

## RESEARCH ARTICLE OPEN ACCESS

# Genomic Assessment of Australian White Sharks (*Carcharodon carcharias*) Challenges Previous Evidence of Population Subdivision

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## ABSTRACT

**Aim:** The white shark (*Carcharodon carcharias*) is one of the world's largest and most recognisable marine predators but has suffered significant declines since the mid-twentieth century. Conservation efforts remain complicated by persistent knowledge gaps associated with white shark biology and ecology, including the biological connectedness of white shark populations. We re-assess patterns of population genetic structure in Australian white sharks, where two subpopulations—eastern and southern-western—are currently recognised based on previous animal tracking and genetic assessments.

**Methods:** Population genomic analyses are performed using tissues from ~650 individual white sharks and ~7000 single nucleotide polymorphism (SNP) loci generated through reduced genome representation sequencing. We test for evidence of genetic structure and relatedness among sharks from eastern and southern Australia and use population genetic simulations to assess the likely strength of inter-generational migration between regions.

**Results:** This study challenges the current paradigm of population structure in Australian white sharks, showing a lack of genetic structure between white sharks from eastern and southern Australia. These findings are further supported by population genetic simulations and kinship analyses indicating high levels of intergenerational migration and relatedness between regions. Consistent with recent reports from eastern Australia, we also detected high levels of relatedness among juvenile and subadult white sharks and estimated the overall effective population size ( $N_e$ ) of Australian white sharks to be less than 500 individuals. Furthermore, we provide evidence of a potential reduction in  $N_e$  over the last two generations.

**Main Conclusions:** Overall, these findings highlight the need to consider this revised estimate of genetic structure when discussing the management and conservation of the species. Our results also raise concerns for the conservation of Australian white sharks highlighting risks of potential inbreeding, and reductions in population fitness and resilience. We discuss the need for further research and the importance of ongoing population monitoring.

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## 1 | Introduction

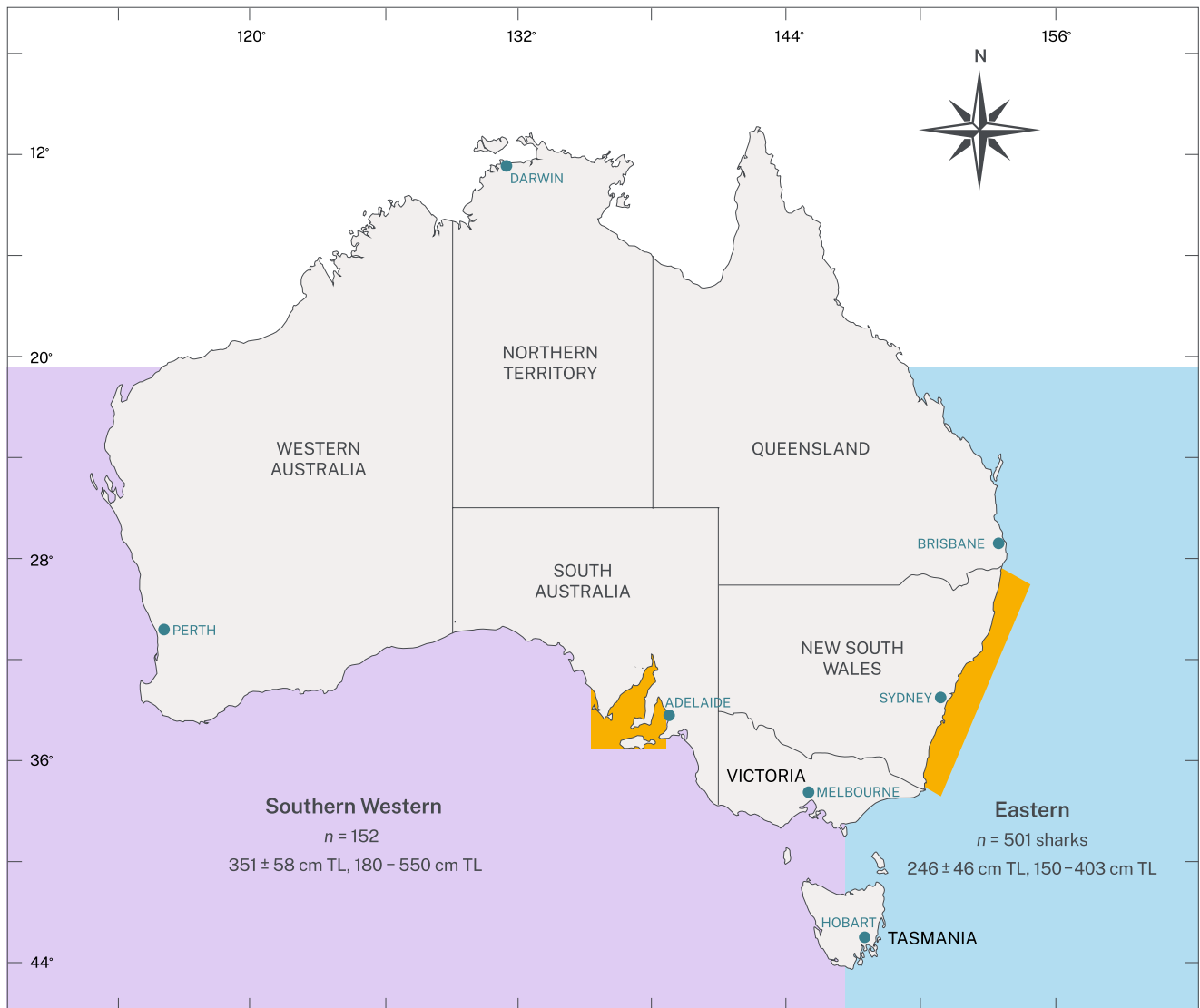
The white shark, *Carcharodon carcharias*, is one of the world's largest and most recognisable marine predators, and a functionally important regulator of marine biodiversity and ecosystem function in temperate and subtropical oceanic environments (Bruce 2008; Galván-Magaña et al. 2019). However, white shark populations have suffered major declines since the 1950s due to overexploitation by commercial fisheries, trophy hunting for jaws or teeth and lethal shark control programmes (Dewar et al. 2013; Ellis and McCosker 1991; Rigby et al. 2019). Globally, white shark populations have declined by up to 80%–90% (e.g. in the Northwest Atlantic Ocean and Australia's east coast; Curtis et al. 2014; Rigby et al. 2019; Roff et al. 2018), leading to concerns for the conservation of the species and the health and structure of marine ecosystems (Hammerschlag et al. 2019, 2022). Despite strategic fisheries management and conservation programmes (Department of Climate Change, Energy, the Environment and Water (DCCEEW) 2013; Dewar et al. 2013), and population recovery in some regions of the world (e.g. Northeast Pacific—Dewar et al. 2013), the species remains listed as Vulnerable by the IUCN Red List (Rigby et al. 2019). Furthermore, conservation efforts remain complicated by persistent knowledge gaps associated with white shark biology and ecology, including information on population structure and biological connectivity across parts of the species range (Huveneers et al. 2018; Spaet, Patterson, et al. 2020).

Understanding the biological connections across species' ranges is essential for quantifying the spatial boundaries and sizes of different populations (Bertram et al. 2022; Hohenlohe, Funk, and Rajora 2021), identifying key habitats for protection (Gallagher et al. 2021; Hays et al. 2019) and determining the spatial reach of disturbance events, including the spread of novel diseases (Storfer et al. 2017; Whiterod et al. 2016). Additionally, this information is prudent for gauging the genetic fitness and resilience of populations, which is particularly important when dealing with threatened species (Hoffmann and Sgrò 2011; Miller et al. 2020). To date, telemetry and population genetic studies have played an important role in describing patterns of connectivity between white shark populations within and between the world's oceanic basins. Telemetry studies from the Indo-Pacific and Atlantic oceans indicate that white shark movement is largely limited to local ocean basins and coastal shelf waters in temperate regions (Anderson, Burns, et al. 2021; Bruce and Bradford 2012; Francis, Duffy, and Lyon 2015; Franks et al. 2021). These findings are largely corroborated by population genetic studies indicating limited population genetic structuring within ocean basins, but significant genetic structuring between ocean basins (Andreotti et al. 2016; Blower et al. 2012; Davenport 2022; Jorgensen et al. 2010; O'Leary et al. 2015; Tanaka et al. 2011; Wagner et al. 2024). Despite the importance of these telemetry and genetic studies, most have been constrained by small sample sizes, with genetic studies often further limited to the use of small numbers of genetic markers that can lack sensitivity for resolving fine-scale patterns of genetic structure.

Information on white shark population connectivity and spatial ecology is urgently needed in Australia (Huveneers

et al. 2018), where historical white shark declines are estimated to have exceeded 90% (Roff et al. 2018). At a national level, the species is listed as Vulnerable under the Environmental Protection and Biodiversity Conservation Act (1999) and is the subject of a national recovery plan (Department of Climate Change, Energy, the Environment and Water (DCCEEW) 2013). Conservation management of white sharks in Australia is complicated by increasing frequencies of human-shark interactions, sometimes resulting in human casualties, leading to public demands for shark control and culling programmes (Meeuwig, Harcourt, and Whoriskey 2015; Riley et al. 2022). The shark management programme (SMP), led by the New South Wales Department of Primary Industries, involves the largest shark tracking project in the world, where more than 1300 juvenile and subadult white sharks have been captured, tagged and tracked using a combination of satellite and acoustic telemetry approaches since 2015 (Lee et al. 2021; Spaet, Patterson, et al. 2020; Spaet, Butcher, et al. 2022). Comprehensive monitoring of white sharks has also been occurring in South Australia, where ~180 white sharks have been tagged with acoustic transmitters since 2013 to monitor the efficacy of the regulations used to manage Australia's white shark cage-diving industry (Niella et al. 2022). These and previous tagging programmes have shown a combination of high residency and constrained movement to temperate coastal shelf waters within the respective regions of capture in some sharks, and large-scale movements (e.g. >8000 km) between eastern, southern and western Australia (Bradford et al. 2020; Spaet, Butcher, et al. 2022; Spaet, Manica, et al. 2020) and between Australia, New Zealand, New Caledonia and Papua New Guinea in other sharks (Spaet, Patterson, et al. 2020). The combination of diverse movement patterns and uncertain levels of gene flow among white sharks from eastern and southern-western Australia highlights the need for rigorous investigations of population genetic structure. Despite this uncertainty, sharks from eastern and southern-western Australia are currently assumed to be distinct biological entities and treated as such for conservation and management purposes by government authorities (Department of Climate Change, Energy, the Environment and Water (DCCEEW) 2013; Figure 1).

Studies on the population genetics of Australian white sharks have demonstrated inconsistent patterns of genetic structure across the species' continental range. Pardini et al. (2001) reported a lack of significant genetic differentiation among white sharks from eastern and southern-western Australia using a small number of microsatellite markers and a single mitochondrial locus. In contrast, Blower et al. (2012) reported significant genetic structure between sharks from these regions using the same mitochondrial locus and comparatively weak but significant genetic structure at one of six microsatellite loci (a locus not genotyped by Pardini et al. 2001). The findings of Blower et al. (2012) support the possibility of female reproductive philopatry and sex-biased dispersal in Australian white sharks, which is in line with previous studies on white sharks from other parts of the world (Pardini et al. 2001) as well as other elasmobranchs (Phillips et al. 2021). However, as discussed by Blower et al. (2012), more rigorous investigations using larger sample sizes and additional marker systems are needed to help resolve the true patterns of overall population



**FIGURE 1** | Assumed population subdivision of Australian white sharks (*Carcharodon carcharias*), where sharks from eastern and southern-western Australia are considered isolated gene pools. Regions encompassing sampling locations are shown in orange shaded boxes, and total sample sizes and representative animal total length (average total length including standard error, and length ranges) for each region are provided.

genetic structure in Australian white sharks and to help implement spatially appropriate shark conservation and management programmes.

In this study, we use samples from ~650 individual sharks to assess the population genetic structure of Australian white sharks using > 7000 SNP loci derived from reduced genome representation sequencing. Specifically, we assess contemporary patterns of biological connectivity between white sharks from eastern and southern Australia by testing for evidence of genetic differentiation between regions and sex-biased dispersal. We also use population genetic simulations to estimate the strength of intergenerational gene flow between regions and perform kinship analyses to characterise levels of relatedness among sharks from each region. Outputs from this study challenge the current paradigm regarding the connectivity and spatial ecology of Australian white sharks and provide an essential resource for managing this charismatic and functionally important marine predator.

## 2 | Methods

### 2.1 | Sample Collections

Tissue biopsies were collected from 501 juvenile and sub-adult white sharks (average total length = 2.45 m) from eastern Australia by the SMP team between 2015 and 2021 (Tate et al. 2019; Table S1). Individual sharks were captured using Shark-Management-Alert--in-Real-Time (SMART) baited drumlines, set daily by government contractors and scientists, approximately 500 m offshore and at depths of 8–22 m, and at 45 locations spanning the New South Wales coastline between Tathra (−36.723°, 149.993°) and Lennox Head (−28.789°, 153.604°). Upon capture, sharks were secured alongside the boat, physically tagged, and assigned a unique identification number and metadata including the time and location of capture, sex and body measurements (precaudal, fork and total length) were recorded (Table S1). Fin clips were taken from each individual and were placed in ethanol and stored at −20°C

until ready for sequencing. Additionally, muscle biopsies were collected from 152 adult and large subadult (average total length = 3.50 m) white sharks between November 2000 and June 2022 from five locations in South Australia (Figure 1; Table S1). Sharks were attracted to cage-diving or research vessels using a combination of attractants (bait and chum mixture) (Huveneers et al. 2013; Niella et al. 2023). Biopsies were taken from diving cages or from above the water's surface using a single 16–20 mm rubber 1.0–1.2-m spear gun, with a spear tip modified into a hollow 1-cm diameter stainless steel biopsy probe (Meyer, Fox, and Huveneers 2018), targeting the dorsal or upper flank musculature directly below the dorsal fin. Biopsies were immediately frozen (−20°C) and transported to the laboratory where white muscle tissue was dissected from the subdermal tissue and skin and stored in 100% ethanol until required for genetic analysis. Genetic samples from Western Australia were not available, but an ongoing acoustic tracking study assessing the residency of white sharks at the Neptune Islands, South Australia (Niella et al. 2023), is providing insights into the cross-jurisdictional movements between South Australia and Western Australia. Out of 180 white sharks tagged with acoustic tags, ~33% have been detected in Western Australia, while white sharks tagged in Western Australia have also been detected at the Neptune Islands (C. Huveneers, unpublished data). Previous acoustic and satellite tagging has also shown frequent movements between South Australia and Western Australia (Bradford et al. 2020; Spaet, Patterson, et al. 2020). In addition, genetic studies have also demonstrated a lack of population genetic structure and admixture between white sharks from South Australian and Western Australia (Blower et al. 2012; Davenport 2022). These observed movements and existing genetic datasets suggest that while additional genetic samples from Western Australia would be beneficial, sampling at the Neptune Islands is expected to be representative of the presumed southern-western subpopulation.

## 2.2 | DNA Extraction and SNP Genotyping

Total genomic DNA was extracted from 10 to 15 mg tissue from each sample by Diversity Arrays Technologies (DART Pty Ltd. Canberra, Australia) using a NucleoMag 96 Tissue Kit (Macherey-Nagel, Düren, Germany) coupled with NucleoMag SEP (Ref. 744,900) to allow automated separation of high-quality DNA on a Freedom Evo robotic liquid handler (TECAN, Männedorf, Switzerland). Sequencing for SNP genotyping was performed using the genome-wide and high-density DARTseq platform specifically developed for *C. carcharias* (Sansaloni et al. 2011). This technology uses a combination of genome complexity reduction methods, including a DNA digestion and ligation step using *pstI/nlaIII* restriction enzymes, followed by PCR and quantification (Kilian et al. 2012; Sansaloni et al. 2011). After this, samples were standardised, pooled for sequencing using an Illumina HiSeq2500 instrument, filtered and assembled using the DARTseq analytical pipeline. The DARTseq algorithm uses technical replicates to calculate genotyping reproducibility and Mendelian inheritance patterns to filter paralogous regions and sequencing errors (Kilian et al. 2012; Sansaloni et al. 2011).

Genotyping with the DARTseq platform yielded a total of 20,900 SNP markers. These were subsequently filtered, retaining only a single SNP per tag, removing secondaries and monomorphic

loci, applying a minimum minor allele frequency of 2%, reproducibility of 80% and a Hamming distance threshold of 0.2 to control for the influence of linkage disequilibrium between loci. For an initial assessment of relatedness among shark pairs, we applied a strict set of parameter settings, applying a locus and individual call rate of 90%. For estimates of population differentiation, following the correction for first- and second-degree relatives (discussed below), we applied a slightly less strict set of parameter settings, allowing locus and individual call rates to be 80%. All bioinformatic processing involving SNP calling was performed using the package *dartR* ver 1.9.9.1 (Gruber et al. 2018).

## 2.3 | Tests for Relatedness and Population Genetic Structure

We used two complementary analytical approaches to infer patterns of relatedness among individual white sharks. First, we used *SNPRelate* (Zheng et al. 2012), implemented within the R package (R Core Team 2021) to calculate relatedness between all shark pairs, with relatedness categories (first-, second- and third-degree relationships) inferred from co-ancestry coefficients ( $\theta$ ) and accompanying  $K_0$  and  $K_1$  coefficients (Table S2). Next, we used the R package *SEQUOIA* v2.0.7 (Huisman 2017) to assign pairs of individuals (dyads) to relationship categories (first- and second-degree relationships only) to all shark pairs. *SEQUOIA* provides a conservative hill-climbing algorithm to construct a high-likelihood pedigree from SNP genotypes. *SEQUOIA* is optimised for SNP datasets, jointly considers a variety of alternative relationship categories (e.g. grandparents/grand-offspring in addition to parents/offspring) and allows the consideration of more than two generations at a time. We performed *SEQUOIA* analyses by setting *MaxSibIter* to 20 and using the *GetMaybeRel* function. Following tests for relatedness, we generated a SNP data matrix corrected for relatedness for downstream tests of population differentiation, acknowledging the inclusion of genotypes from close relatives could bias estimates of genetic structure between regions. To achieve this, we randomly selected an individual for all first- and second-degree relative pairs and removed them from the data frame.

To control for sampling bias, we performed tests for population genetic differentiation on datasets including all sharks (both related and unrelated) and excluding related individuals (described above). To test for population genetic structure, we calculated descriptive statistics using the *Hierfstat* package version 7 (Goudet 2005), including allelic richness ( $r$ ) per population averaged over loci, observed ( $H_O$ ) and expected ( $H_E$ ) heterozygosity and Weir and Cockerham's inbreeding coefficients ( $F_{IS}$ ) and global estimate of population differentiation ( $F_{ST}$ ; Weir and Cockerham 1984) with 95% confidence limits determined using permutation (10,000). We also tested for private alleles using the *gl.report.pa* function in the package *dartR* ver 1.9.9.1 (Gruber et al. 2018). We subsequently used the *Poppr* package version 2.9.3 (Kamvar, Brooks, and Grünwald 2015) to perform an analysis of molecular variation (AMOVA), where variation was partitioned within and between regions (eastern and southern Australia). A graphical depiction of genetic structure among sampling locations was undertaken using Discriminant Analysis of Principal Components (PCA) implemented in the R



package *adegenet* (Jombart 2008; Jombart and Ahmed 2011) using the find clusters approach. In addition, a principal components analysis (PCA), also implemented in *adegenet* (ref), was used to summarise patterns of genetic differentiation between individuals across sampling locations. The first two principal components explaining the majority of variation across loci were plotted. Finally, we conducted a Bayesian analysis to estimate the number of population clusters within the SNP dataset using *STRUCTURE* (Pritchard, Stephens, and Donnelly 2000). *STRUCTURE* estimates the most likely number of distinct population clusters, assigns individuals to clusters and identifies migrants and admixed individuals using genetic data only. To determine the number of populations ( $K$ ), we ran ten independent simulations for  $K=1-5$  with 10,000 burn-in and 100,000 data iterations. We did the analyses using the admixture model of population structure (i.e. individuals draw some fraction of their genome from each of the  $K$  populations) and set allele frequencies as independent among populations. We estimated the most likely  $K$  using Evanno's delta  $K$  (Evanno, Regnaut, and Goudet 2005).

We tested for evidence of sex-biased dispersal using two separate analytical approaches. First, we conducted tests for genetic structure in male and female sharks separately. Sexes were partitioned prior to SNP filtering into separate genomic data frames, after which SNPs were called for each dataset following the procedures outlined above applying a locus and individual call rate of 80%. Again, the *Hierfstat* package version 7 (Goudet 2005), was used to generate global estimates of population differentiation  $F_{ST}$ ; (Weir and Cockerham 1984) for each dataset, with 95% confidence limits determined using permutation (10,000). Second, we used population assignment tests to provide further tests for evidence of sex-biased dispersal. Assignment tests were performed using empirical allele frequencies and sex data for all unrelated individuals and the *sex bias* function in the package *GenAlEx* v.6.6 (Peakall and Smouse 2006). This method generates an assignment index correction (AIC) value for each sex following the method of Mossman and Waser (1999). Sex-biased dispersal is indicated when there is a significant difference between the mean AIC values, where the more dispersive sex has a negative mean AIC value, and least dispersing sex shows a positive mean AIC. Analyses were performed on 500 randomly selected SNP loci (due to computational limitations of the programme) and significance was determined using a nonparametric Mann-Whitney test (Nachar 2008).

## 2.4 | Effective Population Size and Population Genetic Simulations

We calculated the genetic effective population size ( $N_e$ ; the number of breeding individuals) for the Australian white shark population using *NeEstimator* v.2.1 (Do et al. 2014). We conducted the analysis on the full dataset containing genotypes from both related and unrelated sharks, using the linkage disequilibrium method and random mating model, with parametric estimates of 95% confidence intervals. We also performed separate analyses on eastern (juvenile/subadult) and south-western (adult/large subadult) white sharks to determine potential intergenerational changes in  $N_e$ . Following this, we subsequently ran individual-based forward-time population genetic simulations in *simuPOP* (Peng and Kimmel 2005) using the model outlined in Lowell et al. (2023) to infer the likely numbers of effective migrants per generation required to drive our observed pattern of differentiation among eastern and southern Australian white sharks ( $F_{ST}=0.003$ , 95% CIs: 0.002–0.003). The most important assumptions of the model were as follows: fixed number of populations ( $n=2$ ) of equal size ( $N_e=250, 500, 1000$ ) that interact through specified migration rates by probability per generation ( $m=1\%, 5\%, 10\%, 20\%$  and  $30\%$ ). We chose this range of effective population sizes (250, 500, 1000) to account for various estimates generated here and in previous studies on white sharks (Blower et al. 2012; Blower et al. 2024). We initialised genotypes with observed (empirical) allele frequencies from all unrelated sharks at all independent SNP loci, assuming random mating. We ran simulations for 10, 50 and 100 generations of drift with 10 replicates, with global  $F_{ST}$  (Weir and Cockerham 1984) calculated from each subpopulation averaged over each replicate run.

## 3 | Results

### 3.1 | Tests for Relatedness and Population Genetic Structure

A total of 644 white sharks from New South Wales (499 sharks) and South Australia (145 sharks) were successfully genotyped with SNP calling for tests of relatedness yielding a total of 5367 SNP loci (Table S2). The assignment of relationship categories between all shark pairs was highly consistent between independent kinship analyses, including 99% and 83% agreement in the resolution of first- and second-degree relationships, respectively (Table S3), identifying 287

**TABLE 1** | Estimates of relatedness among 644 white sharks from eastern and southern Australia. Assigned relationship categories include; first-degree relationships, parent–offspring (PO) and full-sibling (FS); second-degree relationships, half-sibling (HS), grandparent (GP), niece/nephew (NN); third-degree relationships, cousins (CO).

Relationship category	Within eastern	Within southern	Between eastern and southern	Total relationships
1st degree (PO)	0	0	1	1
1st degree (FS)	275	12	0	287
2nd degree (HS, GP, NN)	511	29	23	563
3rd degree (CO)	770	52	55	877

full-sibling, 563 second-degree and 877 third-degree relationships (Table 1). Relatedness tests among southern Australian adult white sharks indicated 12 full-sibling relationships, 29 second-degree and 52 third-degree relationships from a total of 145 sharks. In contrast, a comparably higher frequency of closely related sharks was detected among eastern Australian juvenile-subadult sharks, including 275 full-sibling relationships, 511 second-degree and 770 third-degree relationships from a total of 499 sharks. Relatedness estimates between shark pairs from eastern and southern Australia indicated 1 first-degree (parent-offspring relationship), 23 second-degree and 55 third-degree relationships (Table 1).

Following the removal of related animals, a data frame consisting of genotypes representing 274 unrelated sharks (including 162 eastern and 112 southern Australian sharks) and 6253 SNP loci (Table S2) was used for tests of population genetic differentiation. We observed comparable levels of genetic diversity between sharks from eastern and southern Australia ( $r$ : 1.99 and 1.99;  $H_E$ : 0.25 and 0.26;  $H_O$ : 0.26 and 0.26 respectively) and limited genetic structure between regions ( $F_{ST}$ =0.003, 95% CIs: 0.002–0.003), further supported by a rarity of private alleles between regions (only four private alleles detected across all SNP loci). Similar values were observed when analyses were performed on all individuals (including both related and unrelated individuals;  $F_{ST}$ =0.004, 95% CIs: 0.003–0.005). Despite high levels of relatedness among sharks (particularly within eastern Australia) inbreeding coefficients did not differ significantly from zero when related individuals were excluded ( $F_{IS}$ =0.000 (eastern) and 0.028 (southern),  $p>0.05$ ) or included in the analyses ( $F_{IS}$ =0.000 (eastern) and 0.028 (southern),  $p>0.05$ ). AMOVA further supported the lack of significant SNP variation between regions (0.25%,  $p>0.01$ , while between-individual variation within regions explained 99.75%,  $p<0.01$ ). DAPC and STRUCTURE analyses also indicated a lack of differentiation between regions ( $K=1$ ; Figures S1 and S2). PCA also indicated a lack of differentiation between regions, with the first two principal components explaining only 1.6% of the total variation within the dataset, and individuals from both regions forming a single overlapping population cluster (Figure S3).

Our analyses indicated a lack of evidence for sex-biased dispersal in Australian white sharks. Genetic analyses conducted on female sharks consisted of 121 unrelated individuals (87 and 34 from eastern and southern Australia respectively) and 7401 SNP loci, while analyses performed on male sharks consisted of 146 unrelated individuals (75 and 71 from eastern and southern Australia respectively) and 6990 SNP loci. In both cases, we found limited genetic structure with both estimates of global  $F_{ST}$  being weak and close to zero (females,  $F_{ST}$ =0.002, 95% CIs: 0.002–0.003; males=0.003, 95% CIs: 0.003–0.004). Population assignment tests also indicated a lack of evidence for sex-biased dispersal with the differences in mean AIC scores between sexes being insignificant (females AIC=0.662, Std Err=0.558; males AIC=−0.722, Std Err=0.066;  $p=0.239$ ).

### 3.2 | Effective Population Size and Population Genetic Simulations

Given the lack of genetic structure observed among white sharks from eastern and southern, we pooled all genotypes (including

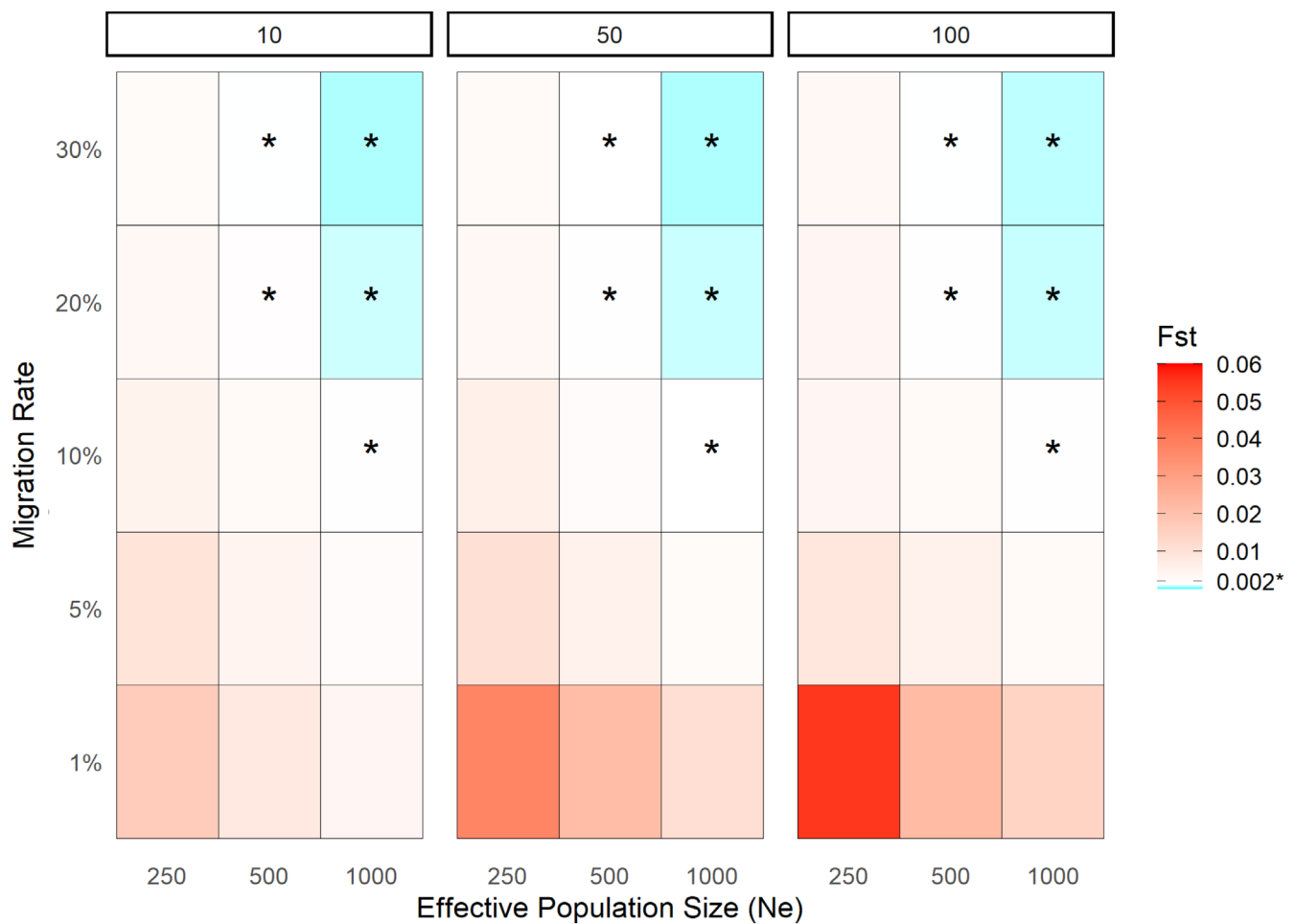
related sharks) from each region to estimate overall  $N_e$ , which was calculated to be 469 (95% CIs: 467–470). However, we detected notable differences in  $N_e$  when eastern (juvenile/subadult; 316, 95% CIs: 315–317) and southern (adult/large subadult; 545, 95% CIs: 540–550) white sharks were separated for analysis pointing to possible intergenerational reductions in  $N_e$ . We subsequently used this information to inform population simulations to test the effect of various levels of gene flow on genetic structuring in Australian white sharks (Figure 2). Based on an  $N_e$  of 250–500, according to our current study and (Blower et al. 2024), a theoretical effective migration rate of at least 20% (and potentially >30%) per generation is required to achieve an  $F_{ST}$  equal to our observed global estimate of 0.003 (95% CIs: 0.002–0.003).

## 4 | Discussion

Our study represents the most comprehensive assessment of population genetic structure in Australian white sharks, making use of a high-density panel of genomic SNP loci and large sample sizes made possible by two long-term white shark monitoring programmes. These resources allowed us to overcome some of the limitations of previous genetic studies and to gain new insights into the strength of biological connections between white sharks from eastern and southern Australia. Overall, we observed weak evidence for genetic structure between sharks from eastern and southern Australia, with no evidence for sex-biased dispersal. Most analyses indicate a single panmictic population, although a very low, but significant estimate of genetic differentiation ( $F_{ST}$ ) was observed. Our simulations suggest that frequent gene flow and intergenerational migration between these regions is likely contributing to this pattern of weak differentiation, which is further supported by the detection of related sharks between regions. Collectively, these findings indicate white sharks from eastern and southern Australia treated as a single panmictic population for management purposes. Finally, we provide further evidence for high levels of relatedness between white sharks from eastern Australia, estimate the overall effective population size ( $N_e$ ) of Australian white sharks to be less than 500, and detect a potential reduction in  $N_e$  over the last two generations, raising concerns for the conservation of the species in Australia. Overall, these findings challenge the previous evidence of population structure in Australian white sharks and highlight the need for revised management and conservation approaches.

### 4.1 | Biological Connections Between Australian White Sharks

We provide multiple lines of evidence pointing to a single panmictic population of white sharks across Australia. Our analyses indicate limited genetic structuring among white sharks from eastern and southern Australia with our estimates of population differentiation being similar to those reported in previous studies ( $F_{ST}$ =0.009, Blower et al. 2012;  $F_{ST}$ =0.001, Davenport 2022). Despite correcting for relatedness among shark pairs, we found that this had little effect on estimates of genetic structure (all sharks included,  $F_{ST}$ =0.004; related sharks excluded,  $F_{ST}$ =0.003), suggesting that previous estimates of genetic structure are also unlikely to be biased. Our



**FIGURE 2** | Simulated effects of varying number of white sharks (*Carcharodon carcharias*) migrants per generation on global  $F_{ST}$  among eastern and southern Australia ( $n=2$ ) with effective population sizes ( $N_e$ ) of 250, 500 and 1000, and simulations run for 10 generations (left), 50 generations (centre) and 100 generations (right). \* indicates where the predicted  $F_{ST}$  is less than the observed  $F_{ST}$  value of 0.003 (95% CIs: 0.002–0.003).

population genetic simulations suggest that the magnitude of  $F_{ST}$  observed by our and previous studies can be obtained despite substantial gene flow between eastern and southern Australia, with our conservative estimates being 20% migration per generation (assuming an  $N_e$  of 500, estimated in the current study), and possibly exceeding 30% (assuming an  $N_e$  of approximately 250 as indicated by (Blower et al. 2024)). Furthermore, we demonstrate a large number of related individuals between regions, providing further evidence for biological connections between eastern and southern Australia, and supporting the recognition of a single panmictic population. We acknowledge that genetic structure relating to Western Australia or Queensland cannot be discounted due to samples from these regions being unavailable. Samples from these locations would have assisted in assessing spatial patterns of gene flow across the Australia-wide white shark distribution. However, a substantial body of literature based on genetic and tracking studies points to white sharks from southern and western Australia, and across the east coast being connected and mixed gene pools (Blower et al. 2012; Bradford et al. 2020; Bruce et al. 2019; McAuley et al. 2017; Rogers and Drew 2018; Pardini et al. 2001; Spaet, Patterson, et al. 2020; Spaet, Butcher, et al. 2022). Consequently, our findings point to Australian white sharks being panmictic across their distribution.

Despite our findings indicating a lack of genetic structure among Australian white sharks, several early telemetry studies suggested limited movement of white sharks between southern-western and eastern Australia (Bradford et al. 2020; Bruce and Bradford 2012; McAuley et al. 2017). However, several factors might have biased the abilities of previous telemetry studies to record frequent movements between these regions. While the number of acoustic receivers deployed in Australia has grown over the last decade through the Integrated Marine Observing System (IMOS), which enables large-scale collaborative animal tracking research (Hoenner et al. 2018; Brodie et al. 2018), some of these studies reported movements based on detections from their regional study sites only rather than large-scale movements. For example, McAuley et al. (2017) did not report on detections of sharks tagged in New South Wales, while limited acoustic receivers were deployed in South Australia at the time of the study by Bruce and Bradford (2012). Some of these tracking studies were based on a relatively small sample size (e.g.  $n=22$ , Bruce and Bradford 2012;  $n=43$  Bradford et al. 2020), which is sufficient for describing movement patterns on local and regional scales (Sequeira et al. 2019), but might be insufficient to assess the extent of movement patterns and connectivity between eastern and southern-western regions. However, more recent tracking studies indicate that inter-regional movement

of white sharks is more common than previously assumed. For example, Spaet, Patterson, et al. (2020) revealed one white shark caught in northern NSW to travel north into southern Queensland before heading south to Western Australia and back to northern NSW three times over a 3-year period, as well as several white sharks also caught in northern NSW venturing into southern ocean waters. Bradford et al. (2020) reported that white sharks tagged at the Neptune Islands and in Spencer Gulf in South Australia travelled to both the western and eastern coasts of Australia, including Tasmania, and reached the southern waters of New Zealand (Bradford et al. 2020; Rogers and Drew 2018). Furthermore, recent studies show that a number of acoustically tagged white sharks are migrating between eastern and southern-western Australia (Spaet, Patterson, et al. 2020). Consequently, multiple lines of evidence now point to a lack of population subdivision in Australian white sharks.

This combined evidence for panmixia raises the possibility of life stage structuring in Australian white sharks, where adults and juveniles have largely nonoverlapping distributions. Tracking studies to date have been biased towards different life stages across the two regions, with a bias towards juveniles and small subadults in eastern Australia and large subadults and adults in southern-western Australia (Bruce and Bradford 2012; McAuley et al. 2017; Spaet, Butcher, et al. 2022). This is largely due to the rare abundance of adult white sharks (over 3.5 and 4.5 m total length for males and females respectively) in eastern Australia (Spaet, Manica, et al. 2020; Tate et al. 2021) and comparatively low frequencies of juveniles (<3 m total length) in southern-western Australia (Robbins and Booth 2012). Even if small juveniles occur in southern-western Australia, with several possible hotspots having been identified (e.g. O'Connell et al. 2023), they do not appear to be in the same concentration or abundance as seen in eastern Australia. Indeed, many studies have demonstrated nonrandom aggregations of white sharks of similar age and size classes, which have been linked to differences in resource and habitat requirements of different life stages (Anderson, Clevestine, et al. 2021; Schilds et al. 2019). However, distinctive distributions between adult and juvenile white sharks in Australia have not been previously recognised but help to explain the discrepancy between the present study and previous tracking studies.

Although our study points to a single panmictic population of white sharks in Australia, the spatial boundaries of the population still remain uncertain and require further investigation. Evidence from previous genetic and telemetry studies suggest at least weak biological connections between sharks from southern-western Australia and South Africa, and connections between eastern Australia and New Zealand, but a lack of connectivity between white sharks from the northern and southern hemispheres (Andreotti et al. 2016; Bernard et al. 2018; Davenport 2022; Jorgensen et al. 2010; O'Leary et al. 2015). Our study highlights the need for a reassessment of the global population genetic structure in white sharks. Although there have been some attempts over the last two decades, most have been limited by small sample sizes and a dependency on small numbers of traditional genetic markers. More rigorous assessments using larger sample sizes, targeted spatial sampling and modern genomic approaches will therefore greatly assist in resolving

intercontinental and global patterns of biological connectivity in white sharks.

## 4.2 | Lack of Evidence for Sex-Biased Dispersal

Contrary to previous reports, we found no evidence for sex-biased dispersal in Australian white sharks. Pardini et al. (2001) first reported evidence of male-biased dispersal among white sharks from the Pacific and Indian Ocean basins using a combination of maternally inherited mitochondrial haplotype and biparentally inherited microsatellite data. More recently, Blower et al. (2012) used the same analytical approach to report possible male-biased dispersal in Australian white sharks, providing evidence of genetic structure among female sharks from eastern and southern Australia. In contrast, our analyses indicate a lack of genetic structure in both male and female Australian white sharks, challenging the notion of sex-biased dispersal. This discrepancy is likely due to differences in genetic marker systems with varying sensitivities for resolving contemporary patterns of gene flow and population genetic structure. Estimates obtained using uniparentally inherited loci, such as mitochondrial and chloroplast DNA, may not reflect contemporary population structure due to slow mutation rates and the possible influence of both selection and nonauthentic nuclear orthologues (Allendorf 2016; Ballard and Pichaud 2014; Churchill Cihlar et al. 2020). More recently, high-density biparentally inherited markers (i.e. SNP loci) have been shown to be effective and reliable for tests of sex-bias dispersal (including in elasmobranchs), overcoming some of the limitations of uniparentally inherited loci (Banks and Peakall 2012; Phillips et al. 2021). Despite these limitations, unpublished findings from Davenport (2022) support our conclusions in providing evidence of a lack of mitochondrial differentiation between eastern and southern Australian white sharks. Specifically, Davenport (2022) demonstrated shared mitochondrial haplotypes between regions and the formation of a single mixed mitochondrial clade based on haplotype network analyses and substantially larger sample sizes compared to previous studies.

Our findings are further corroborated by several tracking studies from Australia that point to both male and female white sharks making inter-regional migrations and being equally vagile (e.g. Bradford et al. 2020; Rogers and Drew 2018; Spaet, Manica, et al. 2020; Spaet, Patterson, et al. 2020). Specifically, Bradford et al. (2020) reported no statistical difference in the overall length of tracks between male and female white sharks (both sexes having similar longitudinal ranges of ~4000 km), while Spaet et al. (2020) provided evidence of both male and female juvenile/subadults tagged off the east coast of Australia venturing into southern ocean waters. Collectively, these findings point to a lack of sex-biased dispersal in Australian white sharks.

## 4.3 | High Levels of Relatedness Among Juvenile and Subadult White Sharks

Our analyses are consistent with Blower et al. (2024) in revealing a concerning high degree of relatedness among juvenile and subadult white sharks from eastern Australia but also shows



that the degree of relatedness among adults and large subadult white sharks from southern Australia was markedly less notable. White sharks are long-lived animals with a maximum life span of up to 73 years (Hamady et al. 2014) and a generation time of approximately 23 years (Mollet and Cailliet 2002). Therefore, it is possible that the observed low levels of relatedness among the adult population are a relic of the past and historical levels of relatedness in the population prior to the declines during the 1970s and 1980s (Roff et al. 2018). It is possible that we are now observing signs of inbreeding in the juvenile and subadult white sharks, which are likely to be second- and third-generation offspring since the population crash. While significant inbreeding coefficients were not observed, this is expected as there has been limited generational turnover since the population crash and opportunities for drift and potential inbreeding to influence allele frequencies and genetic diversity at the population level. Risks of inbreeding are plausible given the low overall  $N_e$  estimates of 400–500, which is similar to those previously reported for eastern Australian white sharks (Blower et al. 2012). More recently, Blower et al. (2024) conducted rigorous assessments of  $N_e$  in Australian white sharks indicating that  $N_e$  could be less than 300, highlighting the possible vulnerability of Australian white sharks to risks of inbreeding and genetic drift, and reductions in population fitness. We build on the findings of Blower et al. (2024) detecting a potential reduction in  $N_e$  over the last two generations (juvenile/subadult population,  $N_e = 316$ ; adult/large subadult population,  $N_e = 545$ ). These findings require more rigorous examination in line with Blower et al. (2024), but further emphasise the possible susceptibility of the population to negative demographic processes. Collectively, these findings have significant implications for the conservation status of white sharks in Australia and highlight the need for further research and ongoing population monitoring.

#### 4.4 | Management Implications

This new paradigm in the population structure of the Australian white shark is pertinent when assessing the potential impacts of current and emerging threats, and the suitability of management responses. Existing threats to white sharks are spatially diverse across Australia, including commercial fisheries (i.e. bycatch), illegal hunting and bather protection programmes (targeted culling and netting operations), wildlife tourism and expansion of offshore infrastructure (Niella et al. 2023; NSW Department of Primary Industries 2023; Qld Department of Agriculture and Fisheries 2020). While commercial fishing was historically recognised as a key threat to the species, targeting of sharks by this sector in Australia has been reduced to extremely low levels over the last decade. Furthermore, bycatch of this species by commercial fishers is unlikely to be a key threat to the recovery of the Australian white shark population (Macbeth et al. 2009; Macbeth and Grey 2015). Considering our findings, localised threats should be considered a potential risk to the entire Australian white shark population rather than a single subpopulation. Similarly, white shark monitoring programmes should assume trends in population abundance observed at regional scales to be reflective of range-wide trends at the continental scale (Blower et al. 2024; Hillary et al. 2018). However, the apparent structuring between the two regions based on life stages (primarily juvenile and small subadults on the east coast and

large subadults and adults in southern-western Australia), leads to differences in age, maturity stage, diet, habitat use and movement patterns (Clark et al. 2023; Nazimi et al. 2018; Robbins and Booth 2012; Bruce and Bradford 2015). While white sharks of a broad size range, that is, from young-of-the-year to large adults, can be found in both regions, the predominant ontogenetic variation between regions remains an important management consideration and complicates population-wide assessments. Further studies assessing population connectivity at the ecological scale (e.g. via tracking studies) rather than evolutionary scale (e.g. via genetic studies) would help further elucidate the population dynamics of white sharks in Australia.

## 5 | Conclusions

Understanding the biological connections across species' ranges is essential for informing biodiversity management, including conservation planning for vulnerable species. Despite efforts to characterise these connections among the world's white shark populations, patterns of connectivity within and between ocean basins remain uncertain and continue to hinder the management. Making use of a large collection of tissue samples and modern genotyping approaches, we demonstrate that white sharks from eastern and southern Australia constitute a single panmictic population, challenging previous evidence of population subdivision. These findings highlight the importance of large sample sizes and large panels of genomic markers for resolving patterns of genetic structure and provide a resource for the spatial management and conservation of this important marine predator.

#### Author Contributions

This project was conceptualised by Adam D. Miller, Paul A. Butcher, Craig D. H. Sherman and Andrew R. Weeks. Sampling of shark biopsies was led by Paul A. Butcher and Charlie Huvaneers, while genotyping was undertaken by Zach S.R. Clark, Jessica J. Fish and Adam D. Miller with bioinformatic support from Owen J. Holland and Madeline Toomey. Writing of the manuscript was led by Zach S.R. Clark and Adam D. Miller with assistance from all authors.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

All genomic datasets are publicly available in the DRYAD archives ([10.5061/dryad.51c59zwb](https://doi.org/10.5061/dryad.51c59zwb)).

## Peer Review

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## Supporting Information

Additional supporting information can be found online in the Supporting Information section.