Table S2a) (all classifications based on CAP leave-one-out allocation).

While there were differences among combinations of locations, overall classification success was low or close to that expected by chance alone when pooling adjacent locations within jurisdictions, including pooling NSW and COMM (overall classification accuracy 42% and 53%, respectively) (Table 1, Table S2b,c). However, sample distribution across the multivariate space highlighted potential broader east to west patterns among regions, with generally fewer misclassified individuals between locations or jurisdictions at greater geographic distances. Trends in misclassification highlighted potential groupings among SA/western VIC and WA, versus eastern VIC, TAS and NSW/COMM (Fig. 3, Figure S2). Shape variation between Port Fairy and Corner Inlet (VIC), suggested most Port Fairy samples (12 out of 15) were misclassified to

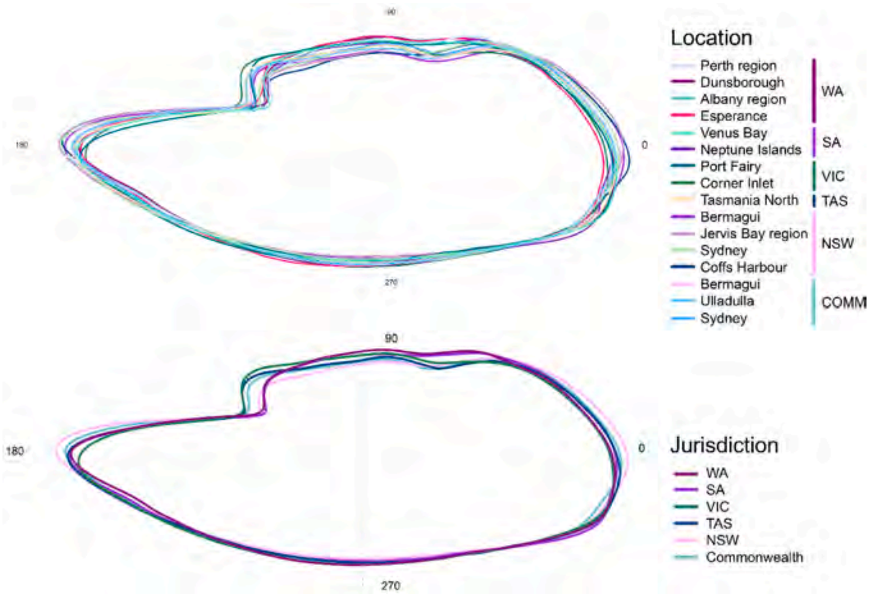

Fig. 2. Discrete wavelet analysis of silver trevally (*Pseudocaranx georgianus*) otolith shape for each location (top) and jurisdiction (bottom). Vertical colour lines in top panel reflect locations by jurisdiction. Jurisdictions are Western Australia (WA), South Australia (SA), Victoria (VIC), Tasmania (TAS), New South Wales (NSW) and Commonwealth (COMM).

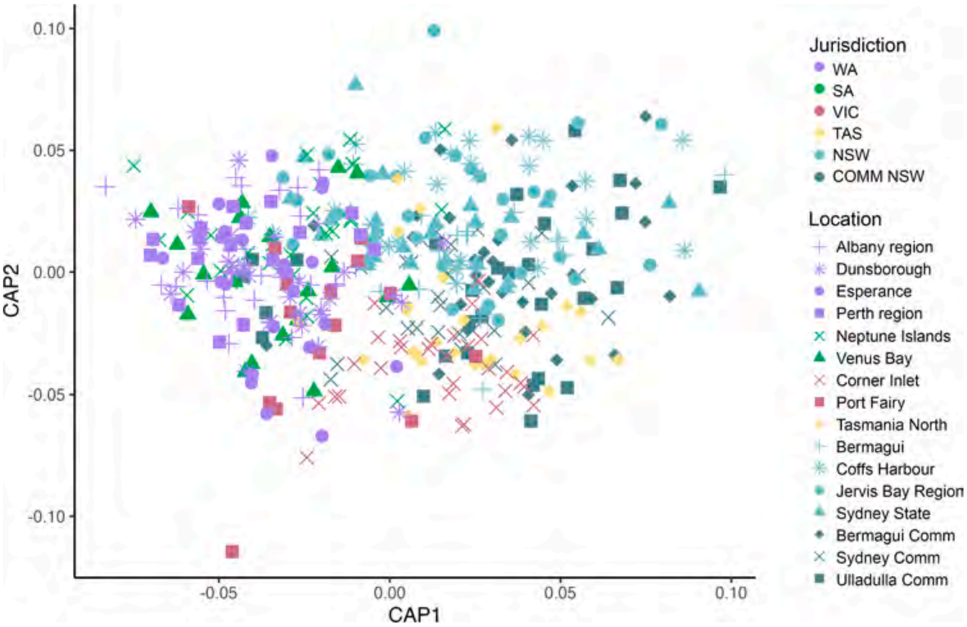

Fig. 3. Ordination plot of the canonical analysis of principle coordinates (CAP) for wavelet coefficients comparing otolith shape of silver trevally across all sampling locations (overall correct classification 21%). Jurisdictions are Western Australia (WA), South Australia (SA), Victoria (VIC), Tasmania (TAS), New South Wales (NSW) and Commonwealth (COMM NSW).

the WA-SA cluster, which suggested a transition zone between eastern and western groups lies east of Port Fairy. Grouping Port Fairy with WA-SA increased overall classification to 86% (as well as for both VIC sites to 90% and 84%) (Table S2d-e).

3.2. *Otolith chemistry*

The elemental composition of otolith edges of silver trevally differed significantly among locations (Pseudo-$F_{(23,655)} = 16.7$, $P < 0.001$) and jurisdictions (Pseudo-$F_{(5655)} = 28.5$, $P < 0.001$) (Sr:Ca and Ba:Ca ratios are shown as examples in Figure S3).

Elemental signatures did not provide high discriminatory power across all locations (42% overall correct classification accuracy, based on CAP leave-one-out allocation) (Table 1, Fig. 4). Nonetheless, individual locations with high and moderate correct classification accuracies included Coffs Harbour (NSW) (84%), Jervis Bay (NSW) (77%), Corner Inlet (VIC) (67%) and Sydney (NSW) (67%) (Table S3a). Overall, CAP analysis of jurisdictions, and when pooling NSW state with COMM, also returned moderate overall classifications (59–67%, based on CAP leave-one-out allocation) and similar to shape, sample distribution across the multivariate space highlighted trends among east to west regions that were further explored (Table 1, Fig. 4, Table S3b-e). Pooling jurisdictions at a broad east-west scale, and with a transition area between SA and VIC, or within VIC, increased overall classification success to 76% - 78%, respectively (Table 1, Fig. 4, Table S3f-g, Figure S4).

Compared to the broader scale analysis of population structure,

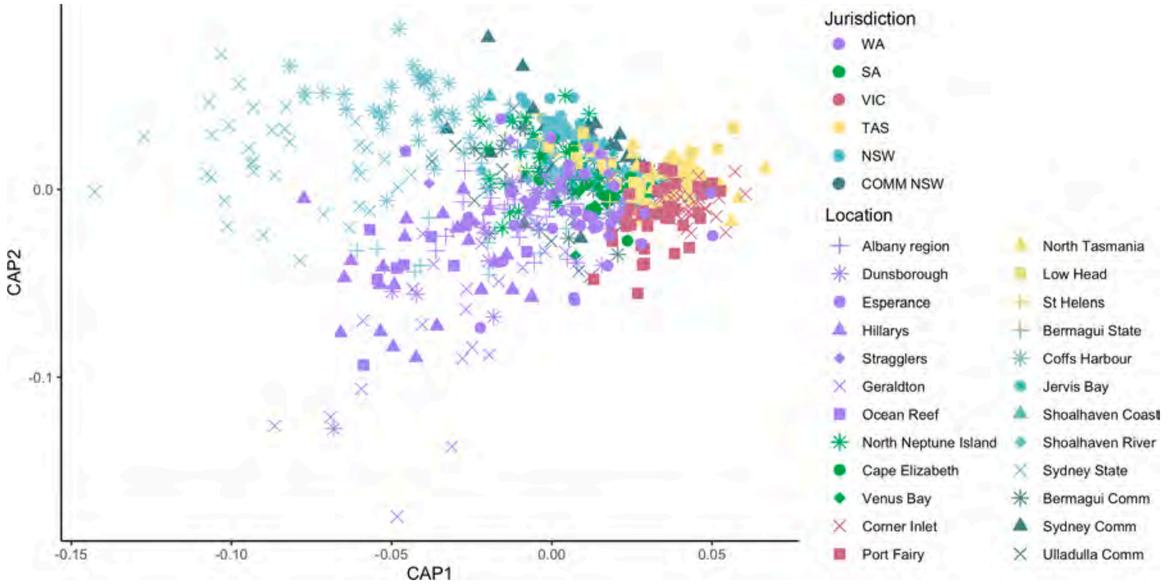

Fig. 4. Ordination plot of the canonical analysis of principle coordinates (CAP) for otolith chemical composition of silver trevally (*Pseudocaranx georgianus*) across all locations (42% overall correct classification accuracy). Jurisdictions are Western Australia (WA), South Australia (SA), Victoria (VIC), Tasmania (TAS), New South Wales (NSW) and Commonwealth (COMM NSW).

investigating patterns of otolith chemistry at smaller spatial scales within jurisdictions revealed potential for sub-structuring or the ability to discriminate individual collection locations (Table S4). In VIC, fish from Corner Inlet and Port Fairy were accurately classified with a very high overall correct classification of 94%. Within NSW, overall correct classification to sample location was 70%, with high accuracy (>85%) for sites such as Sydney, Coffs Harbour and Jervis Bay. Discrimination between NSW state- and Commonwealth-managed locations had an overall 78% accuracy.

3.3. Integrating otolith shape and chemistry

Integrating both otolith markers did not provide additional information on structuring when compared to analysing markers individually (38.4% overall classification). The results returned similar patterns delineating an apparent east – west grouping around VIC (88% overall correct classification).

3.4. Genomic diversity, genetic differentiation and migration

DArTseq produced an initial dataset of 64,239 SNPs for 599 individual silver trevally. After filtering, we retained high quality data for 543 individuals at 2526 SNPs (Table S5- S6). Genomic diversity was relatively similar across locations (H_E: 0.058 – 0.078, H_O: 0.056 – 0.078), with low population-level inbreeding coefficients (F_{IS}: −0.0161 – 0.0437) and moderate percentages of polymorphic loci (31.03% – 59.98%) (Table 2).

The PCA revealed three main genomic clusters, with two distinct clusters in Australia, one along the east and the other along the southern coast of Australia, and a third cluster around NZ (Fig. 5). The first and second principal components (PC1 and PC2) explained 8.66% and 1.09% of the genetic variance, respectively. Similarly, ADMIXTURE identified $K = 3$ as the optimal clustering across the continent, revealing distinct populations in NZ, the east coast of Australia (i.e. Coffs Harbour, NSW to Corner Inlet, VIC and northern Tasmania, TAS) and the southern coast of Australia (i.e. Cape Elizabeth, SA to Geraldton, WA) (Fig. 6). Notably, the NZ population exhibited a degree of admixture with ancestry of the Australian east coast population.

There was low genetic differentiation based on F_{ST} pairwise comparisons within each of the three major regions (i.e. eastern and southern Australia, and NZ) (eastern Australia: 0.0022 – 0.0122; southern Australia: 0.0017 – 0.0106; NZ: −0.0003 – 0.001) (Figure S5). In contrast, southern Australia showed high genetic differentiation from both the eastern Australia and the NZ regions (southern Australia – eastern Australia: 0.330 – 0.411; southern Australia – NZ: 0.323 – 0.367). Moderate genetic differentiation was detected between samples from the eastern Australian coast and NZ (0.0251 – 0.0321).

Nil to very low levels of recent migration were detected between pairs of geographic regions (maximum of 3.59%; Table S6, Figure S6). No evidence of asymmetric migration was detected, except for the higher, but still low, rate of migration from NZ into Australia's east coast compared to the opposite direction.

3.5. Isolation by coastline distance

The Mantel test uncovered significant isolation-by-distance (IBD) across the entire sampling region ($p < 0.05$, $R^2 = 0.78$). However, analyses conducted separately within each population showed no evidence of IBD (NZ: $p = 0.83$; east coast: $p = 0.47$; south coast: $p = 0.055$) (Figure S7). Thus, the IBD signal across the entire sampling regions is likely an artifact of the biogeographic separation and divergence among the three inferred coastal populations (eastern and southern Australia, and NZ), rather than a true spatial constraint of species within each coastline.

4. Discussion

We employed otolith shape and chemistry along with genomic analyses to investigate the population structure and connectivity of silver trevally across its full range in Australia and New Zealand (NZ). Findings from each approach consistently revealed the existence of two biologically distinct stocks in Australia: a southern population spanning from Western Australia (WA) to western Victoria, and an eastern population extending from eastern Victoria to northern New South Wales (NSW), encompassing north-eastern Tasmania and the Commonwealth-managed waters off NSW. Analyses indicated strong connectivity within each biological stock but little to no evidence of ongoing connectivity between the Australian populations. Furthermore, the availability of tissue samples from three regions off NZ allowed us to demonstrate genomic differentiation across the Tasman Sea, thereby extending the study to the species' entire known distribution.

In Australia, the boundary between the two identified silver trevally biological stocks was found at Bass Strait, between Port Fairy and Corner Inlet. In this region, the Bassian Isthmus connected mainland Australia

Table 2
Genomic diversity estimates for silver trevally (*Pseudocaranx georgianus*) at 20 locations based on 2526 SNPs.

Jurisdiction	Location	N	%PL	H_O	H_E	F_{IS}
Commonwealth	Sydney	40	59.98	0.0616	0.0610	0.0030
	Ulladulla	29	56.93	0.0603	0.0619	0.0422
	Bermagui	31	54.20	0.0627	0.0614	-0.0046
New South Wales	Coffs Harbour	23	45.88	0.0564	0.0575	0.0403
	Shoalhaven	18	42.40	0.0628	0.0637	0.0429
	Jervis Bay	9	31.03	0.0614	0.0604	0.0437
Victoria	Corner Inlet	30	54.67	0.0637	0.0628	0.0027
Tasmania	North Tasmania	38	58.39	0.0610	0.0608	0.0097
South Australia	Spencer Gulf	35	53.21	0.0694	0.0688	0.0068
	Venus Bay	18	49.11	0.0781	0.0779	0.0284
Western Australia	Esperance	40	59.34	0.0694	0.0676	-0.0131
	Albany-Lights Beach	43	54.00	0.0692	0.0673	-0.0161
	Dunsborough-Siesta Park	39	54.49	0.0639	0.0633	0.0044
	Preston Beach	2	12.07	0.0632	0.0482	0.0181
	Stragglers-Rottnest Island	18	45.79	0.0688	0.0663	-0.0094
	Hillarys-Ocean Reef-Two Rocks	34	55.97	0.0702	0.0688	-0.0059
	Geraldton	21	44.97	0.0648	0.0635	0.0045
New Zealand	East Coast, South Island	24	48.46	0.0661	0.0660	0.0196
	West Coast, South Island	27	50.08	0.0662	0.0674	0.0359
	North Coast, North Island	24	48.73	0.0658	0.0667	0.0346

Notes: Number of individuals after filtering (N), percentage of polymorphic loci (%PL), observed heterozygosity (H_O), expected heterozygosity (H_E), and inbreeding coefficient (F_{IS}).

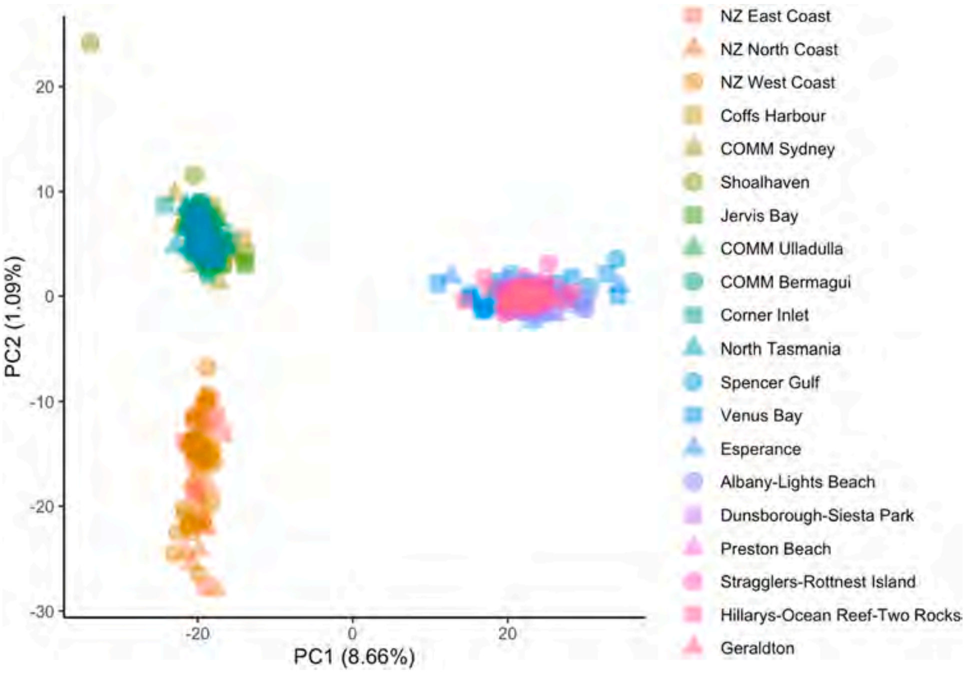

Fig. 5. Principal Component Analysis (PCA) of 543 silver trevally (*Pseudocaranx georgianus*) individuals from 20 sampled locations along the coasts of Australia and New Zealand. Each point represents one individual, colour coded by sampling location. Locality names starting with 'COMM' relates to locations under the Commonwealth-managed fisheries. NZ: New Zealand.

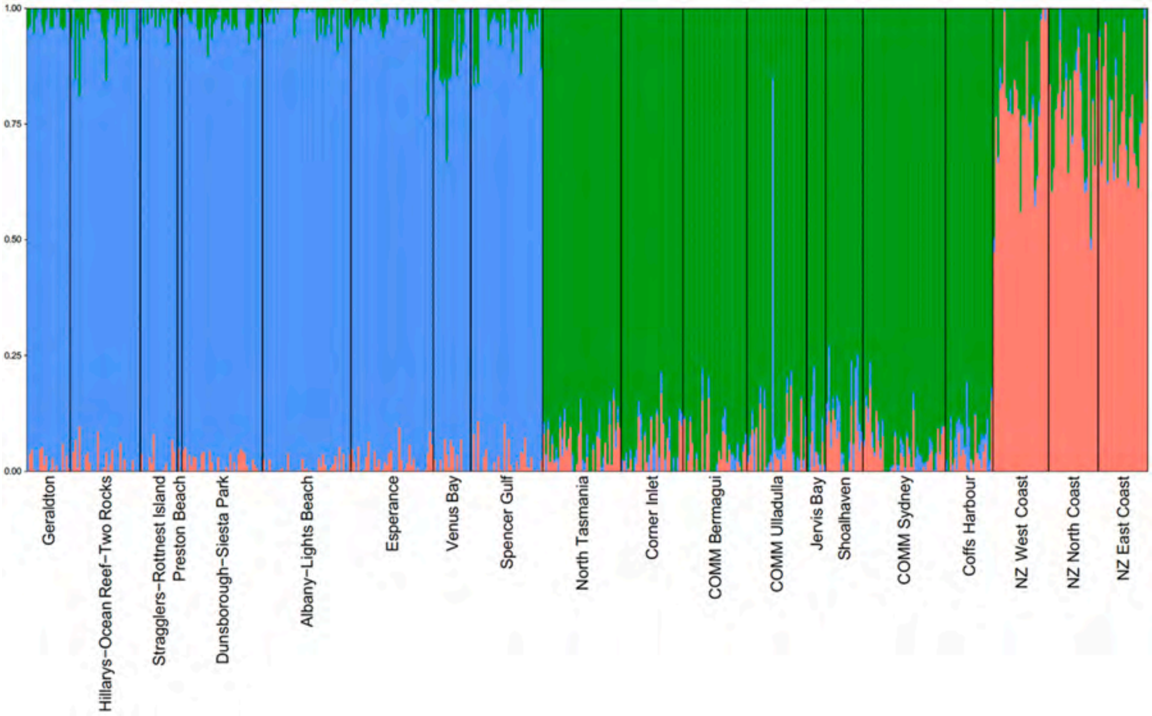

Fig. 6. ADMIXTURE with $K = 3$, showing distinct populations of silver trevally (*Pseudocaranx georgianus*) in New Zealand, east coast and south coast of Australia. Locality names starting with 'COMM' relate to locations under the Commonwealth-managed fisheries. NZ: New Zealand.

with Tasmania during the Last Glacial Maximum (Lambeck and Chappell, 2001). This vicariant historical feature is considered a major biogeographic barrier that hindered population connectivity, restricted colonisation, and promoted geographic isolation and evolutionary divergence in multiple coastal marine species (reviewed in Colgan, 2016; Teske et al., 2017). Similarly broad patterns of population differentiation, or in some cases phylogenetic divergence and speciation, between the eastern and southern coasts of Australia have been reported for barnacles, echinoderms, gastropods and other teleosts with a wide range of dispersal potential (e.g., Waters and Roy, 2003; Waters, 2008; York et al., 2008; Shaddick et al., 2011; Colton and Swearer, 2012; Moore and Chaplin, 2014; Barnes et al., 2016; Bertram et al., 2023).

Our findings suggest a strong influence of biogeographic and environmental factors on the population structure of silver trevally, with pronounced divergence occurring at the interface between two major oceanic currents in the region (White et al., 2010). The observed population boundary likely reflects genetic differentiation through restricted connectivity among populations, driven initially by a land barrier to east-west exchange and potentially maintained to present day by variations in habitat availability, temperature, and coastal circulation (Wells and Okada, 1996; Lambeck and Chappell, 2001). The eastern population occupies a range dominated by the poleward-flowing East Australian Current (EAC), which transports warm tropical waters toward temperate zones, whereas the southern population occurs in the Indian Ocean, characterized by a complex system of warm surface flows and cooler deep-water currents (Oke et al., 2019; Duran et al., 2020). The interaction between these warm and cool currents creates strong environmental gradients in temperature, water density, nutrient availability, and salinity, forming a semi-permeable barrier that likely reinforces population isolation (Unal and Bucklin, 2010). Otolith analyses broadly supported these inferences, reflecting a combination of environmental, physiological, and genetic influences on shape and element composition, though the boundary was less clear (Clarke et al., 2011; Stransky, 2014; Reis-Santos et al., 2023). Variations in environmental conditions, including temperature, salinity, depth, and food availability, influence otolith shape in tandem with genetic factors, and likely contribute to the observed differences in otolith rostrum and dorsal margins (Assis et al., 2020; Vignon, 2020; Mahé et al. 2024). Overall, coastal environmental conditions and oceanographic processes appear to influence reproductive dynamics, dispersal, and the contemporary population dynamics of silver trevally.

Within jurisdictions, otolith chemistry suggested potential finer-scale structuring. Silver trevally from coastal locations in NSW were distinguished with reasonable confidence from those in offshore Commonwealth waters, suggesting differences in habitat use over recent timescales represented by otolith edge chemistry. This is consistent with tagging and telemetry studies from WA, NSW, and NZ that report limited adult movements (James, 1980; Fairclough et al., 2011; Fowler et al., 2018). These differences, and the larger magnitude of variation in Ba:Ca, also reflect known upwelling regions across southern Australia (Woodson et al., 2013; Grammer et al., 2015) However, fine-scale heterogeneity also highlights the scale dependence of otolith chemical variation and challenges associated with analysing many source locations, particularly in marine environments where chemical signatures are more homogeneous (Sturrock et al., 2012; Reis-Santos et al., 2023). While variability among proximate locations improves discrimination, it can impact classifications when pooling or comparing across larger spatial scales. The fact that otolith chemistry can differ between nearby locations suggests limited recent adult movement, highlighting the potential for localised depletion from fishing, where there may be reduced replenishment from adult migration. Resolving these knowledge gaps will require greater sampling effort and additional research into life history and biology of the species in the region.

Although we detected relatively higher rates of connectivity between NZ and the population on the east coast of Australia compared to connectivity between the two Australian populations, the overall pattern suggests these three geographic regions are functionally isolated from one another. Environmental gradients across the Tasman Sea, particularly given its broad spatial range and depth, may act as a barrier to gene flow between populations (Smith et al., 1996; Doubleday et al., 2009). Over geological timescales, marine connectivity and hydrological interactions between Australia and NZ have been intermittent, with prevailing ocean currents shifting significantly across the Tasman Sea in response to glacial cycles (Nees, 1997; Ashe and Wilson, 2020). This barrier may cause a large range of environmental gradients, including differences in water mass, nutrient availability and temperature (Scott, 1981; Matear et al., 2013; Henschke et al., 2015), along with complex eddy activity across the region (Scott, 1981; Everett et al., 2012). While trans-Tasman dispersal has been observed in some species such as long-spined sea urchins (*Centrostephanus rodgersii*) and common dolphins (*Delphinus delphis*) (Banks et al., 2007; Ashe and Wilson, 2020; Thomas et al., 2021), several marine teleosts with high dispersal potential, such as jackass morwong (*Nemadactylus macropterus*), Australian salmon (*Arripis* spp.) and striped trumpeter (*Latris lineata*) (Grewe et al., 1994; Tracey et al., 2007; Moore and Chaplin, 2014), have exhibited restricted connectivity across the Tasman Sea, similar to the divergence observed in silver trevally. This highlights the strength of this barrier even for species with high dispersal potential.

Our multi-disciplinary approach provided a comprehensive, large-scale assessment of the stock structure of silver trevally across its distribution. Genomic analyses provided strong evidence for population separation at the multi-generational scale, while regional genomic patterns indicated high connectivity within each population reflecting substantial gene flow within each oceanic region. Otolith-based analyses revealed broadly similar clustering, but offered complementary resolution at the within-lifetime scale, capturing environmental and physiological influences reflected in otolith shape and chemistry (Stransky, 2014; Reis-Santos et al., 2023). Future research should examine how seasonal variability and ontogenetic development influence the spatial distribution of silver trevally across life stages. Age-composition data from NSW commercial fisheries indicate pronounced differences between estuarine and offshore catches, with estuarine individuals typically less than five years old, whereas offshore fish range from three years to over 20 years of age (Rowling and Raines, 2000). This pattern suggests potential ontogenetic movement from the inshore to offshore environment (Rowling and Raines, 2000). A similar inshore–offshore distinction has been documented in WA, where larger, older individuals occur in deeper waters and exhibit markedly different lengths at the same age (Farmer et al., 2005). However, it remains uncertain whether these patterns reflect shifts in habitat use during ontogeny or represent distinct assemblages within the same species. In both cases, stock assessment models for silver trevally may need to account for such spatial segregation by including explicit spatial structure within the model. Inshore-offshore segregation is currently accommodated in east-coast models via separation of NSW estuarine, NSW inshore, and Commonwealth fishery fleets (Burch et al., 2023). The separate selectivity functions estimated for each fleet allow for differences in the availability of size classes across the inshore-offshore transition.

Building on these findings, assessing temporal variations in both genomic and otolith datasets will allow deeper insights into dispersal, recruitment dynamics and spawning behaviour (Clarke et al., 2015; Egan et al., 2019; Quintero-Galvis et al., 2020). Chemical analysis of otoliths can uncover patterns of seasonal aggregation and ontogenetic migration (reviewed in Campana et al., 2007, redfish *Sebastes* spp.; Gauthier et al., 2024, Atlantic halibut *Hippoglossus hippoglossus*; Widdrington et al., 2025, Eteline snapper *Etelis* sp.). Such work would require a spatiotemporal sampling design or analysis across the otolith growth axis (i.e., full life history) to capture potential ontogenetic or spawning-related shifts in habitat use. However, this will also depend on sufficient seasonal variation in chemical signatures to resolve such movements. While in early stages, there is growing interest in using trace element concentrations to reconstruct reproductive cycles, and in exploring hormone or diet derived markers in hard or soft tissues to provide insights into these dynamics (Sturrock et al., 2014; Li et al., 2019; Reis-Santos et al., 2023).

Advanced genomic studies focused on identifying adaptive genetic variations will be critical for understanding the demographic and evolutionary processes shaping connectivity patterns of silver trevally under current and future climate scenarios (Grummer et al., 2019; Brauer et al., 2026). This effort could be strengthened by applying whole-genome data, which offers greater resolution of adaptive diversity across the genome and enables the study of population resilience to environmental change (Allendorf et al., 2010; Bernatchez et al., 2024). By combining population dynamic knowledge acquired from both otolith and genomic data, researchers can improve the conceptualisation of life history strategies within each population (Leis et al., 2011; Parada et al., 2017; Pirotta et al., 2018). This, in turn, can be used to guide the implementation of stock-specific management measures, including minimum legal lengths and catch quotas based on life-history simulations. (Eayrs et al., 2014; Catalán et al., 2025).

5. Conclusions

Our study employed a multidisciplinary approach, combining otolith and genomic analyses, to clarify the stock structure of the commercially and recreationally important silver trevally (*Pseudocaranx georgianus*) across Australia. Our results identified two distinct biological stocks: one spanning coastal waters from Western Australia to western Victoria, and another extending from eastern Victoria to northern New South Wales, including northeastern Tasmania and the Commonwealth-managed waters off New South Wales. The boundary of these biological stocks lies in the region between Port Fairy and Corner Inlet, a division likely shaped by the historical Bassian Isthmus and maintained by contemporary oceanographic processes. Our findings underscore the importance of cross-jurisdictional collaboration for effective fisheries management. Additionally, finer-scale population structure and preferences in habitat use may exist within each broader biological stock. Further, the New Zealand population differed to Australia. Future research should aim to better understand recruitment dynamics, variation in life-history traits, and fine-scale connectivity within and between the identified biological stocks.

Ethical Statement

All procedures were performed in compliance with relevant laws and institutional guidelines and the appropriate institutional committee(s) have approved them.

CRediT authorship contribution statement

Zoriana H.T. Lam: Writing – review & editing, Writing – original draft, Formal analysis. **Rowan C Chick:** Writing – review & editing, Resources. **Jonathan Sandoval-Castillo:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Formal analysis, Data curation. **Corey P. Green:** Writing – review & editing, Resources. **John Stewart:** Writing – review & editing, Writing – original draft, Resources, Project administration, Investigation, Funding acquisition, Data curation, Conceptualization. **Julian Hughes:** Writing – review & editing, Resources. **Ashley M. Fowler:** Writing – review & editing, Resources. **Luciana M. Möller:** Writing – review & editing, Investigation, Funding acquisition, Conceptualization. **Peter Ritchie:** Writing - review & editing, Resources. **Michael Drew:** Writing – review & editing, Resources. **Bronwyn M. Gillanders:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization. **Nils C. Krueck:** Writing – review & editing, Resources. **Rhiannon A. Van Eck:** Data curation, Formal analysis, Writing – review & editing, Methodology, Investigation. **Sean R. Tracey:** Writing – review & editing, Resources. **Patrick Reis-Santos:** Writing – review & editing, Writing – original draft, Resources, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **David V. Fairclough:** Writing – review & editing, Writing – original draft, Resources. **Charlie Huveneers:** Writing - review & editing, Resources. **Beheregaray Luciano:** Writing – review & editing, Writing – original draft, Supervision, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Maren Wellenreuther:** Writing - review & editing, Resources.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fishres.2026.107751.

Data availability

Data will be made available on request.

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