



Genome-wide evaluation of Scylla serrata (giant mud crab) population structure between and within two continental shelf regions of northern Australia

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ABSTRACT

Context. Offshore spawning and larval distribution of the wide ranging Scylla serrata (giant mud crab) provides genetic connectivity potential across large spatial scales. Aims. We examined the genetic connectivity of S. serrata between and within two large continental shelves of northern and eastern Australia, to inform fisheries assessment and management. Methods. Over 300 individuals were sampled from 14 locations, within 6 oceanographic regions, across the 2 continental shelves, providing 40,364 single nucleotide polymorphisms (SNPs) for analysis. Key results. Results indicated a single genetic stock along the eastern continental shelf of Australia with no evidence of north to south structuring. A separate genetic stock on the northern continental shelf of Australia was indicated, with evidence supporting a degree of east-west structuring of S. serrata populations within the Gulf of Carpentaria. Conclusions. The spatial extent of genetically connected S. serrata metapopulations is likely dependent on the oceanographic features of a region. The spatial scale of S. serrata stocks should be assessed on a case-by-case basis, confirmed by empirical evidence (e.g. SNP analysis) given connectivity is likely dependent on regional oceanographic conditions. **Implications**. The outcomes of this study have implications for management of fished *S. serrata* stocks, especially where fishing mortality may (or may not) have effects beyond the jurisdiction of interest.

Keywords: Australia, east Australian current, fish stock, genetic connectivity, Gulf of Carpentaria, single nucleotide polymorphisms, stock structure.

Introduction

Defining the number and spatial extent of wild populations is critical for effective monitoring, assessment and management of exploited species (Waples and Naish 2009; Ovenden et al. 2015). It is well recognised that when a population (also known as a stock) is subject to harvest pressure by fisheries and the population dynamics are not adequately characterised, it can lead to unviable estimates of mortality, reproduction and recruitment (Hilborn et al. 2020). Where species distributions transcend jurisdictional boundaries, population and management units do not always align, which can lead to ineffective management (Flood et al. 2016). Therefore, ascertaining the population structure of a species is vital to ensuring that management units and associated controls are implemented at a biologically relevant level to improve the prospects of sustainable harvest (Waples

Scylla serrata (giant mud crab) is a species of swimmer or paddler crab (family Portunidae), which is widely distributed throughout coastal waters of the Indo-Pacific, with three other species in the genus: S. olivacea, S. paramamosain and S. tranquebarica (Keenan et al. 1998; Le Vay 2001). Within Australian waters, S. serrata are a widely sought after and harvested species by recreational, commercial and Indigenous fishers. Harvesting of mud crabs (S. serrata and S. olivacea) within Australia takes place from Exmouth Gulf in Western Australia, across northern Australia to the New South Wales-Victoria border, with approximately two-thirds of the national harvest occurring along the east coast (Kirke *et al.* 2023). Each jurisdiction independently manages and assesses mud crab fisheries, with management variably employing a mix of input controls (e.g. limited commercial licences and gear limits) and output controls (i.e. sex-harvest policy, minimum size-limit, total allowable commercial catch, individual transferable quotas and possession limits for recreational fishers). The distribution of *S. serrata* is continuous across the four Australian jurisdictions in which it occurs (Kirke *et al.* 2023). The need for inter-jurisdictional cooperation in management across the species extent is unclear at present, but modelling of critical processes (spawning, dispersal and recruitment) have been shown to cross jurisdictional boundaries (e.g. Hewitt *et al.* 2022a).

Scylla serrata has a life history that spans inshore estuarine habitats (juveniles and adults) with offshore waters (female spawning migration). Juveniles and adults are typically associated with mangrove-lined estuaries, whereas spawning females migrate offshore where stable, warm, saline waters provide optimal conditions for egg development and larval survival (Quinn and Kojis 1987; Hill 1994). The eggs of S. serrata hatch after ~15 days at 28°C and become planktonic larvae, progressing through five zoea stages the duration of which (3–4 weeks) is strongly related to water temperature and salinity (Hill 1974; Hamasaki 2003). Zoea 5 larvae metamorphose into megalopae, which use tidal currents to return to inshore habitats.

Offshore spawning allows larvae to disperse widely in ocean currents, with dispersal patterns influenced by regional oceanography and seasonal currents and winds (Wolanski 1993; Hewitt *et al.* 2022a; Charles *et al.* 2024). Timing of spawning migrations varies geographically: on the eastern shelf it generally occurs from spring to early autumn at subtropical latitudes (Heasman *et al.* 1985; Hewitt *et al.* 2022b), whereas in tropical latitudes spawning can extend from September to March, with evidence of year-round activity in some regions (Hill 1994; Knuckey 1999). Females are highly fecund, producing on average 4.5 million eggs per batch, and may spawn multiple times within a single intermoult period (Mann *et al.* 1999). The female spawning migration to offshore waters is thought to support connectivity between regions (Hill 1994).

Earlier genetic analysis of the mitochondrial *Cox-1* region provided evidence for distinct *S. serrata* stocks in the western Indian Ocean, north-western Australia and eastern Australia including the western Pacific Ocean (Fratini *et al.* 2010). Within Australian waters, genetic stock structure based on allozymes, and mitochondrial DNA (mtDNA) indicated considerable genetic structuring on a meso-scale across the western and northern continental shelves, but minimal genetic structuring along the eastern continental shelf within 18–28°S (Gopurenko and Hughes 2002). Simulations of *S. serrata* larval dispersal and recruitment along eastern Australia indicated broadscale connectivity (Hewitt *et al.* 2022a; Charles *et al.*

2024) that was consistent with Gopurenko and Hughes (2002). Hewitt *et al.* (2022*a*) suggested that their simulated larval dispersal demonstrated an overall north-to-south source–sink metapopulation structure for *S. serrata* on the east-Australian shelf, but also showed the East Australian Current (EAC) separation zone (28–31°S) likely created a 'soft boundary' to connectivity where estuaries south of this zone were supplied with recruits from local spawning. Further stock structure analysis of *S. serrata* using nuclear markers was recommended to further resolve stock structure along eastern Australia (Gopurenko and Hughes 2002).

Study of genetic population structure in crustaceans has recently advanced with the application of genome-wide single nucleotide polymorphism (SNP) assays. In many cases, study of SNPs has resulted in the identification of genetic differentiation over finer spatial scales than previously revealed using mitochondrial markers. The blue swimmer crab Portunus pelagicus had historically showed contrasting population structure throughout south-east Asian waters based on different marker systems (microsatellite, mtDNA and SNPs) (Chai et al. 2017; Dang et al. 2019; Supmee et al. 2020). Recent work using SNPs showed strong differentiation between central and northern Vietnam waters, which arose through the restriction of gene flow by complex biophysical factors (Dang et al. 2019). Similar findings have also been observed for other crustaceans using genome-wide SNP assays, including ornate spiny lobster Panulirus ornatus (Farhadi et al. 2022), American lobster Homarus americanus (Benestan et al. 2015) and whitefingered mud crab Rhithropanopeus harrisii (Tepolt et al. 2020). In contrast to these examples of fine-scale genetic heterogeneity, SNP analysis has also confirmed the presence of broadscale connectivity in invertebrates such as the swimming crab Charybdis feriata (He et al. 2024) and reef bugs Thenus australiensis (McMillan et al. 2024). A common element in maintenance of connectivity among crustacean populations is the presence of biophysical characteristics that support broadscale geneflow by the dispersal of larvae or eggs.

In *S. serrata*, genetic population structure across management jurisdictions throughout eastern and northern Australia remains uncertain. To address this uncertainty, we quantified genetic and demographic connectivity of *S. serrata* using a genome-wide SNP panel across this region. The study was designed to ensure spatially representative sampling across east Australian management boundaries to inform inter-jurisdictional resource assessment and management arrangements.

Methods

Muscle tissue samples of *S. serrata* (n = 328 individuals) were obtained from the northern and eastern continental shelves of Australia between November 2020 and June 2024 (Table 1). Tissue samples were obtained though fishery-independent sampling conducted under General Fisheries Permit 210183,

Table 1. Genetic sample locations for *Scylla serrata* collected from the northern and eastern Australian continental shelves, jurisdiction (State or Territory) and oceanographic region.

Shelf	Sample location	State or Territory	Latitude (°S)	Oceanographic region	n
Northern	Roper River	NT	14.76	Western GoC	20
	McArthur River	NT	15.84	Western GoC	19
	Karumba	Qld	17.39	Eastern GoC	28
	Mapoon	Qld	12.03	Eastern GoC	20
Eastern	Princess Charlotte Bay	Qld	14.47	Above EAC jet	19
	Hinchinbrook	Qld	18.36	Above EAC jet	30
	Mackay	Qld	21.46	Above EAC jet	28
	Gladstone	Qld	23.76	Above EAC jet	28
	Moreton Bay	Qld	27.69	EAC jet	32
	Tweed River	NSW	28.17	EAC jet	18
	Clarence River	NSW	29.42	EAC separation	20
	Macleay River	NSW	30.87	EAC separation	20
	Wallis Lake	NSW	32.17	Mesoscale eddy	19
	Port Stephens	NSW	32.72	Mesoscale eddy	19

NT, Northern Territory; Qld, Queensland; NSW, New South Wales; GoC, Gulf of Carpentaria; EAC, East Australian Current. Oceanographic region based on Wolanski (1993) and Hewitt *et al.* (2022*a*).

Marine Park Permit P-MPP-100155117 and Marine Park Permit G22/46474.1, as well as fishery-dependent sampling either at sea (Queensland, Qld) or through landed commercial product (New South Wales, NSW; and the Northern Territory, NT). Additional samples were collected under collaborations with FRDC 2021-119 and TMSFB000012. Animal ethics approval for this research was received from the Queensland Department of Primary Industries Animal Ethics Committee (permit number CA 2021-10-1554). Fourteen collection locations were specifically included to test for differentiation within and between each continental shelf, within and between the management jurisdictions of Qld, NSW and the NT (Fig. 1), their importance as major harvest locations and position relative to possible biogeographic barriers to gene flow. Sex was recorded for all individuals, with size (carapace width or length) and weight recorded where possible. Tissue samples were stored in 90% ethanol at -20°C until extraction.

Small amounts of biological tissue (<15 mg) were transferred to a well plate and sent to Diversity Arrays Technology for DNA extraction and sequencing (DArT Pty Ltd, Canberra, ACT, Australia). The SNP loci were discovered and genotyped following the DArTseq protocol (Kilian *et al.* 2012) for all samples. Quality control, read assembly and SNP calling were undertaken using proprietary DArTseq analytical pipelines (*DArTsoft14*, see https://dartsoft14.user-guide.diversityarrays.cloud/) described in detail by Georges *et al.* (2018).

SNP quality filtering

Genetic markers returned from DArT were further filtered in R (ver. 4.4.1, R Foundation for Statistical Computing, Vienna, Austria, see https://www.r-project.org/) and RStudio (ver. 2024.09.0, Posit Software, PBC, Boston, MA, USA, see https:// posit.co/products/open-source/rstudio/) using the dartR (ver. 2.7.2, see https://CRAN.R-project.org/package=dartR; Gruber et al. 2018) and dartRverse packages (ver. 1.0.2, see https://cran.r-project.org/package=dartRverse; Gruber et al. 2018). To assess the impact of different thresholds on the underlying population structure, a range of different filters and associated thresholds were evaluated including (1) sexlinked loci (Robledo-Ruiz et al. 2023), (2) loci with reproducibility less than 99 or 96%, (3) loci with read depth less than 5 or greater than 70, (4) samples with greater than or equal to 40% missing data and new monomorphic loci generated by the removal of those samples, (5) loci with greater than 1 or 10% missing data and (6) loci with minor allele frequency (MAF) less than 1 or 5% and loci in short linkage-disequilibrium (secondary SNPs within the same locus). Furthermore, samples with higher-than-average individual heterozygosity, indicating potential cross-contamination, were detected with the dartR package. Samples that were flagged as potential duplicates, related or cross-contaminated were removed based on results from the R packages radiator (ver. 1.2.8, T. Gosselin, see https://thierrygosselin.github.io/ radiator/) and SNPRelate (ver. 1.38.1, see https://github. com/zhengxwen/SNPRelate; Zheng et al. 2012). Loci deviating from Hardy-Weinberg equilibrium were assessed using Fisher's exact test ($\alpha = 0.05$, *P*-value) with unadjusted test results compared with P-values corrected for multiple testing using the FDR BH method (Supplementary Table S1) (Waples 2015).

Loci were evaluated for the potential to be under selection using the differentiation-based (F_{ST}) approach in *OUTFLANK* (ver. 0.2, see https://github.com/whitlock/OutFLANK; Whitlock and Lotterhos 2015) (through dartR), and the principal component analysis (PCA)-based method in PCADAPT (ver. 4.4.1, see https://CRAN.R-project.org/package=pcadapt; Luu et al. 2017; Privé et al. 2020). OUTFLANK was used with a FDR q-value of 0.05, 0.1 minimum heterozygosity required and trimming of 5% loci from both tails of the distribution. The number of principal components (PCs) to retain in PCADAPT (K) was determined according to the scree plot of eigenvalues, selecting K (PCs) before the curve in the scree plot reaches an asymptote (Luu et al. 2017). PCADAPT was performed using a minimum MAF of 0.05. Correction for multiple testing was conducted with the FDR method of Benjamini and Hochberg (1995) and a cutoff q-value threshold of 10% was used to identify outliers. The results obtained with the two methods were compared and only loci identified as outliers by both methods were considered potential outliers and removed. From these analyses, we progressed data analysis on a full dataset that included all

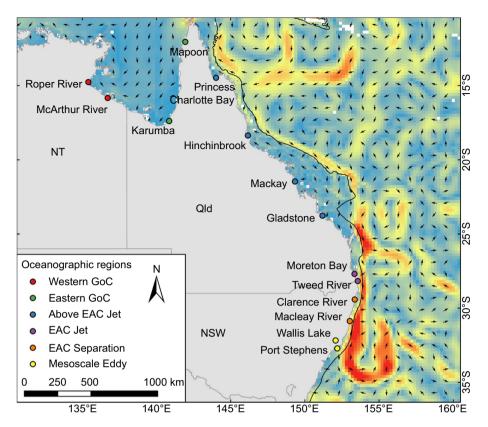


Fig. 1. Map of *Scylla serrata* collected from the northern and eastern Australian continental shelves showing sample locations, jurisdictional boundaries and oceanographic regions listed in Table 1. The 200-m depth contour is in black. Colour display: IMOS OceanCurrent DM02 product, illustrating surface current speed (blue, low; to red, high) and surface current direction (arrows), example data 3 September 2020.

loci and a neutral dataset that excluded outliers. Datasets resulting from other filters (Tables S1–S3) are provided in the Supplementary material.

Population genetic structure analyses

Genetic population structure was analysed across the full set of samples (including individuals from all locations), as well as separately for the northern continental shelf Gulf of Carpentaria (GoC) and eastern continental shelf (Qld and NSW - see Table 1) to allow for within shelf variability to be characterised (see Table 1 for allocations of collection locations to a continental shelf). Genetic differentiation among sampling locations was assessed across multiple analytical methods. Firstly, pairwise F_{ST} between locations were calculated following the method of Weir and Cockerham (1984) as implemented in dartR. Associated P-values were estimated using 10,000 bootstraps based on the following α values: 0.001, 0.01 and 0.05. To compensate for multiple comparisons, we consider 0.001 as representing statistical significance, with the latter two α values being included to inform interpretations and reduce the risk of a false negative outcome among pairwise comparisons (Waples and Gaggiotti 2006; White et al. 2019). Secondly, we explored the SNP dataset across all locations using a model-based clustering method, sparse non-negative matrix factorisation (SNMF) (R package LEA, ver. 4.5, see https://bioconductor.org/ packages/release/bioc/html/LEA.html; Frichot and François 2015), which is comparable to STRUCTURE (Pritchard et al. 2000) but produces a least-squares estimate of ancestral (source) populations given *K* ancestral populations. To explore the appropriate number of ancestral populations, we plotted the minimum entropy criterion against K ranging within 1–14, searching for the inflection point in the plot where additional cross-entropy loss was minimal (Forester et al. 2018). Thirdly, PCAs were conducted on the filtered datasets through dartR. Finally, isolation by distance was assessed through a Mantel test implemented in *dartR* using F_{ST} between locations as the genetic distance and Euclidean distance based on latitude and longitude coordinates as geographic distance. All other parameters were set to the default values.

Results

SNP filtering and identification of non-neutral loci

A total of 40,364 SNPs were scored and filtered from 328 individuals (Tables S1 and S2). The major filtering steps

included detection and removal of the following: locus call rate less than 0.99 (19,502 SNPs excluded) and MAF (6399 SNPs excluded). Importantly, a large number of sex-linked loci (n = 747) in a ZW sex chromosomes system was also removed, including 497 sex-biased, 71 z-linked, 47 w-linked and 132 gametolog loci (Supplementary Fig. S1). In addition, several individuals (two from Gladstone, one from Tweed river and one from Mackay) were also removed after filtering for an individual call rate greater than 60%, and filtering out individuals with high genetic similarity, relatedness, high individual heterozygosity or a combination of these (n = 3,Tables S4-S6, Fig. S2-S4). No loci out of Hardy-Weinberg equilibrium were detected. OUTFLANK identified 101 putative outliers, whereas *PCADAPT* identified 198 putative outliers. which included 88 outlier loci identified by OUTFLANK. Only these 88 outliers were removed in the neutral dataset.

After filtering, the final full dataset included 4713 SNPs from 321 individuals, and the neutral dataset included 4625 SNPs from 321 individuals (Tables S2 and S3). Analytical results from these two datasets are presented below and provide the basis of the discussion and interpretation. Analyses were replicated on additional datasets outlined in Table S3 to support evaluation of filtering effects. The results of these analyses are presented in the Supplementary material (Fig. S8–S14).

Between-shelf genetic structure

The level of genetic connectivity among sample locations was estimated using pairwise F_{ST} comparisons for both the neutral and full datasets. Pairwise comparisons among all locations indicated significant differences with moderate F_{ST} values $(P < 0.001; F_{ST} 0.012-0.019)$ between the northern and eastern continental shelf locations (Fig. 2a). However, once the outlier loci were removed (i.e. neutral dataset), pairwise $F_{\rm ST}$ values between each of the northern continental shelf locations and each of the eastern continental shelf locations were reduced to one-quarter of the full dataset value (Fig. 2b). Ancestry analyses using SNMF inferred an inflection point of the minimum cross entropy plot at K = 2 for the main data set (4713 loci) but K = 1 for neutral dataset (Fig. 3). Ancestry assignment plots showed clear differentiation across both K = 2 and K = 3 scenarios between the northern and eastern continental shelf samples when using the full dataset (Fig. 3a). This signal was reduced in the ancestry assignment when using the neutral dataset, with only minor differences present in the K=3 scenario (Fig. 3b). The PCA results were consistent with both the F_{ST} and SNMF analyses, illustrating the presence of one cluster that included the northern continental shelf locations (GoC) and a second cluster including all locations from the eastern continental shelf (Qld and NSW). The main axis of the PCA separated these two clusters, explaining 1.5% of differentiation (Fig. 4a). However, as with the other analysis types, the differentiation between the two clusters was reduced once the 88 outlier loci were removed (Fig. 4b).

Within-shelf genetic structure

Comparisons of pairwise $F_{\rm ST}$ between locations within the eastern continental shelf (i.e. Qld and NSW) were predominantly non-significant (P > 0.001) across both full and neutral dataset. However, there were several pairwise comparisons where P-values fell in the range of 0.01–0.05, including Mackay (Qld) with Macleay River and Port Stephens (NSW), as well as Wallis Lake (NSW) with Gladstone (Qld) and Macleay River (NSW) (Fig. 2a).

The only significant differences among locations in the northern continental shelf for the full dataset (P < 0.001, $F_{\rm ST} = 0.003 - 0.007$) were between locations from the western oceanographic region (Roper and McArthur Rivers, NT) and those from the eastern oceanographic regions (Karumba and Mapoon, Old). In the neutral dataset, only the difference between Roper River and Mapoon at the two extremes remained significant at P < 0.001. Non-significant comparisons with P-values in the range of 0.05–0.01 and low F_{ST} values (0.001-0.002) occurred between some GoC locations such as Karumba and Mapoon or between Roper and McArthur Rivers for both datasets. Evaluation of the SNMF ancestry analyses on the full dataset (Fig. 3a) indicated limited variation among locations from the eastern continental shelf. Similarly, when evaluating the SNMF ancestry analyses for the neutral dataset, there was no such clear differentiation in ancestry assignment for the eastern continental shelf (Fig. 3b).

Owing to the separation of northern and eastern continental shelf locations identified in prior analyses, the isolation by distance analysis was undertaken among locations within each shelf to ensure differences were assessed across a consistent spatial gradient. When only eastern continental shelf samples were analysed (datasets #6 and 8, Table S3, Fig. S13), Mantel tests showed a non-significant relationship, indicating no isolation by distance (i.e. no latitudinal structuring of *S. serrata*) from locations within the eastern continental shelf. This was consistent with the within-shelf ancestry analyses and pairwise $F_{\rm ST}$ values. When only northern continental shelf samples were analysed (datasets #5 and 7, Table S3, Fig. S14), the Mantel test was significant with or without outliers (P = 0.0417, $r^2 = 0.511$ or 0.655 respectively), indicating a weak pattern of isolation by distance.

Discussion

Our study did not detect any evidence for genetic population structure in *S. serrata* among locations along the 2500 km of the Australian eastern continental shelf from 14.5°S (Princess Charlotte Bay) to 32.7°S (Wallis Lake). The presence of low fixation indices and homogeneous clustering among eastern

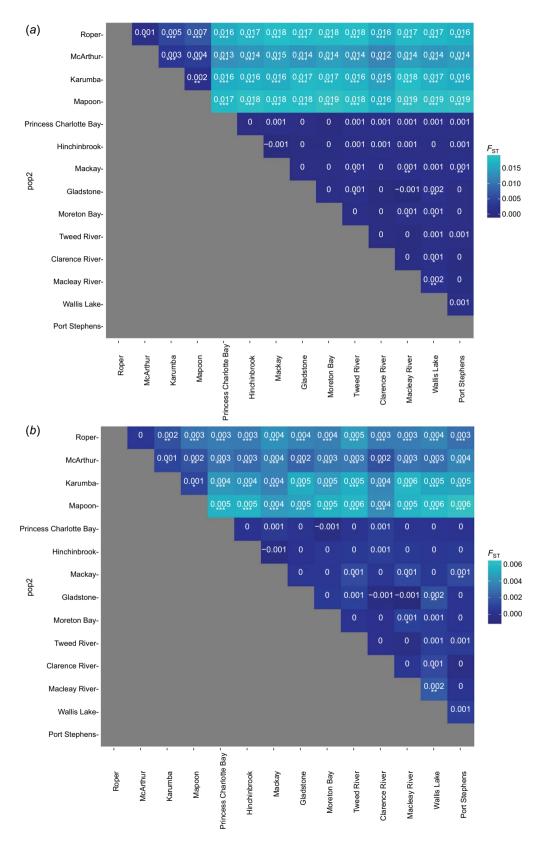


Fig. 2. Population pairwise fixation index values (F_{ST}) for *Scylla serrata* sampled from the northern and eastern Australian continental shelves (ordered as per Table 1) for (a) full dataset and (b) neutral dataset. Probabilities are significant at: ****, P < 0.001; ***, P < 0.001; and *, P < 0.05. Darkest blue cells indicate a F_{ST} of zero.



Fig. 3. Sparse non-negative matrix factorisation analysis of 321 *Scylla serrata* sampled from the northern and eastern Australian continental shelves (ordered as per Table 1) showing individual ancestry coefficients to the ancestral genetic cluster (K) for the full dataset under (K) K = 2 and (K) K = 3 scenarios, as well as for the neutral dataset (K) K = 2 and (K) K = 3 scenarios.

continental shelf locations indicates broadscale genetic connectivity (Kritzer and Sale 2004), as inferred by larval dispersal and recruitment simulations (Hewitt *et al.* 2022*a*; Charles *et al.* 2024). Our study detected strong genetic differentiation between the eastern and northern continental shelves, consistent with previous mtDNA analyses (Gopurenko and Hughes 2002). The results are consistent with metapopulation spatial structuring for the northern continental shelf but provided new evidence indicative of minor east–west spatial structuring within the GoC. This concurs with results from preliminary larval dispersal simulations for *S. serrata* in the GoC indicating a degree of demographic stock structuring (as defined in Ovenden *et al.* 2015), likely attributable to the GoC's oceanographic features (Patterson 2020).

Population structure has been reported in other parts of the *S. serrata* broad geographic range, including the Western Indian Ocean, Northern Indian Ocean and Central Indo-Pacific (Gopurenko and Hughes 2002; Fratini *et al.* 2010; Saher *et al.* 2019). Previous mtDNA analysis reported a single haplotype (A1) present in all Australian shelf regions, although much reduced at locations north of 18°S (Gopurenko and Hughes 2002). The low occurrence rate of the A1 haplotype in the far north of the eastern Australian shelf (i.e. Cape Grenville, 12°S) was interpreted as representing strong genetic structuring, potentially as a consequence of a barrier to geneflow, such as the bifurcation point of the South Equatorial Current (see Steinberg and Lowrey 2018; Charles *et al.* 2024 for further details). The SNP analysis presented

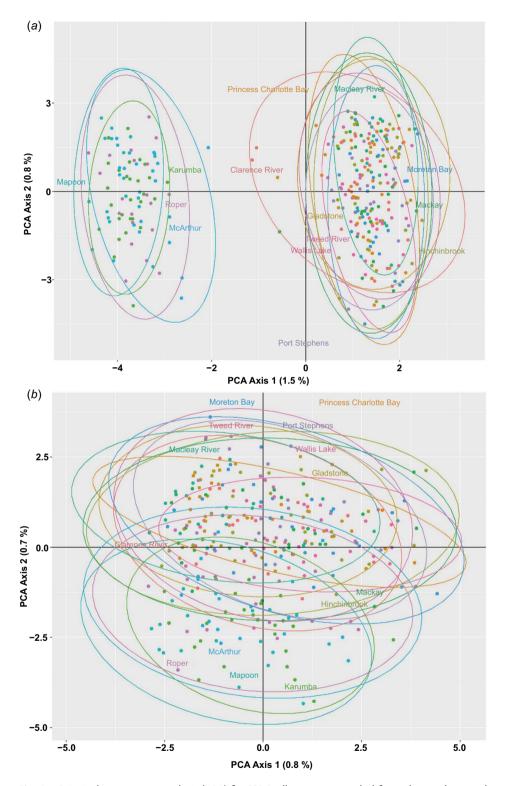


Fig. 4. Principal component analysis (PCA) for 321 *Scylla serrata* sampled from the northern and eastern Australian continental shelves (Table 1), and plots provided for (a) full dataset and (b) neutral dataset. Inertia ellipses are centred on the mean coordinates of point from each sampling location (plotted in different colours). Width and height of ellipses illustrate variance on each axis.

herein did not detect genetic structuring between the far north of the eastern Australian shelf (i.e. Princess Charlotte Bay, 14°S) and more southern locations, which somewhat contrasts with the mtDNA results of Gopurenko and Hughes (2002).

Recent simulation of *S. serrata* larval dispersal along the east Australian continental shelf indicated overlap in connectivity between 14 and 18°S (Princess Charlotte Bay and Hinchinbrook Channel), as well as between 12 and 14°S (Princess Charlotte Bay and Cape Grenville) (Charles *et al.* 2024). This can likely be attributed to the complexity of the oceanographic conditions within the Great Barrier Reef area (Wolanski *et al.* 2024).

The oceanographic complexity of the eastern continental shelf of Australia has been a driver of variable stock structure across a range of benthic invertebrates that inhabit the northern section of this shelf (i.e. within the Great Barrier Reef). For example, McMillan et al. (2024) found no genetic differences for Moreton Bay bugs Thenus australiensis sampled within 14.5-25°S (~1500 km), due to larval dispersal and associated connectivity. Similarly, spanner crabs Ranina ranina have been found to have broadscale stock connectivity across the eastern continental shelf of Australia (Brown et al. 1999), which was surmised to be facilitated through larval dispersal dependent on the area's oceanographic features (Schilling et al. 2022). By contrast, Scata et al. (2024) detected genetic differences for Ballot's saucer scallop Ylistrum balloti between samples north of 22°S to those south of 22°S. The winter spawning of Y. balloti, when oceanographic conditions in the central Great Barrier Reef often results in little to no drift (Rose et al. 1988; Wolanski et al. 2024), likely contributes to different larval dispersal patterns in this species, compared to S. serrata, T. australiensis and R. ranina that predominately spawn over spring-summer. The above examples demonstrate how the relationship between the phenology of reproduction and temporal features in oceanography influence and shape the population structure of benthic invertebrates.

Although the east coast of Australia is a complex seascape that spans a vast latitudinal gradient, the GoC is a comparatively remote and data-limited location on the northern continental shelf. This region has much less complexity in its oceanographic features (e.g. major currents or topographic change), which are primarily driven by tides and seasonal wind patterns (Li et al. 2006; Patterson et al. 2023). However, these features were still sufficient to drive a level of genetic structuring in the SNP data, concurring with early results of mtDNA analysis (Gopurenko et al. 2003) despite sample locations only being 500 km apart, and offshore spawning (Hill 1994) potentially enabling connectivity by larval drift. Simulation of *S. serrata* larval dispersal indicated that oceanographic features limited the degree of connectivity between the western and eastern GoC (Patterson 2020).

The SNP analysis presented herein also did not detect genetic structuring between locations sampled at the southern end of the east Australian continental shelf where *S. serrata* occurs, which supports the results of larval simulation by Hewitt *et al.* (2022*a*). We note that our results may be limited in their ability to detect demographic independence among *S. serrata* samples from the eastern continental shelf. As discussed by Ovenden *et al.* (2015), genetic connectivity

can be maintained by an insignificant number of migrants who successfully contributed to recruitment.

The outcomes of this study further inform assessment and management of *S. serrata* throughout east Australian waters. The lack of spatial genetic differentiation supports the maintenance of a single genetic stock for *S. serrata* within the Qld east coast, but with consideration of cross-jurisdictional assessment and management between Qld and NSW. To further clarify mechanisms for gene flow, further research into *S. serrata* effective larval source locations, through quantification of their spawning migration (when and where) on each continental shelf would assist in refining larval dispersal models.

Supplementary material

Supplementary material is available online.

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Data availability. The data collected during the current study are stored on a secure server within the Department of Primary Industries, Queensland, and are available for access or re-use on request.

Conflicts of interest. The authors declare that they have no conflicts of interest.

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