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Novel multimarker comparisons address the genetic population structure of silvertip sharks (*Carcharhinus albimarginatus*)

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Abstract. The silvertip shark (*Carcharhinus albimarginatus*) is a reef-associated shark, with an intermittent distribution across the Indo-Pacific Ocean. Owing to global declines, the species is listed as Vulnerable under the International Union of Conservation for Nature Red List. Samples from 152 *C. albimarginatus* were collected from three locations: Papua New Guinea (PNG), east Australia and Seychelles. Samples were analysed using mitochondrial, microsatellite and double-digest restriction-associated DNA (ddRAD) generated single nucleotide polymorphism markers. As expected across a vast oceanic expanse, no gene flow was identified between south-west Pacific locations and Seychelles for any marker (population differentiation measured using Φ_{ST} values 0.92–0.98, F_{ST} values 0.036–0.059). Mitochondrial DNA indicated significant population structuring between PNG and east Australia ($\Phi_{ST} = 0.102$), but nuclear markers suggested connectivity between these geographically close regions ($F_{ST} = 0.000$–0.001). In combination with known telemetry movements for *C. albimarginatus*, our results suggest stepping-stone patterns of movement between regions is likely driven by reproductive requirements. The use of three distinct marker types in this study has facilitated a powerful genetic description of the population connectivity of *C. albimarginatus* between the three sampled regions. Importantly, the connectivity described between PNG and east Australia should be used as a guide for managing the south-west Pacific stock of *C. albimarginatus*.

Additional keywords: elasmobranch, fisheries management, microsatellite, mitochondrial DNA, reef shark, population genetics, single nucleotide polymorphisms.

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Introduction

Defining the scale of connectivity among marine populations and identifying the factors driving the exchange of individuals is pivotal to our understanding of population dynamics (Cowen *et al.* 2006). Understanding how and why animals move (or remain resident) is essential for conservation ecology, with such knowledge directly applied to spatial management planning (Palumbi 2003; Espinoza *et al.* 2014). Species that exhibit migrations across jurisdictional boundaries or beyond national jurisdictions altogether can complicate management efforts because international cooperation is required (Ovenden *et al.* 2015; Hays *et al.* 2016; Chin *et al.* 2017).

Genetic methods are commonly used to examine the stock structure and connectivity of wild species to assist management and conservation planning (Knutsen *et al.* 2003). Genetic tools (in the form of 'markers') can uncover a variety of biological information important for connectivity and population structure estimates (Ovenden *et al.* 2015). Markers widely used for population genetic studies include short regions of mitochondrial (mt)DNA (Avise 2012) and nuclear microsatellite loci (Selkoe and Toonen 2006). Advances in next-generation sequencing technology enable the screening of loci across whole genomes and multiple individuals, thereby providing geneticists access to thousands of loci commonly in the form of single point mutations referred to as single nucleotide polymorphisms (SNPs; Morin *et al.* 2004). SNPs are increasingly being used for population structure studies (Morin *et al.* 2004; Hess *et al.* 2011; Jeffries *et al.* 2016; Momigliano *et al.* 2017; Pazmiño *et al.* 2018); however, their biallelic nature means that SNPs contain less information per locus then multiallelic microsatellites (Coates *et al.* 2009).

Nevertheless, in studies where thousands or more SNP loci are used, they are proving powerful enough to resolve fine-scale population structure (Rosenberg *et al.* 2003; Morin *et al.* 2004; Liu *et al.* 2005; Rašić *et al.* 2014; Vendrami *et al.* 2017).

Depending on the marker selected, genetics can explore historic and contemporary population patterns as well as compare differences in male and female connectivity among populations (Feutry *et al.* 2017). One of the most important genetic measurements for marine spatial management is estimating the level of connectivity among populations. The extent of genetic subdivision identified in a population can help define the geographic boundary of a stock (Nielsen *et al.* 2009; Allendorf *et al.* 2010; Ovenden *et al.* 2015). The application of population genetics has been successful in uncovering genetic stock structures and providing robust estimates for spatial management in many marine species (Appleyard *et al.* 2002; Blaber *et al.* 2005; Salini *et al.* 2006; Ovenden *et al.* 2009; Horne *et al.* 2011; Pazmiño *et al.* 2018). The silvertip shark *Carcharhinus albimarginatus* is one species that will benefit from connectivity assessments because of its discontinuous distribution in the Indo-Pacific and recent global population declines (Espinoza *et al.* 2016). Occurring on continental shelves, offshore islands and coral reefs, *C. albimarginatus* inhabits tropical waters to depths of 800 m (Bond *et al.* 2015). Listed as Vulnerable under the International Union for Conservation of Nature (IUCN) Red List, globally *C. albimarginatus* has undergone a rapid decline in biomass of a predicted 30% over 54 years, as estimated from survey data (Espinoza *et al.* 2016). Declines are attributed to heavy fishing pressure from longline, gill net and purse seine fisheries throughout its range (Bond *et al.* 2015).

In Australia, *C. albimarginatus* is the second most commonly sighted shark species within the Great Barrier Reef (GBR; Heupel *et al.* 2009). Although not targeted, it is predicted that *C. albimarginatus* makes up bycatch in commercial and recreational coral trout line fisheries along the east coast of Australia (Heupel *et al.* 2009) and have also been identified during examination of illegal, unreported, unregulated (IUU) fishing practises in northern Australia (Marshall 2011). In locations such as Papua New Guinea (PNG), *C. albimarginatus*, along with many other species of sharks, is caught in greater numbers than in Australia (Kumoru 2003; White 2007). Connectivity of *C. albimarginatus* in the region is not well understood, making management challenging given the differences in catch rates between Australia and PNG.

To test the extent of connectivity among regional locations and improve our understanding of the genetic structure of *C. albimarginatus*, we analysed genetic variation in mtDNA, microsatellites and SNPs. By using combinations of mitochondrial and nuclear DNA markers, our understanding of genetic subdivision in broadly distributed marine species has advanced rapidly (Waples 1998; Hellberg *et al.* 2002). For sharks in particular, microsatellites have been a popular marker for delineating contemporary genetic structure (Keeney *et al.* 2003; Feldheim *et al.* 2007; Karl *et al.* 2011; Daly-Engel *et al.* 2012; Bernard *et al.* 2016). Recently, however, there has been a rise in the number of studies using suites of SNPs to measure genetic variation in the nuclear genome (Momigliano *et al.* 2017; Pazmiño *et al.* 2018). Ongoing improvements in sequencing technology enable thousands of genome-wide SNPs to be easily screened (Baird *et al.* 2008; Sansaloni *et al.* 2011; Peterson *et al.* 2012), with many studies finding the informativeness and power of SNPs to be high (Rosenberg *et al.* 2003; Morin *et al.* 2004; Liu *et al.* 2005; Rašić *et al.* 2014; Vendrami *et al.* 2017).

Previous genetic studies of *C. albimarginatus* have primarily focused on identifying the species within fish markets (Liu *et al.* 2013); as such, no population genetic assessment has been undertaken for the species. In this study we collected samples from three Indo-Pacific Ocean countries, namely Seychelles, PNG and Australia, to identify what level of connectivity or genetic stock structure was occurring between these nations, each with varied capacities for fisheries exploitation and management. The patchy and isolated distribution of *C. albimarginatus* throughout its range suggests that each location could be a distinct population, in which case connectivity would be low. Based on findings from telemetry studies (Espinoza *et al.* 2015*a*) and similar population genetic assessments of reef shark species (Vignaud *et al.* 2014; Pazmiño *et al.* 2017), we expected gene flow to be restricted between our three sampled locations.

Materials and methods

Sample collection and DNA extraction

In all, 152 *C. albimarginatus* DNA samples were obtained from three locations across the Indo-Pacific (Fig. 1). These locations were chosen to focus on the cross-jurisdictional management of *C. albimarginatus* between PNG and Australia. One distant location (Seychelles) was selected to provide contrast to the south-west Pacific locations. Collection from Seychelles and east Australia occurred at one and two sites respectively, whereas PNG samples were obtained from several sites throughout the Bismarck and Solomon seas (Fig. 1). Throughout 2015–16, samples from PNG were collected on board fishing vessels, from fish markets and local villages by observers. Fisheries-independent samples from Seychelles and east Australia were collected between 2013 and 2017 by researchers from Environment Seychelles and James Cook University respectively. A fin clip was taken, with individuals subsequently released. For sharks landed by commercial and artisanal fishers, a piece of vertebrae chord or muscle was collected. Associated biological data were also collected for each individual, including sex, total length (TL) and maturity stage.

DNA was extracted using the Wizard SV Genomic DNA Purification system (Promega, Sydney, NSW, Australia); tissue extractions were undertaken using SV minicolumns (Promega) with some modification to the manufacturer's instructions (i.e. overnight tissue digestion at 55˚C, 30 µL of supernatant used to elute the DNA and DNA elution times were increased by 2 h). Total genomic gDNA was eluted in DNase-free water and quantified (ng μL^{-1}) on a NanoDrop 8000 (Thermo Fisher Scientific, Melbourne, Vic., Australia), after which the DNA concentration was standardised to 15–25 ng of gDNA.

Mitochondrial DNA

To characterise similarity among and between samples from various locations, we amplified 994 bp of the mtDNA control region (CR) using the forward primer PRoL2 and reverse primer PheCacaH2 (Pardini *et al.* 2001). Polymerase chain reactions (PCR) were conducted in 25-µL reaction volumes with 15–25 ng of gDNA, GoTaq Green Master Mix (Promega, Madison, WI,

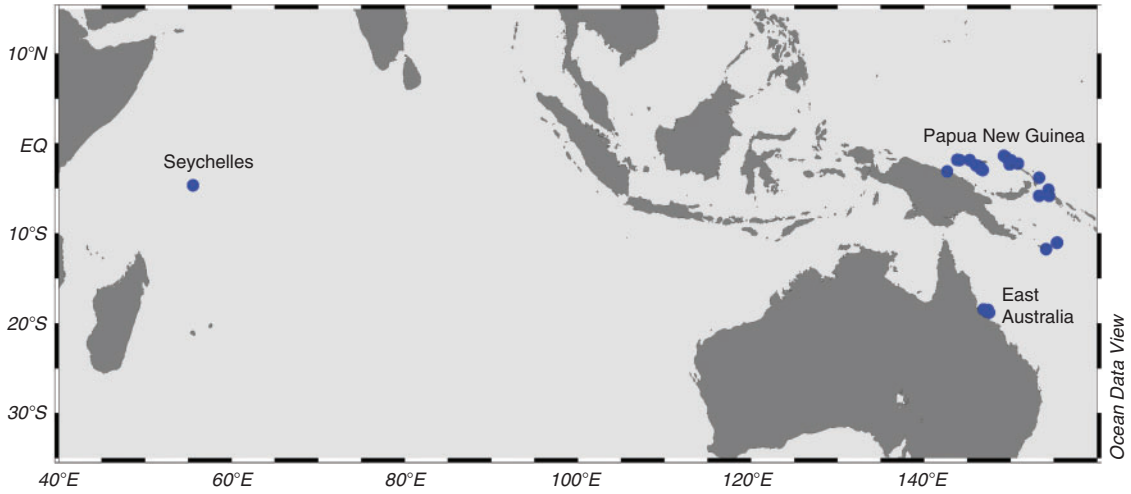

Fig. 1. Sample collection for *Carcharhinus albimarginatus* within the Indo-Pacific Ocean. West Indo-Pacific location: Seychelles; south-west Pacific locations: Papua New Guinea and east Australia. Circles represent sample collection sites.

USA), 1 μL of bovine serum albumin (Promega) and 10-μM primers. The PCR used the following thermocycler parameters: initial hold at 94°C for 5 min, followed by 35 cycles of 94°C for 30 s, 58°C for 30 s and 72°C for 1 min, with a final extension of 72°C for 10 min. Successfully amplified PCR products were sequenced bidirectionally using a BigDye Terminator Cycle Sequencing Kit (ver. 3.1; Invitrogen Life Technologies, Carlsbad, CA, USA) and an annealing stage of 58°C for 5 s for 25 cycles. Cycled sequence products were cleaned using a CleanSEQ kit (Beckman Coulter, Sydney, NSW, Australia) and run on an ABI 3130XL AutoDNA sequencer (Applied Biosystems, Foster City, CA, USA) at the CSIRO Marine Laboratories (Hobart, Tas., Australia). Sequences were screened and aligned using Geneious (ver. 10.2.3, Biomatters, Auckland, New Zealand). Molecular diversity indices, including haplotype and nucleotide diversities, were calculated using Arlequin (ver. 3.5, see http://cmpg.unibe.ch/software/arlequin35/; Excoffier and Lischer 2010). To visualise haplotype structure between locations, median-joining network analysis was constructed using POPart (ver. 1.7, see http://popart.otago.ac.nz, accessed 13 March 2018; Bandelt *et al.* 1999).

Microsatellites

Microsatellite loci were one of two types of codominant, biparentally inherited markers used to test for population distinctiveness among individuals across sample locations. Samples were genotyped using 12 newly designed polymorphic microsatellite loci, as outlined in the Supplementary material, the methods of which included next-generation sequencing microsatellite loci detection, characterisation and optimisation of microsatellite primers (including GenBank accession numbers; see Table S1 of the Supplementary material). In order to accurately size alleles, amplified products were run alongside GeneScan 500 Liz on an ABI 3130XL AutoDNA sequencer (Applied Biosystems) in the CSIRO Marine Laboratories. Genotypes were scored using the Microsatellite plug-in in Geneious (ver. R10.2.3, Biomatters). Allele frequencies are given in Table S2 of the Supplementary material. MICRO-CHECKER (ver. 2.2.3, see http://www.nrp.ac.uk/nrp-strategic-alliances/elsa/software/microchecker/; Van Oosterhout *et al.* 2004) was used to check for potential scoring errors and the presence of null alleles. At each locus and location, we calculated the number of alleles (n_A), expected (H_E) and observed (H_O) heterozygosities, allelic richness (A_R), fixation indices (F_{IS}) and deviations from Hardy–Weinberg Equilibrium (HWE) using the R package '*diveRsity*' (see https://cran.r-project.org/web/packages/diveRsity/index.html; Keenan *et al.* 2013; Table 1; Table S3 of the Supplementary material). To detect non-random associations of alleles among multiple loci, exact tests for linkage disequilibrium were undertaken using GENEPOP on the web (ver. 4.2, see http://genepop.curtin.edu.au/; Raymond and Rousset 1995).

Single nucleotide polymorphisms

We used a reduced-representation next-generation sequencing approach to obtain SNPs from across the *C. albimarginatus* genome. We sent gDNA to the Australian Genome Research Facility (AGRF; www.agrf.com.au, accessed 1 December 2018) for library preparation (including ligation of barcoded adapters, size selection of pooled digested–ligated fragments and amplification of libraries by PCR using indexed primers) and sequencing according to their in-house genotype-by-sequencing (GBS) methodology (Elshire *et al.* 2011). This is a reduced representation approach similar to double-digest restriction-associated DNA (ddRAD; Peterson *et al.* 2012), which sequences short sections of the genome selected from restriction enzyme cut sites (the enzymes *Pst*I and *Mse*I were used). The libraries from each of the two plates of DNA were sequenced on four lanes of an Illumina NextSeq 500 platform flow cell (Illumina, San Diego, CA, USA) with 150 cycles in mid-output mode resulting in over 410 million 100-bp single-end reads. AGRF processed the raw reads using their in-house STACKS pipeline (ver. 1.47, see http://catchenlab.life.illinois.edu/stacks/; Catchen *et al.* 2013). The STACKS program aligns sequence reads into matching stacks from which loci are formed and SNPs are detected. The parameters used to define a 'stack' were as follows: minimum depth coverage of two (m), one mismatch

Table 1. Summary of various measures of genetic diversity for mitochondrial (mt)DNA, microsatellites and single nucleotide polymorphism (SNP) datasets across the three *Carcharhinus albimarginatus* sampling locations

The table describes, for each location, the number of individuals successfully amplified per marker (*n*), the observed (H_O) and expected (H_E) heterozygosity, the number of polymorphic sites (S; for SNPs, one site equals one locus), number of haplotypes (H), haplotype diversity (*h*), nucleotide diversity (π; given as the mean ± s.d.), allele richness (A_R) and the inbreeding coefficient (F_{IS}). The total number of individuals collected is given with the location name

	Seychelles ($n = 31$)	Papua New Guinea ($n = 98$)	East Australia ($n = 23$)
mtDNA CR 994 bp			
n	26	75	19
S	1	8	1
H	2	12	2
h	0.073	0.818	0.498
π ($\times 10^2$)	0.007 ± 0.017	0.14 ± 0.10	0.05 ± 0.05
Microsatellites (12 loci)			
n	30	64	23
A_R	3.63	4.7	4.67
H_O	0.393	0.446	0.434
H_E	0.366	0.466	0.457
F_{IS}	−0.08	0.105	0.072
SNPs (6461 loci)			
n	20	53	19
S	4128	4965	6014
A_R	1.95	1.95	1.95
H_O	0.13	0.127	0.126
H_E	0.152	0.142	0.139
F_{IS}	0.115	0.095	0.067

allowed between sample tags (n), a minimum of five reads to call a homozygote and a minor allele frequency per stack of 0.05–1 for calling heterozygotes. All resulting SNPs were further filtered using R packages '*vcfR*' (see https://cran.r-project.org/web/packages/vcfR/index.html; Knaus and Grünwald 2017), '*adegenet*' (see https://cran.r-project.org/web/packages/adegenet/index.html; Jombart 2008) and '*dartR*' (see https://cran.r-project.org/web/packages/dartR/index.html; Gruber *et al*. 2018) according to the following criteria: (1) only one SNP per tag; (2) average read depth >5; (3) no missing data per SNP; (4) minor allele frequency >0.02; (5) no loci out of HWE; and (6) heterozygosity per individual between 0.11 and 0.18. This heterozygosity threshold was selected because of excessive low and high heterozygosity likely representing poor DNA quality or sample contamination respectively (see Fig. S1 of the Supplementary material). Step-wise filtering and SNP retention is described in Table S4 of the Supplementary material. Missing data per SNP were filtered step-wise; first, SNPs were filtered with a 30% missing data threshold, after which they were filtered again with no missing data threshold at the end of the filtering process (Table S4). This was to reduce the number of SNPs in the final suite and decrease computation time. Summary statistics, including H_E and H_O, F_{IS} and A_R, were calculated using R package '*diveRsity*' (Keenan *et al.* 2013).

Power analyses

In order to determine the theoretical statistical power of the microsatellite and SNP loci to resolve genetic differentiation, we ran a power analysis using POWSIM (ver. 4.1, see http://internt.zoologi.su.se/~ryman/; Ryman and Palm 2006). The settings of effective population size (N*e*) and generations of drift (t) were selected to represent F_{ST} values generated from pairwise comparisons identified in this study (for the F_{ST} equation, see Ryman and Palm 2006). Empirical allele frequencies used in POWSIM calculations for microsatellites and SNPs were identified using the R package '*PopGenReport*' (see https://cran.r-project.org/web/packages/PopGenReport/index.html; Adamack and Gruber 2014). The parameters of the Markov chain were fixed to 10 000, 1000 and 10 000 for dememorisations, batches and iterations per run respectively. A total of 1000 replicates of each run was completed for microsatellites, and 200 replicates were completed for SNPs.

Population structure

In order to test for genetic homogeneity between locations, we calculated the pairwise fixation indices, Φ_{ST} for mtDNA and F_{ST} for the nuclear markers (microsatellites and SNPs) using Arlequin (ver. 3.5) and the R package '*StAMPP*' (see https://cran.r-project.org/web/packages/StAMPP/index.html) respectively (Excoffier and Heckel 2006; Pembleton *et al.* 2013). Each analysis consisted of >10 000 bootstraps generating confidence intervals and *P*-values for each pairwise comparison. Significance levels of all pairwise tests were corrected for multiple comparisons with a sequential Bonferroni procedure (BF $P =$ conventional *P*-value 0.05 divided by the number of tests per marker type; Rice 1989).

To estimate the number of genetic groups based on the microsatellite data, we used Bayesian algorithms implemented in STRUCTURE (ver. 2.3.4, https://web.stanford.edu/group/pritchardlab/structure_software; Pritchard *et al.* 2000).

STRUCTURE analysis was run using an admixture model with correlated allele frequencies, a burn-in length of 50 000 followed by 1 000 000 Markov Chain Monte Carlo with K (number of clusters) set between 1 and 7, with 8 runs for each K value. Given STRUCTURE's inability to accurately cluster individuals to populations at low levels of differentiation (Latch *et al.* 2006), as is the case for east Australian and PNG comparisons, a LOCPRIOR approach similar to that of Falush *et al.* (2003) was used with *a priori* location information. In addition, to overcome our unbalanced sample sizes, an alternative ancestry prior of $\alpha = 0.33$ was used, as suggested by Wang (2017).

Estimation of the number of genetic groups identified with SNP loci was undertaken using maximum likelihood algorithms in ADMIXTURE (see http://software.genetics.ucla.edu/admixture/; Alexander and Lange 2011). ADMIXTURE estimates individual ancestry from SNP datasets using similar statistical models as STRUCTURE, but is computationally faster (Alexander and Lange 2011). The unsupervised clustering algorithm implemented in ADMIXTURE was applied with K varying from 1 to 9 with 20 000 bootstraps. A 100-fold cross-validation was set to determine the number of clusters with the lowest cross-validation error.

We conducted an alternative assessment of genetic clusters for microsatellites and SNPs using a discriminant analysis of principal components (DAPC) in the R package '*adegenet*' (Jombart *et al.* 2010). DAPC identifies clusters by sequential clustering and model selection; this multivariate analysis does not require populations to be in HWE or linkage equilibrium (Jombart 2008; Jombart *et al.* 2010). As per instructions (Jombart 2008), one-third of the Principle Components (PCs) were retained and all discriminant eigenvalues were used (<5 for both microsatellites and SNPs).

Kinship inference

To account for potential family bias (see Feutry *et al.* 2017; Devloo-Delva *et al.* 2019), the filtered SNP data were analysed to identify kinship as described in Hillary *et al.* (2018). Briefly, after allele frequencies were estimated, duplicate or replicate individuals were checked based on the number of identical genotypes. Full sibling pairs (FSPs) and parent–offspring pairs (POPs) were estimated, based on a likelihood ratio of two individuals to be either unrelated (UP) or a FSP or POP. At each locus, this likelihood score was calculated based on the expected probabilities that two individuals will share a genotype (according to the identity-by-descent theory; Thompson 2013) and the observed genotypes between the pair of individuals. The log transformation of the mean of each locus-specific score compared between individuals (i.e. pseudo-log likelihood or 'PLOD' score) allows us to determine the kin relationship. mtDNA haplotypes were used to assess the proposed kin groupings. FSPs and POPs were distinguished based on their cohort data. For simplicity, we only used SNPs to infer kinship because these have proven to perform with high resolution and precision (see Hellmann *et al.* 2016; Attard *et al.* 2018).

Results

By genotyping the same set of samples with a range of markers, we maximised our ability to discern population structure with available samples. The number of samples successfully analysed for each marker is given in Table 1. Sample dropout (i.e. the loss of samples from analyses) was due to a range of factors (e.g. poor-quality gDNA) that affected sequencing and genotyping success. All samples were checked for inadvertent duplication using SNPs to ensure no double sampling occurred, and no duplicates were identified. Following the kinship inference using SNPs, three FSPs and three POPs were identified in our data with individuals retained in analyses. The removal of sibs (that are not a sampling artefact) can introduce more bias than their retention, as suggested from empirical and simulated datasets (Waples and Anderson 2017). Further description of kinship results is below in the Kinship inference section.

Mitochondrial DNA

To investigate the relationship among mitochondrial genomes, we sequenced 994 bp of the mtDNA CR across 120 individuals, resulting in 14 haplotypes (GenBank accession numbers MH213460–MH213474). Most samples were represented by three haplotypes: two within the south-west Pacific and one located in the west Indo-Pacific (Fig. 2). The number of haplotypes per location ranged from 2 (Seychelles and east Australia) to 12 (PNG); as a result, nucleotide diversities were greatest for PNG (0.14 ± 0.10 s.d.; Table 1). All south-west Pacific haplotypes were separated from the west Indo-Pacific haplotypes by a 9-bp difference (Fig. 2).

Microsatellites

In all, 12 microsatellite loci were successfully genotyped in 117 individuals across the 3 locations. All loci were shown to be polymorphic in PNG, whereas three (ALS11, ALS14, ALS51) and two (ALS11, ALS51) loci were monomorphic in Seychelles and east Australia respectively (Table S3). Consequently, n_A ranged from 1 to 22; the widely variable alleles per locus was also represented in H_o values ranging from 0.00 to 0.900 (Table S3). MICRO-CHECKER (Van Oosterhout *et al.* 2004) indicated some evidence for the presence of null alleles per location (at 2 of 36 loci). To test the significance of these results, all loci were checked for departures from HWE. Four of thirty-six tests (ALS1, ALS7, ALS42 and ALS51) were found to deviate significantly from HWE in either PNG or east Australia. Because no single locus deviated at every location, no further action was taken and all 12 loci were included in further analyses. In addition, assessment of linkage disequilibrium between any two loci per population found no significant association was present. Per location, loci were moderately polymorphic across all populations, with average A_R of 3.63–4.70 and average H_o of 0.393–0.446 (Table 1).

Single nucleotide polymorphisms

ddRAD genotyping and the STACKS pipeline returned 717 800 SNP reads. After additional stringent quality filtering (Table S4), we identified a total of 6461 SNPs polymorphic across the three locations in 92 individuals (Table 1; genlight file of data available at https://doi.org/10.25919/5c25869707896). The number of polymorphic loci per population varied, with east Australia having the highest (6014) and the Seychelles having the lowest (4128; Table 1). A_R was identical between locations

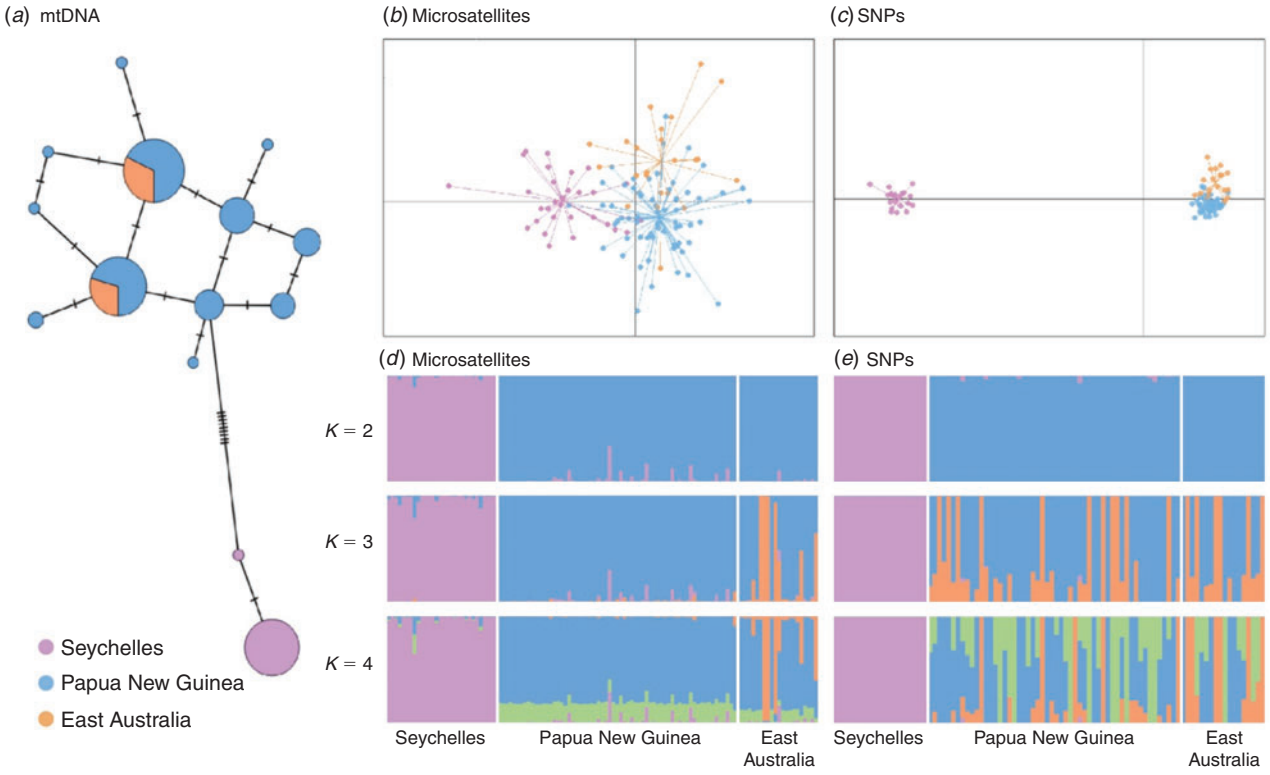

Fig. 2. Various measurements of population structure using each marker. (*a*) Mitochondrial (mt)DNA (control region) median-joining network analysis from POPart (ver. 1.7, see http://popart.otago.ac.nz, accessed 13 March 2018). Haplotype frequencies are relative to the size of the circles; colours represent sampling locations, as indicated. The number of strokes joining nodes represents the number of mutations between two haplotypes (across the 994-bp fragment). (*b*, *c*) Scatterplots created using discriminant analysis of principal components (DAPC) showing variation between individuals (dots) and populations (colours) for microsatellites (*b*) and single nucleotide polymorphism (SNP) markers (*c*). (*d*, *e*) Corresponding cluster analyses using 12 microsatellite loci conducted in STRUCTURE (*d*) and 6461 SNPs using ADMIXTURE (*e*). Colours represent different clusters as defined by *K* values.

(1.95) and average H_o was small and similar between locations, ranging from 0.126 to 0.130 (Table 1).

Power analysis

Power simulations suggested the 12 microsatellite loci would be sufficient to recognise population differentiation for F_{ST} values between 0.01 and 0.05 (power to detect >98%), but the power quickly declined with decreasing F_{ST}; for example, detecting differentiation of $F_{ST} = 0.001$ was calculated to be detected only 10% of the time (Table S5 of the Supplementary material). In contrast, the SNP dataset provided consistently high power (1) for every F_{ST} scenario tested (Table S5).

Population structure

An assessment of fixation indices for spatial population structure identified varying differentiation between locations depending on the marker used. Samples within PNG were tested for genetic homogeneity (based on all three marker types) between sample collection sites (location data available in Table S6 of the Supplementary material). Homogeneity could not be rejected; therefore, subsequent analyses including PNG samples were considered to represent a single population. For maternally inherited mtDNA, pairwise Φ_{ST} estimates between Seychelles and the south-west Pacific locations, PNG and east Australia, were very high and significantly different ($\Phi_{ST} = 0.920$ and $\Phi_{ST} = 0.980$ respectively; $P < 0.000$; Table 2). Low (albeit significant; $P < 0.000$) differentiation between PNG and east Australia was identified, with a Φ_{ST} value of 0.102.

The significance levels of microsatellite pairwise comparisons were similar to those of mtDNA, although F_{ST} values were far lower, ranging from <0.000 to 0.050. Again, the Seychelles was found to be significantly differentiated from south-west Pacific locations (PNG $F_{ST} = 0.036$, $P < 0.000$; east Australia $F_{ST} = 0.050$, $P < 0.000$), but no genetic differentiation was identified between PNG and east Australia ($F_{ST} = 0.000$; Table 2). Both Arlequin (which permutes genotypes between populations) and *StAMPP* (which bootstraps across loci) estimated pairwise F_{ST}; the F_{ST} values reported here are from Arlequin (*StAMPP* calculations yielded identical results; data not shown).

Estimates of population structure using nuclear SNP markers were similar to the microsatellite results. Pairwise F_{ST} values were slightly higher than for the microsatellites (SNP $F_{ST} = 0.001$–0.059). Significant structuring between populations was found for the Seychelles and south-west Pacific locations ($P < 0.000$), whereas again low and (after Bonferroni correction) non-significant differentiation between PNG and east Australia was identified ($F_{ST} = 0.001$, $P = 0.017$; Table 2).

Table 2. Global and pairwise genetic differences (Φ_{ST} and F_{ST}) calculated from a 994-bp mitochondrial (mt)DNA control region (CR), 12 microsatellite markers (unbiased G_{ST} estimate given in parentheses) and 6461 single nucleotide polymorphisms (SNPs) for *Carcharhinus albimarginatus*

P-values are given above diagonal; pairwise Φ_{ST} and F_{ST} values are given below the diagonal. Asterisks denote significant *P*-values following Bonferroni correction ($P < 0.0167$)

		Seychelles	Papua New Guinea	East Australia
mtDNA (global $\Phi_{ST} = 0.889$)	Seychelles		0.000*	0.000*
	Papua New Guinea	0.92		0.005*
	East Australia	0.98	0.102	
Microsatellites (global $F_{ST} = 0.025$)	Seychelles		0.000*	0.000*
	Papua New Guinea	0.036 (0.018)		0.505
	East Australia	0.050 (0.025)	0.000 (0.000)	
SNPs (global $F_{ST} = 0.037$)	Seychelles		0.000*	0.000*
	Papua New Guinea	0.057		0.017
	East Australia	0.059	0.001	

The Bayesian clustering analysis STRUCTURE was run using microsatellite loci to determine what, if any, genetically similar clusters could be assigned. The natural log of probability ($\ln P$) and ΔK could not discern whether $K = 1$ or $K = 2$ due to the low $\ln P$ scores between $K = 1$ and $K = 2$ (Fig. S2 of the Supplementary material). Therefore, STRUCTURE results are presented for a range of K values to explore subdivision. Clustering scenario $K = 2$ was consistent with geographic location because STRUCTURE clearly separated individuals from the Seychelles into a cluster distinct from those from the south-west Pacific (Fig. 2). In addition, when $K = 3$, some individuals exclusively in the east Australia location were assigned to a separate cluster. The unsupervised clustering algorithm from the ADMIXTURE software was able to determine an optimal K using SNP markers. We identified an optimal $K = 2$ clusters, based on the lowest cross-validation error (Fig. S3 of the Supplementary material). The ADMIXTURE plot for two clusters identified more distinct separation between the Seychelles and the south-west Pacific locations than the microsatellite STRUCTURE plot. Moreover, no structure was visible between PNG and east Australia, even when increasing the number of clusters. DAPC analysis using microsatellite loci showed individuals across all three locations to occasionally overlap along the *x*- and *y*-axes (Fig. 2). Conversely, DAPC analysis for SNPs identified two clearly defined clusters consistent with geographic locations. The Seychelles individuals belonged to one cluster separated along the *x*-axis, whereas individuals from PNG and east Australia made up the second cluster, closely located but slightly partitioned, along the *y*-axis (Fig. 2).

Kinship inference

Three FSPs and three POPs were identified in our data (PLOD scores 0.024–0.181; Fig. S4 and Table S7 of the Supplementary material). Following identification of related individuals, mtDNA haplotypes were checked for similarities. All FSP and POP individuals had matching mtDNA haplotypes with the exclusion of one POP (10177 and 10219), which had a single point mutation along the 994-bp CR sequence from thymine (T) in the mother to cytosine (C) in the daughter. Related pairs were captured in the same locations with a maximum of 11 days between capture. The estimated age and relationship of individuals identified in the analysis is given in Table S5.

Discussion

Population genetic analysis of *C. albimarginatus* in the Indo-Pacific region may suggest that some level of gene flow and genetic connectivity is present between PNG and east Australia. Conversely, no connectivity was identified between the two Pacific locations and the Seychelles, suggesting that the Indian Ocean presents a strong barrier to gene flow between these locations. Both suites of microsatellites and SNPs were deemed powerful enough to identify population structure (as indicated in POWSIM analyses) at low levels of genetic differentiation. Our findings make important comparisons between nuclear markers, providing greater confidence in our results and help describe the genetic stock structure for *C. albimarginatus* in the region.

All three marker types detected substantial genetic subdivision between individuals in the Seychelles and south-west Pacific locations. The lack of genetic connectivity between the two regions is consistent with our understanding that many marine taxa, in particular reef-associated sharks, rarely transverse expansive ocean basins (McKibben and Nelson 1986; Chapman *et al.* 2005; Lowe *et al.* 2006; Heupel *et al.* 2010; Whitney *et al.* 2012; Dudgeon *et al.* 2013; Momigliano *et al.* 2015). The reasonably high pairwise differentiation values identified across all three markers are a strong indication that very little (or possibly no) migration is occurring across the ocean basins (i.e. resulting in the exchange of genes, where individual migrants successfully join the local population). Similar levels of population subdivision between ocean basins have been recorded for tope sharks *Galeorhinus galeus* (mean $\Phi_{ST} = 0.750$), spiny dogfish *Squalus acanthias* ($\Phi_{ST} = 0.744$, $F_{ST} = 0.055$) and the scalloped hammerhead *Sphyrna lewini* (mean $\Phi_{ST} = 0.499$ and $F_{ST} = 0.041$; Chabot and Allen 2009; Veríssimo *et al.* 2010; Daly-Engel *et al.* 2012). Several other complementary lines of evidence support the low likelihood of *C. albimarginatus* individuals migrating across the Indian Ocean.

Globally, *C. albimarginatus* have a patchy and isolated distribution, exclusively inhabiting coral reefs and bathymetric structures on continental shelves (Last and Stevens 2009).

Exhibiting pelagic behaviours, *C. albimarginatus* primarily occupy depths between 0 and 60 m (Espinoza *et al.* 2015*a*), but on occasion deep dive to 400–800 m (Bond *et al.* 2015; Espinoza *et al.* 2016). Coral reefs provide refuge, foraging grounds and breeding opportunities for *C. albimarginatus* (Espinoza *et al.* 2014); these essential requirements likely facilitate residency within a single ocean basin. It would be of interest to sample alternative west Indian Ocean locations, including Madagascar and the east African coast, to quantify levels of gene flow between these more closely located regions. In addition, sampling from a mid-point of the species distribution across the Indian Ocean (e.g. east Indian coast or Sri Lanka) would allow us to test whether stepping-stone migrations are occurring across the ocean basin.

Genetic connectivity between PNG and east Australia was described by several tests, and the low F_{ST} values (0.000–0.001) in nuclear markers suggests some level of gene flow between these regions. Cluster analyses completed in ADMIXTURE and DAPC for SNPs identified genetic connectivity between PNG and east Australia, consistent with microsatellite STRUCTURE results (Fig. 2).

This study was unable to reject the null hypothesis of genetic homogeneity between PNG and east Australia for *C. albimarginatus*. If confirmed by future studies with higher sample numbers and more collection locations, then connectivity would be similar to other reef-associated species within the western Pacific. Patterns of high gene flow at similar spatial scales have been reported in other reef sharks, including the whitetip reef shark *Triaenodon obesus* (Whitney *et al.* 2012), blacktip reef shark *C. melanopterus* (Vignaud *et al.* 2014), grey reef shark *C. amblyrhynchos* (Momigliano *et al.* 2017), *S. lewini* (Ovenden *et al.* 2009) and tiger shark *Galeocerdo cuvier* (Holmes *et al.* 2017). More widely, factors that curtail dispersal across the Indo-Pacific include ocean depth (Ovenden *et al.* 2009; Karl *et al.* 2012), body size (Espinoza *et al.* 2015*a*, 2015*b*), temperature (Verissimo *et al.* 2011), reproduction (Momigliano *et al.* 2017) and oceanographic features (Dudgeon *et al.* 2009). The body size of *C. albimarginatus* is larger than most pelagic reef-associated sharks, suggesting its dispersal potential may be similar to that of other large-bodied sharks, including *S. lewini* and blue sharks *Prionace glauca* (Ovenden *et al.* 2009).

The genetic homogeneity identified between Australia and PNG does not strictly indicate that individuals are exchanging between PNG and the east coast of Australia. Certainly our identification of related pairs would suggest some level of familiar residency is occurring. On Wheeler Reef, east Australia, and Sudest Island, PNG, mothers were captured in the same locations as their pups. In addition, a sibling pair in Manus Island, PNG, with an estimated age of 6–7 years was collected in the same location. All offspring and sibling pairs identified had not yet reached estimated age at maturity (Smart *et al.* 2017*a*). Tagging studies have found *C. albimarginatus* to remain fairly resident at coral reefs, but some individuals are recorded leaving an acoustic array for a short period of time before returning; a behaviour suggested to be associated with reproduction with individuals in neighbouring reefs (Espinoza *et al.* 2015*a*). Mating occurring between proximal individuals leads to patterns of close relatedness at fine scales and creates genetic gradients at large scales (Schwartz and McKelvey 2009). For example, patterns of high gene flow identified in *C. amblyrhynchos* are thought to be facilitated by nearby coral reefs representing stepping stones, allowing for the existence of genetic connectivity along the continental shelf (Momigliano *et al.* 2017). Telemetry work completed by Espinoza *et al.* (2015*a*) suggested that *C. albimarginatus* individuals are dispersing to breed with individuals on neighbouring reefs. If a stepping-stone style of migration is occurring, this would homogenise gene flow between the two locations, with subtle population structure between locations possible but undetected by our genetic methods and sampling regime. Our results work towards supporting this hypothesis, but further robust testing using more temporally similar sampling at locations between PNG and east Australia is required to better understand the effect of geographic distance on gene flow and whether any subtle population structure is apparent.

Although the nuclear data are unable to reject our null hypothesis of genetic homogeneity between PNG and east Australia, the mtDNA data point to low ($\Phi_{ST} = 0.102$) but significant population subdivision between the two sampling areas. However, this is not an unexpected finding and has been observed in other mitochondrial studies of some reef sharks. mtDNA is maternally inherited, and many reef sharks show strong population subdivision between regions with discontinuous coastline (Blower *et al.* 2012; Daly-Engel *et al.* 2012; Geraghty *et al.* 2014; Osgood and Baum, 2015; Corrigan *et al.* 2016). Structure identified using mtDNA (and a correctly designed sampling strategy) is often linked with female-mediated residency or philopatry, whereby female sharks remain at a site or return to a natal site to give birth (Chapman *et al.* 2015). The low yet significant mtDNA population structure identified between PNG and east Australia may suggest female *C. albimarginatus* exhibit residency or philopatric behaviour. Although studies have found no significant difference in male and female movements, tagging was conducted for juvenile *C. albimarginatus* individuals and therefore cannot provide insight into putative philopatry (Espinoza *et al.* 2015*a*). Kinship inference provides some qualitative evidence of philopatry, with the identification of a POP with a 16- to 18-year-old mother and her 7- to 8-year-old female pup present at the same location collected 1 day apart in Sudest Island, PNG. Further investigation of this putative behaviour is warranted, including more kinship studies, tagging of mature male and female *C. albimarginatus*, removing juveniles from genetic analysis (not possible in the present study because of small sample sizes) and locating nursery areas (if any) in order to understand the breeding behaviours of female *C. albimarginatus*.

Often population genetic studies show discrepancies in results between different marker types, in particular nuclear microsatellites and SNPs (Elbers *et al.* 2017; Vendrami *et al.* 2017). The concordant results from our nuclear analyses show both markers indicate similar patterns of gene flow throughout the west Indo-Pacific and south-west Pacific. When compared directly, one microsatellite locus contains more information than a single SNP locus, because microsatellites are multiallelic and SNPs are biallelic (Coates *et al.* 2009). However, comparisons between microsatellites and SNPs and the exclusive use of genome-wide SNPs are becoming more common in population genetic literature. Although small numbers of SNPs are inferior

or provide similar results as microsatellites for population diversity studies (Hamblin *et al.* 2007; Narum *et al.* 2008; Coates *et al.* 2009; Hess *et al.* 2011), once the number of SNP loci increases into the thousands, their power to detect population structure based on genetic informativeness increases (Rosenberg *et al.* 2003; Morin *et al.* 2004; Liu *et al.* 2005; Rašić *et al.* 2014; Vendrami *et al.* 2017). POWSIM estimates from the present study showed that the suites of 12 microsatellite and 6461 SNP markers are both powerful enough to detect genetic population at their relative global F_{ST} values (global $F_{ST} = 0.025$ and 0.037 for microsatellites and SNPs respectively). Thus, the capacity of our study to test and compare the results of nuclear markers (microsatellites and SNPs) has provided a robust assessment of *C. albimarginatus* population structure.

Throughout PNG and Australia, *C. albimarginatus* is captured in commercial, small-scale and IUU fisheries (Kumoru 2003; Marshall 2011; Bond *et al.* 2015; Smart *et al.* 2017*a*). Their susceptibility as bycatch during fishing has led to their Vulnerable status under the IUCN Red List (Espinoza *et al.* 2016), with *C. albimarginatus* at risk of declining populations because they lack the capacity to be harvested sustainably unless fishing is limited to specific age classes (Smart *et al.* 2017*a*). Like many other shark species, *C. albimarginatus* have low fecundity and long generation times, with demographic modelling finding populations unable to tolerate moderate levels of harvesting when all age classes are fished (Smart et al. 2017*b*). It has been demonstrated that low levels of bycatch of young-of-the-year (YOY) up to a maximum size of 100 cm TL is the most sustainable option for *C. albimarginatus* (Smart *et al.* 2017*b*). In contrast, samples collected during this project from the PNG region were harvested in longline fisheries and all individuals, except one, were over 100 cm TL. Furthermore, *C. albimarginatus* individuals collected from artisanal fisheries in PNG have recently been estimated at catch sizes between 68 and 201 cm TL for 28 individuals (Appleyard *et al.* 2018). In northern Australia, IUU fishing has reported a high proportion of adults being targeted (Marshall 2011). Concerningly, populations of *C. albimarginatus* in PNG and Australia will unlikely be able to recover if the breeding adults are persistently removed.

Our study has suggested apparent genetic connectivity between east coast Australia and PNG, each of which has varying degrees of fishing pressure and fisheries management capabilities for this species. Given these results, we suggest the regions are considered and managed as a single genetic stock. We also recommend that both nations consider reducing catches of *C. albimarginatus* over 100 cm TL, possibly by changing gear type and harvesting locations, in order to protect the adult population and avoid recruitment overfishing.

Conclusions

The lack of genetic connectivity between the Seychelles and the two south-west Pacific locations, shown here for both mitochondrial and nuclear DNA, was not unexpected because of the large geographic distance over ocean basins. However, potential genetic connectivity between PNG and east Australia is of great interest. Whether the connectivity identified is an effect of stepping-stone migrations creating a genetic gradient or indicative of direct exchange of individuals between locations cannot be resolved with our available data. In addition, mtDNA differentiation between PNG and Australia may perhaps reflect assumed female philopatry. Our suggestion of genetic connectivity between PNG and east Australia provides important evidence that *C. albimarginatus* may have large home ranges within which movement and mating is extensive.

The use of multiple markers in this study provided a robust comparison, and furthermore adds to the growing literature describing genetic population structure for elasmobranchs based on multiple approaches. Our research highlights the benefits of combining multiple lines of evidence with previously available tagging information to better understand movements of large-bodied marine species, the output of which can provide information to fisheries managers in the region.

Conflicts of interest

Jennifer Ovenden is an Associate Editor for *Marine and Freshwater Research*. Despite this relationship, she did not at any stage have Associate Editor-level access to this manuscript while in peer review, as is the standard practice when handling manuscripts submitted by an editor to this Journal. *Marine and Freshwater Research* encourages its editors to publish in the Journal and they are kept totally separate from the decision-making processes for their manuscripts. The authors have no further conflicts of interest to declare.

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