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Comparative population genomics confirms little population structure in two commercially targeted carcharhinid sharks

Claudia Junge[1,2,3] · Stephen C. Donnellan[4,5] · Charlie Huveneers[6,7] · Corey J. A. Bradshaw[8] · Alexis Simon[1,9] · Michael Drew[7] · Clinton Duffy[10] · Grant Johnson[11] · Geremy Cliff[12] · Matias Braccini[13] · Scott C. Cutmore[14] · Paul Butcher[15] · Rory McAuley[13] · Vic Peddemors[16] · Paul Rogers[6] · Bronwyn M. Gillanders[1,2]

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Abstract

Many shark species are at risk of overexploitation due to their high economic value, slow maturation, and low recruitment compared to most teleosts. However, there is insufficient knowledge about population structure at different spatial scales necessary to optimise fisheries models. We used single-nucleotide polymorphisms (SNPs) obtained through complexity-reduction genome sequencing to quantify the population structure of two highly mobile and commercially fished shark species: bronze whalers (*Carcharhinus brachyurus*) and dusky sharks (*C. obscurus*). We applied a comprehensive approach to test several population-structure hypotheses and signal consistency across methods and marker type. We found that *C. obscurus* was panmictic across Australia and Indonesia and across the Indian Ocean to South Africa based on neutral loci, whereas for *C. brachyurus*, the westernmost Australian samples appeared to be separate from the rest. The southernmost east Australian samples indicated some difference from the rest of Australia and New Zealand based on candidate loci for *C. brachyurus*, and potentially also *C. obscurus*; however, the lack of a reference genome makes the interpretation difficult. Despite similar patterns in both species, subtle and potentially important structure differences emphasise the importance of studying each target species independently rather than assuming similar patterns from closely related species with similar dispersal abilities, as well as considering different marker types in future studies. We found evidence of connectivity across the regions sampled, suggesting that the cumulative effects of regional fisheries and the potential for cross-jurisdictional fishery assessments and management should be considered for Australian, Indonesian, and New Zealand populations.

Introduction

Marine species generally exhibit high gene flow and connectivity across local, regional, and global scales. However, dispersal distances can vary substantially among species, making a unified approach to assessing connectivity and population structure difficult. Dispersal scales range from virtually zero in some sessile species, to thousands of kilometres in highly mobile elasmobranchs (e.g., Bonfil et al. 2005; Gore et al. 2008; Lea et al. 2015; Skomal et al. 2009; Veríssimo et al. 2017). This enables gene flow across vastly different spatial scales, which can lead to varied genetic population sub-structure. Outcomes can indicate: (1) panmixia, a common phenomenon in highly mobile species with large dispersal distances and home ranges (Quintela et al. 2014; Roy et al. 2014; but see Sellas et al. 2015), and is characterised by an absence of mating restrictions among individuals; (2) discrete populations and strong population sub-structure that are often found in species with limited dispersal capacity and narrow home ranges (Barbosa et al. 2013; Benestan et al. 2015), or (3) isolation-by-distance, where genetic similarity decreases as the distance between populations increases. Isolation-by-distance has been observed across all dispersal ranges (Wright et al. 2015) and is often established after the colonisation of new habitats (e.g., Junge et al. 2011). Although isolation-by-distance is a common pattern, distance alone sometimes only partially

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✉ Claudia Junge
claudia.junge@hi.no

Extended author information available on the last page of the article

predicts gene flow and population connectivity (e.g., Ashe et al. 2015).

Quantifying population structure and connectivity is necessary to define units of management and conservation. Species particularly at risk of overexploitation and extinction are high priorities for management and conservation, and these species are often highly valued, slow to mature, and have sporadic or low recruitment (Dulvy et al. 2014; Field et al. 2009; Frisk et al. 2005). Such characteristics are typical of many elasmobranch species that are fished commercially and recreationally (Walker 1998), making it necessary to monitor their harvests. However, ongoing depletion of sharks makes their sustainable harvest a scientific and management challenge (Dulvy et al. 2017).

The sustainable harvest of sharks relies on effective management that requires quantifying population structure and connectivity. For example, a lack of population sub-structure calls for management of the species across its entire distribution, whereas highly structured populations might require different management strategies depending on specific conditions. However, assessing population connectivity and gene flow for many sharks and other elasmobranchs is difficult due to their large dispersal capacity and complex life histories, coupled with difficulties in observing and sampling individuals.

Several approaches to increase the power to detect population structure have recently become available for species that lack reference genomic information—so-called 'non-model' species. It is now feasible and affordable to sequence thousands of markers for hundreds or thousands of individuals. This is achieved via complexity reduction of the genome prior to sequencing through genotyping by sequencing (GBS; Deschamps et al. 2012), restriction-site associated DNA (RAD; Miller et al. 2007) sequencing, or diversity arrays technology (DArT; Wenzl et al. 2004).

Classic population-genetics studies based only on putatively neutral loci to quantify gene flow and genetic drift, and hence, assess population structure, are relevant only within a well-defined theoretical framework. Therefore, analysing loci under selection (hereafter 'candidate loci') might provide additional spatial resolution (Hess et al. 2013; Milano et al. 2014), or reveal associations with environmental variables (e.g., Gaggiotti et al. 2009; Lamichhaney et al. 2012) or life-history traits (Hemmer-Hansen et al. 2014). Such an approach is potentially a more effective way to integrate genetics into fisheries management (Dudgeon et al. 2012; Ovenden et al. 2015). There are now many marine studies using candidate loci to quantify population structure and divergence (e.g., Case et al. 2005; Guo et al. 2015; Milano et al. 2014). This helps to (1) determine weak population structure for highly mobile species (something traditional markers alone struggle to elucidate) and (2) detect markers potentially under selection more efficiently using outlier detection to reduce the background noise that can swamp weak population structure (Pérez-Figueroa et al. 2010). The patterns of neutral and 'adaptive' population structure (using candidate loci) might either be different—with one or the other marker type showing higher sub-structure (e.g., Hess et al. 2013; Limborg et al. 2012)—or the same, where both marker types show the same sub-structure (e.g., Moore et al. 2014) or a lack thereof.

We applied a comprehensive approach using a large number of neutral and sets of candidate, genome-wide single-nucleotide polymorphism (SNP) loci following the population-genomics approach outlined in Luikart et al. (2003) to quantify the population structure of two commercially fished elasmobranch species: the bronze whaler *Carcharhinus brachyurus* (Günther, 1870), and the dusky shark *C. obscurus* (Lesueur, 1818). At a global scale, both species are of conservation concern—*C. brachyurus* is currently listed as Near Threatened in the International Union for Conservation of Nature's (IUCN) Red List of Threatened Species (Duffy and Gordon 2003b), and *C. obscurus* is listed as Vulnerable (Musick et al. 2009). Their life histories are characterised by low growth rates, late sexual maturity (*C. brachyurus*: 13–20 years, *C. obscurus* 17–32 years), and low fecundity (Drew et al. 2017; Dudley et al. 2005; Geraghty et al. 2013; McAuley et al. 2007; Romine et al. 2009; Walter and Ebert 1991), resulting in low recovery potential following depletion (Smith et al. 1998; Rogers et al. 2013a; Bradshaw et al. 2018). Both species are globally distributed: *C. brachyurus* occurs patchily in temperate regions (Duffy and Gordon 2003b), whereas *C. obscurus* occurs in tropical to warm temperate regions. However, both species are sympatric in temperate regions, where they can be misidentified as each other (Jones 2008).

Both species are targeted commercially and recreationally in many parts of their distribution (Bradshaw et al. 2018), as well as being taken with other more productive shark species in mixed-species fisheries. Landings from fisheries are often grouped together with other *Carcharhinus* species as 'whaler sharks', which means that population declines of an individual species are unlikely to be detected (Duffy and Gordon 2003b). Within Australasia and Indonesia, the major fisheries for *C. brachyurus* are in South Australia and upper North Island of New Zealand (Bradshaw et al. 2018), whereas *C. obscurus* are caught mainly in Australia: in southern Western Australia, New South Wales (Duffy and Gordon 2003b; Macbeth et al. 2009; Rogers et al. 2013b; Simpfendorfer et al. 1999) and to a lesser extent, South Australia; *C. obscurus* is rare in New Zealand (Roberts et al. 2015).

Demographic fishery models (e.g., Bradshaw et al. 2013, 2018; McAuley et al. 2007; Otway et al. 2004; Smart et al. 2017) generally require high-quality catch and effort data (Field et al. 2009; Walker 1998) and reliable information on

demography and connectivity. Previous molecular genetic studies based on mitochondrial DNA showed that Australian *C. obscurus* has one of the lowest nucleotide diversities of any large, globally distributed shark (Benavides et al. 2011b), and they are weakly differentiated genetically between the east and west of Australia (Geraghty et al. 2014). Accordingly, they are currently considered and reported as distinct eastern and western biological stocks in Australia (Braccini et al. 2016). However, no investigation of genetic diversity or population structure of *C. obscurus* has yet included southern Australia populations that potentially connect the east and west via gene flow, and studies on *C. brachyurus* across Australia are lacking altogether. In each species, we therefore (1) tested whether the populations are panmictic, discrete, or show evidence of isolation-by-distance within Australasia and Indonesia and (2) compared the patterns shown by neutral versus candidate loci.

Materials and methods

Sampling, DNA extraction, and sequencing

Tissue samples from *C. brachyurus* ($n = 106$ from seven areas; 43 males, 53 females, 10 unknown) and *C. obscurus* ($n = 207$ from 14 areas; 90 males, 110 females, 7 unknown) were collected from Australia, Indonesia, New Zealand, and South Africa between 2001 and 2013 by a combination of fisheries-dependent and -independent surveys, and from recreational fisheries, and shark bite-mitigation programs (Table 1). All samples were stored in 96% ethanol. We combined samples collected from each defined area here as 'sample sets' (Fig. 1; Electronic Supplementary Materials 1 and 2).

We extracted DNA using the DNeasy Blood & Tissue kit (Qiagen) following the manufacturer's instructions. We

Table 1 Geographic collection, sample set details and genetic diversity estimates for *Carcharhinus brachyurus* and *Carcharhinus obscurus*

Country	Collection area	Region	Sample set map # & ID	n	H_e	H_o
C. brachyurus						
Australia	Near Augusta	WEST	3 WEST_SW1	2	(0.288)	(0.374)
Australia	Great Australian Bight	SOUTH	5 SOUTH_GAB	2	(0.260)	(0.260)
Australia	Spencer Gulf	SOUTH	6 SOUTH_SG	34 (1[a])	0.241	0.261
Australia	Gulf St Vincent	SOUTH	7 SOUTH_GSV	39	0.241	0.258
Australia	SE SA, SW Victoria	SOUTH	8 SOUTH_Vic	3	(0.246)	(0.259)
Australia	Near Sydney	EAST	9 EAST_South	8 (2[a])	0.223	0.212
New Zealand	Auckland	EAST	10 EAST_NZL	15	0.230	0.208
Australasian Total				103		
C. obscurus						
Australia	N Shark Bay	WEST	1 WEST_North	26	0.198	0.188
Australia	Near Perth	WEST	2 WEST_Perth	8	0.191	0.159
Australia	Near Augusta	WEST	3 WEST_SW1	10	0.196	0.194
Australia	Near Bremer Bay	WEST	4 WEST_SW2	15	0.199	0.196
Australia	Great Australian Bight	SOUTH	5 SOUTH_GAB	6	0.190	0.178
Australia	Spencer Gulf	SOUTH	6 SOUTH_SG	28	0.199	0.192
Australia	Gulf St Vincent	SOUTH	7 SOUTH_GSV	9	0.195	0.186
Australia	Near Sydney	EAST	9 EAST_South	6	0.193	0.185
Australia	Near Coffs Harbour	EAST	11 EAST_Mid	15	0.197	0.182
Australia	SE Queensland	EAST	12 EAST_North	16	0.202	0.200
Australia	Norfolk Island	EAST	13 EAST_NORF	27	0.193	0.178
Australia	Timor Sea, NT	NORTH	15 NORTH_NT	21	0.189	0.174
Indonesia	Lombok	NORTH	14 NORTH_IDN	7	0.198	0.187
Australasian Total				194		
South Africa	KwaZulu-Natal		ZAF	13	0.191	0.163
Total				207		

Region: regional groupings for hierarchal population differentiation tests

n, number of individuals sampled; genetic diversity estimates: H_e, unbiased expected heterozygosity; H_o, observed heterozygosity shown for the neutral unlinked data sets only

[a]Statistical outliers deleted. Heterozygosity values in () are estimated from < 6 samples

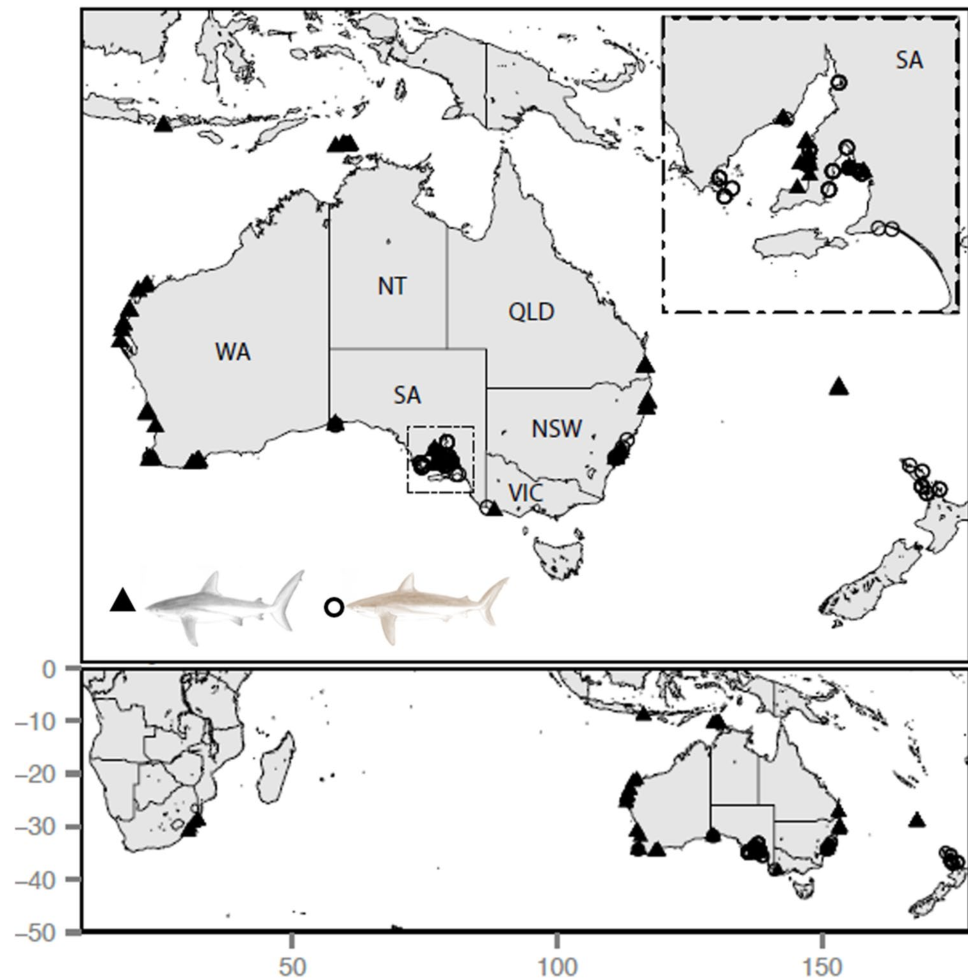

Fig. 1 Sampling locations for *Carcharhinus brachyurus* (circles) and *C. obscurus* (closed upward triangles). Latitudes and longitudes are indicated. (top) Sampling locations across Australia and Indonesia, with insert for locations in the two gulfs in South Australia, and (bottom) overview sampling locations across the Indian and Southern Oceans for both species. *WA* Western Australia, *NT* Northern Territory, *SA* South Australia, *QLD* Queensland, *NSW* New South Wales, *VIC* Victoria

used DArTseq™ technology (Cruz et al. 2013; Kilian et al. 2012) for single-nucleotide polymorphism (SNP) genotyping done by Diversity Arrays Technology (DArT, Canberra). We processed DNA samples in digestion/ligation reactions as described by Kilian et al. (2012), except we replaced the single *Pst*I-compatible adaptor with two different adaptors corresponding to the *Pst*I and *Sph*I restriction-enzyme overhangs for a double digest. Details of the method are in the Electronic Supplementary Material 1 and Donnellan et al. (2015). We originally analysed libraries separately to check for batch effects, and only in the final step completely pooled all libraries and called the final SNPs. We also randomly divided samples from different sample sets across libraries and sequencing lanes to overcome batch effects, as suggested by Leigh et al. (2018).

Data filtering, species identification, and genetic diversity

We detected 50,608 SNPs among 313 individuals across both species with the DArT analytical pipeline. Due to strong morphological similarities of the two species, we first confirmed species identity with a discriminant analysis of principal components of all samples (DAPC) (Jombart et al. 2010) implemented in the R package ADEGENET 1.4-2 (Jombart 2008) R library prior to subsequent analyses. We ran steps 0–2 of our data-filtering pipeline (see Electronic Supplementary Material 3). We assigned individuals to the correct species based on unambiguous clustering results (Electronic Supplementary Material 4).

We then launched the filtering pipeline again, from the beginning with the corrected species IDs (Electronic Supplementary Material 3) including all data, and then, from step 2 onwards, we ran the pipeline independently for each species to retain the most intra-species SNPs.

The data-filtering pipeline comprised 10 quality filters, one outlier individual removal step (step 11), and one linked locus removal step (step 12; summary in Electronic Supplementary Material 3; details in Electronic Supplementary Material 1, section 1.2.). This produced two data sets (Table 2): *brachyurus_ALL_loci*: comprising 3766 loci from 106 *C. brachyurus* in Australia and New Zealand, and *obscurus_ALL_loci*: comprising 8886 loci

Table 2 Overview of loci per species, type of locus, and linkage status

Species	Type of locus	ALL	Unlinked
C. brachyurus	Total	3766	520
	Neutral	2842	**310**
	Candidate loci	31	**13**
C. obscurus	Total	8866	2828
	Neutral	7969	**2478**
	Candidate loci	31	**24**
	Consensus candidate loci	**10**	

Type of locus neutral; candidate as identified by LOSITAN, and consensus loci identified by both LOSITAN and BAYESCAN; linkage status: ALL loci or unlinked loci. The five final data sets are indicated in bold

from 207 C. *obscurus* from 13 Australian and Indonesian and one South African sample set (Table 2).

We used GENODIVE (Meirmans and Van Tienderen 2004) and ADEGENET 1.4-2 (Jombart 2008) to calculate heterozygosities, and allele frequencies, including distributions of minor allele frequency. We did all subsequent analyses for both species focussed on only samples from Australia, Indonesia and New Zealand, unless otherwise indicated.

Linkage disequilibrium, Hardy–Weinberg equilibrium, and outlier loci

We used the GENETICS R library (Warnes and Leisch 2006) to test for locus pairs that are potentially linked, i.e., those loci in linkage disequilibrium. We tested each species' data set separately for pairwise linkage disequilibrium between genetic markers using the function *LD*. After sequential removal (see Electronic Supplementary Material 1), this resulted in two new unlinked data sets, one for each species: *brachyurus_unlinked_loci* with 520 loci and *obscurus_unlinked_loci* with 2828 loci (Table 2). We used these two unlinked data sets for all subsequent analyses (unless otherwise indicated). We also did the same analyses for the full data sets (i.e., unlinked plus linked loci) and did not observe differences in the resulting population-structure patterns. We present the results from the full data sets in the Electronic Supplementary Materials 5–8. We used GENEPOP 4.2.1 (Rousset 2008) to test for deviations from Hardy–Weinberg equilibrium (Electronic Supplementary Material 1).

We used two different F_{ST} outlier detection methods, LOSITAN (Antao et al. 2008) and BAYESCAN (Foll and Gaggiotti 2008) to identify candidate loci that are potentially under positive selection, and loci that could be considered neutral, because the interpretation of outlier loci should be done cautiously (Narum and Hess 2011). Both methods can be sensitive to low sample sizes, so we included only sample sets that had > 8 individuals (i.e., 4/7 for *C. brachyurus*, and 11/13 for *C. obscurus*) to achieve a representative number of alleles. We included only those loci safely identified as 'neutral' in the neutral data sets and excluded all other loci, including those identified as under balancing selection. We subsequently used the BLAST tool to search for sequence matches of the candidate loci that revealed some level of sub-structure.

Population structure

We separated all data sets into neutral and candidate loci, resulting in two data sets per species. We implemented simulations following the strategy of Krück et al. (2013) using POWSIM (Ryman and Palm 2006) to calculate the statistical power to detect genetic differentiation (details in Electronic Supplementary Material 1). We calculated global F_{ST} for the neutral loci for each species separately using GENEPOP and applied the implemented exact *G* test.

We investigated the population structure by two main approaches: (1) classic F_{ST} and population differentiation estimates and (2) cluster analysis. To estimate the differentiation, we calculated pairwise F_{ST} (Weir and Cockerham 1984) and ran exact *G* tests implemented in GENEPOP (details in Electronic Supplementary Material 1), correcting for multiple tests using a sequential Bonferroni method (Rice 1989).

The cluster analyses comprised of: (1) a principal component analysis using ADEGENET and (2) STRUCTURE 2.3.4 (Pritchard et al. 2000). In ADEGENET (Jombart 2008; Jombart and Ahmed 2011), we calculated principal components using the glPca function with default arguments and produced plots using the ggplot2 package (Wickham 2009). We did the same analysis including the South African sample set for *C. obscurus*. In STRUCTURE, we used the admixture model, assuming correlated allele frequencies (Falush et al. 2003; Pritchard et al. 2000) with a burn-in of 300,000 and 700,000 iterations, and the 'locprior' option (Hubisz et al. 2009), with 20 replicate runs for each *k* representing the number of sampled sites. We determined the optimal number of clusters following Pritchard et al. (2000) and Evanno et al. (2005) using STRUCTURE HARVESTER (Earl and vonHoldt 2012) and visualised the results in CLUMPAK (Kopelman et al. 2015).

Subsequently, we tested if there was any structure related to region, distance or sex (detailed in Electronic Supplementary Material 1).

Results

Carcharhinus brachyurus

Descriptive statistics

The expected and observed heterozygosities for the neutral loci ranged from 0.23 to 0.29 and 0.21 to 0.37, respectively; observed heterozygosity was higher than expected in the westernmost Australian sample set (Table 1). The median observed heterozygosity was 0.259 when all and 0.235 when the westernmost samples were excluded. When we analysed all loci together, little heterozygosity was evident (Fig. 2b). However, after removing potentially linked loci, average heterozygosity increased (Fig. 2d), and we used the unlinked loci for all subsequent analyses. Removing the confounding effect of genetic linkage produced the following data set: *brachyurus_unlinked* with 520 loci (an 86% reduction) (Table 2). All sample sets were in Hardy–Weinberg equilibrium in both the neutral and the candidate loci data sets. We detected 13 candidate loci with LOSITAN (Table 2), whereas BAYESCAN detected none, irrespective of the prior settings (Electronic Supplementary Material 5). The BLAST search did not reveal any explanatory sequence matches (data not shown).

Population structure

Global F_{ST} for the neutral loci considering all sample sets was 0.0078 (CI 95% from 10,000 permutations = [0.0043, 0.0113], p value from 1000 permutations < 0.05), and 0.0034 (CI 95% from 10,000 permutations = [5e−04, 0.0064], p value from 1000 permutations > 0.05) if the westernmost sample set (3-SW_WEST) was removed. We found no evidence for population differentiation between pairs of sample sets for neutral loci, whereas the candidate loci showed differentiation in 6 out of 21 pairwise comparisons, involving sample sets within and between regions; half of them involved the Australian EAST sample set (9-EAST_South; Electronic Supplementary Material 6). For each of those 13 candidate loci individually, 0

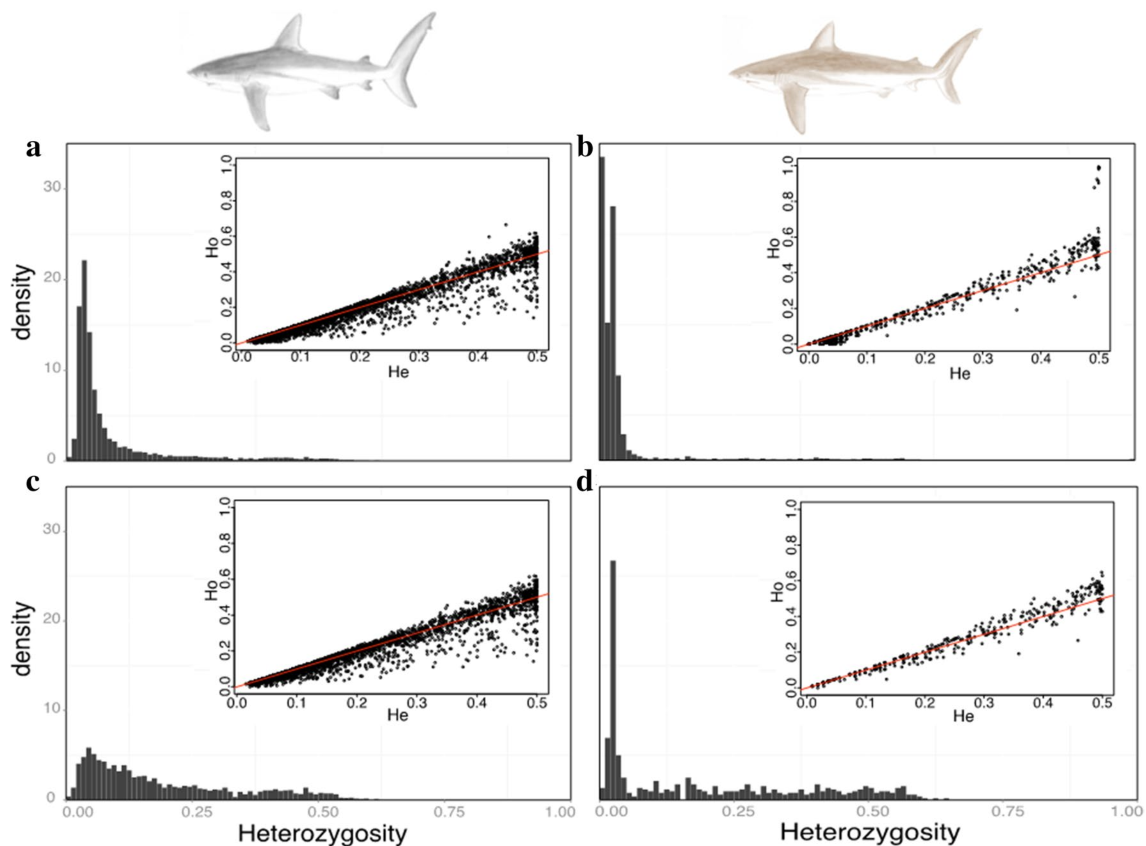

Fig. 2 Observed heterozygosity distribution within species for both species. Shown as densities (= percentage of loci with a given heterozygosity) for **a**, **c** *C. obscurus*; **b**, **d** *C. brachyurus*, including **a**, **b**) all SNPs, and **c**, **d** only unlinked SNPs. Inset: observed versus expected heterozygosity. The red line represents the $y = x$ relation between expected heterozygosity and observed heterozygosity, i.e., the expected 1:1 relationship

to approximately 30% of all pairwise comparisons revealed differences. Pairwise F_{ST} ranged from −0.014 to 0.294 in the candidate locus data set, and from −0.014 to 0.112 in the neutral one (Electronic Supplementary Material 6); in the latter, all comparisons involving the WEST sample set (3-WEST_SW1) had the highest F_{ST}. Power simulations concluded that we have sufficient power to detect differences (for details, see Electronic Supplementary Material 1).

For the neutral loci, STRUCTURE revealed evidence for two population clusters—WEST (3-WEST_SW1) and westernmost SOUTH (5-SOUTH_GAB) formed one cluster, and all other individuals irrespective of sample sets were assigned to the second (Fig. 3b); a cluster possibility for $K=3$ did not reveal any further conclusive sub-structure (Fig. 3c), although it was the most likely number when analysing the unlinked neutral loci only (see Electronic Supplementary Material 7). The same individuals also clustered in the principal components analysis (Fig. 3d). The STRUCTURE analysis of the candidate loci revealed two clusters, separating the EAST (9-EAST_South) from all other (Fig. 3a), whereas the principal components analysis revealed no clear separation (Electronic Supplementary Material 7). We detected no differentiation signal based on distance or sex, but found a differentiation between the EAST and SOUTH regions based on the candidate loci (details in the Electronic Supplementary Material 1).

Carcharhinus obscurus

Descriptive statistics

The expected and observed heterozygosity for the neutral loci ranged from 0.19 to 0.20 and 0.16 to 0.20, respectively. The median observed heterozygosity was 0.186. The general pattern of heterozygosity was similar to *C. brachyurus* (i.e., low but increasing after removing linked loci; Fig. 2a, c). Removing the confounding effect of genetic linkage produced the following data set: *obscurus_unlinked* with 2828 loci, resulting in a 68% reduction of loci (Table 2). All sample sets were in Hardy–Weinberg equilibrium based on the neutral loci. For candidate loci, eight out of 13 sample sets did not conform to Hardy–Weinberg equilibrium. LOSITAN revealed 24 loci and BAYESCAN between two and six loci when using 20 or 10 as prior odds for the neutral model, respectively (Electronic Supplementary Material 5). None of these loci was detected by both programs. However, when testing for candidate loci using all loci (including the linked ones), 10 loci were identified by both programs (see Table 2).

Population structure

Global F_{ST} for the neutral loci was 0.0014 (CI 95% from 10,000 permutations = [7e−04, 0.0021], p value from 1000 permutations > 0.05). None of the pairwise

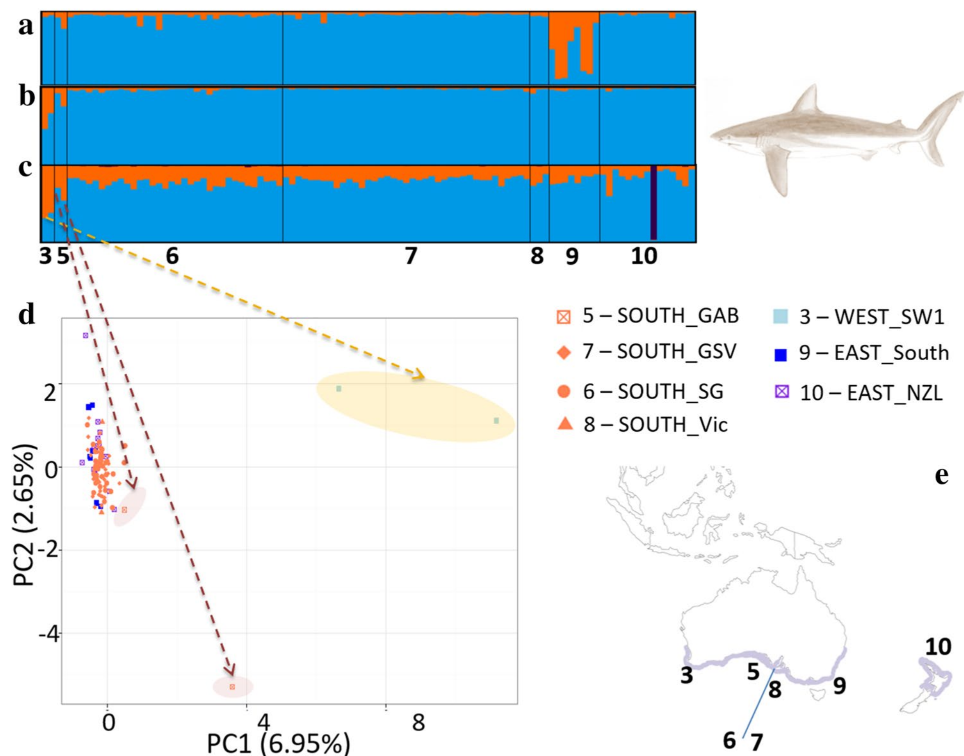

Fig. 3 Cluster analyses for *Carcharhinus brachyurus*. Shown for unlinked loci using STRUCTURE (**a–c**) for **a** candidate loci, and **b**, **c** neutral loci [shown for multiple clusters as recommended Meirmans (2015)] for $K=2$ (**b**) and $K=3$ clusters (**c**) and (**d**) principal component analysis based on 2842 neutral loci from the entire set; **e** distribution of *C. brachyurus* (modified from Duffy and Gordon 2003a) with sample sets indicated: 3–W_SW1, 5–S_GAB, 6–S_SG, 7–S_GSV, 8–S_Vic, 9–E_South, and 10–E_NZ (see Table 1 for abbreviation definitions)

population comparisons showed evidence for differentiation in the neutral data set (pairwise F_{ST} range: −0.008 to 0.011; Electronic Supplementary Material 8). For candidate loci, 38 pairwise comparisons out of 78 showed differentiation (F_{ST} range: −0.032 to 0.210; Electronic Supplementary Material 8). In the 10 candidate loci identified by both LOSITAN and BAYESCAN, all pairwise comparisons involving one EAST sample set (11-EAST_Mid) were differentiated, and approximately half of the comparisons involving one SOUTH sample set (6-SOUTH_GSV) were as well, totalling 18 out of 78. Power simulations concluded that we have sufficient power to detect differences (for details, see Electronic Supplementary Material 1).

There was neither population sub-structure within the Australia–Indonesia region, nor between that region and South Africa, based on F_{ST} and principal component analysis using neutral or candidate loci (Electronic Supplementary Materials 7, 8, and 9; Fig. 4c). No clustering was evident with STRUCTURE for neutral loci (Electronic Supplementary Material 7). For the candidate loci, STRUCTURE revealed $K=2$, but most sample sets showed mixed ancestry without any geographic pattern (Electronic Supplementary Material 7). For the 10 loci jointly detected by LOSITAN and BAYESCAN, there was evidence for $K=2$ or 3 (Fig. 4a, b). One EAST (11-EAST_Mid), one SOUTH (7-SOUTH_SG) sample set and potentially some individuals from neighbouring SOUTH (6-SOUTH_GSV) were separated from the remaining sample sets. We detected no differentiation signal based on distance or sex.

Discussion

Using a comprehensive approach involving 3000–9000 genome-wide SNPs, neutral and candidate loci, and several different analytical methods, we found no evidence for population sub-structure across Australia and Indonesia for the dusky shark (*Carcharhinus obscurus*), but some support for a separation of the westernmost Australian samples for the bronze whaler (*C. brachyurus*) from the rest of Australia and New Zealand based on neutral loci only (albeit based on few samples). For *C. obscurus*, we therefore propose panmixia within Australia and Indonesia as well as across the Indian Ocean, thus rejecting the hypotheses of discrete populations and isolation-by-distance. Although candidate loci generally revealed higher differentiation among populations, we

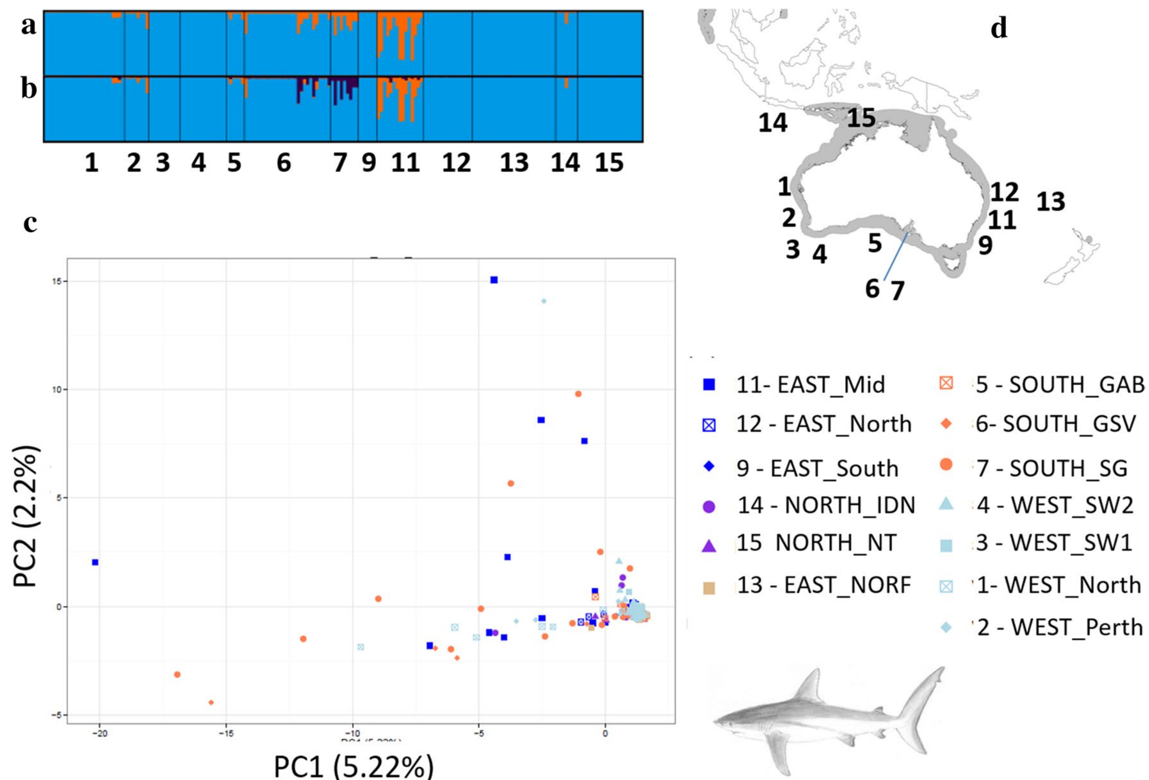

Fig. 4 Cluster analyses for *C. obscurus* using STRUCTURE. Shown for unlinked loci using STRUCTURE (**a**, **b**) consensus candidate loci (10) identified by both, LOSITAN and BAYESCAN, programs for $K=2$–3 clusters [shown for multiple clusters as recommended Meirmans 2015)]; **c** principal component analysis plot based on 7969 neutral loci from the entire set, **d** distribution range of *C. obscurus* (modified from Musick et al. 2009) with the sample sets indicated: 1–W_North, 2–W_Perth, 3–W_SW1, 4–W_SW2, 5–S_GAB, 6–S_SG, 7–S_GSV, 9–E_South, 11–E_Mid, 12–E_North, 13–E_NORF, 14–N_IDN, and 15–N_NT) (see Table 1 for abbreviation definitions)

could not identify any consistent population sub-structure in *C. obscurus*. However, *C. brachyurus* from the east of Australia showed weak differentiation from the rest of Australia and New Zealand using candidate loci, although a clustering could not be conclusively confirmed using principal components analysis. Interestingly, some individuals from the same EAST location showed some admixture as well in *C. obscurus* using STRUCTURE, but we could not confirm a distinct clustering.

Recent studies on the movement and residency of both species in Australia using acoustic and satellite tags have demonstrated some connectivity between South Australia, Victoria, and Western Australia, with several individuals moving between these states (Huveneers et al. 2014; Rogers et al. 2013a, b). Some *C. obscurus* have travelled up to 2736 km between South Australia and Western Australia (Rogers et al. 2013b), and similar large-scale movements have also been recorded in the Northwest Atlantic (Kohler et al. 1998) and off South Africa (Dudley et al. 2005; Hussey et al. 2009); however, there is no direct evidence for movements across the Indian Ocean. Large-scale movements of *C. brachyurus* have also been documented in South Africa (Cliff and Dudley 1992).

Neutral versus candidate loci

The lack of population genetic structure for *C. brachyurus* based on mitochondrial DNA between Australia and New Zealand (Benavides et al. 2011a) suggests that these sharks have substantial gene flow. Our results based on neutral loci confirm panmixia between the two countries, but also show some support for a separation of the western Australia samples, albeit based on a low sample size from the west. This is confirmed by a significant global F_{ST} when including all sample sets but a non-significant result when removing the westernmost samples (3-SW_WEST). We checked those and the other western samples (5-SOUTH_GAB) with respect to DNA quality, sequence quality as well as amount of missing data and we have no reason to conclude that their separation from the rest of the Australian and New Zealand sample sets is due to a sample problem. In contrast, the candidate loci suggest that the east Australian samples (9-EAST_South) differed from all other sample sets, including New Zealand (10-EAST_NZL), the latter being more similar to southern and western Australia samples. However, the reason for this difference requires understanding the function of these candidate loci based on future genome mapping.

Although *C. brachyurus* from EAST Australia was larger than those from SOUTH Australia, a previous study found genetic structure across populations around the globe (Benavides et al. 2011a, b), suggesting that it is unlikely that large *C. brachyurus* in the EAST originated from areas not included in our study. In addition, studies of the movement of *C. brachyurus* using acoustic tags and the Integrated Marine Observing System (IMOS) animal-tracking network (Hoenner et al. 2018) and pop-up satellite archival tags (Huveneers and Drew, unpublished data) show some limited, large-scale movements of *C. brachyurus* between the WEST, the SOUTH, and the south-eastern SOUTH (Victoria). However, these movements occurred across life stages, and predominantly between the SOUTH and the WEST, with no records of sharks mixing between the SOUTH and the EAST. For *C. obscurus*, neutral and candidate loci revealed the same lack of clear population sub-structure. However, the candidate loci showed more variation that was not consistent with geography.

Different gene flow patterns in *C. obscurus*

Previous molecular studies of *C. obscurus* have revealed differing patterns of population structure between eastern and western Australia, from genetic homogeneity using mitochondrial DNA and microsatellites (Benavides et al. 2011b; Ovenden et al. 2009) to weak population structure based on mitochondrial DNA (Geraghty et al. 2014). These have also suggested, but not demonstrated conclusively, limited or no dispersal between Indonesia and Australia (Geraghty et al. 2014; Ovenden et al. 2009). Our results confirm genetic connectivity across the Sunda Shelf Barrier (Timor Trench), a widely recognised biogeographic barrier (Dudgeon et al. 2012), and high gene flow around Australia, including Bass Strait, another biogeographic border for many marine species (e.g., Barnes et al. 2015).

We found no population sub-structure for *C. obscurus* across Australia when analysing almost 3000 neutral loci across differentiation and clustering approaches and irrespective of sex, which was confirmed by a non-significant global F_{ST}. Our finding contrasts with mitochondrial DNA evidence that demonstrated weak differentiation between the east and west of Australia (Geraghty et al. 2014). We observed no evidence of differences between northern Australia (NORTH), situated midway between the east and west coast, and the eastern and western samples. This incongruence between mtDNA and nuclear DNA variation could be due to female philopatry [reviewed in Chapman et al. (2015)]—if females mate and/or give birth close to their natal sites, this can lead to a pattern of local or regional population structuring with gene flow mediated more by males. However, we found no evidence for male-biased dispersal in *C. obscurus*. For candidate loci, we detected many pairwise population differences among males from different samples (29%) compared to the female–female comparisons (5%). This implies that male-biased dispersal is not the driver for population structuring in the Australian–Indonesian *C. obscurus*. Another possibility is that differentiation of mtDNA is driven by selection based on environmental

factors. Under this scenario, mtDNA might be an indicator for demographic connectivity, but this requires confirmation.

Increasing the number of molecular markers is expected to increase the chances of detecting population structure, whereby new technologies enable the sequencing of thousands of loci across the genome to resolve suggestions of weak population structure. However, here we found that even using between 2000 and 8000 neutral loci, there was no sub-structure within Australia and Indonesia for *C. obscurus*, and there were no obvious barriers to gene flow between these areas and South Africa.

Linkage disequilibrium

Although violation of linkage-disequilibrium assumptions can introduce bias when interpreting population genetic data, few genomic studies have incorporated statistical steps and strict testing in their analysis to identify and account for linked markers and the effect of removing such potentially linked markers on their results. We detected many linked loci and reduced our data sets accordingly until only one member per linkage group was retained. Low heterozygosity and minor allele frequencies could mimic linkage between markers due to the prevalence of the most common allele across markers. This is not necessarily a signal of linkage, but the two possibilities might be indistinguishable. When we removed 'linked' loci, there was a reduction of loci with low heterozygosity in both species (most prominent in *C. obscurus*). Removing potentially linked loci resulted in a large reduction of the number of loci, especially for *C. brachyurus*, and it would therefore be worthwhile to test in a future mapping study if pairs showing evidence of linkage disequilibrium are in fact physically linked.

Management implications

Our results provide evidence for high genetic connectivity across Australia and Indonesia for *C. obscurus*, and Australia and New Zealand for *C. brachyurus*. The practical implications of this are that fisheries management needs to be considered across jurisdictional boundaries by taking catches from other states and countries into account in fisheries models (e.g., Bradshaw et al. 2018). For *C. brachyurus*, we found some genetic separation between Western Australia (WEST) and South Australia (SOUTH), with the Great Australian Bight (5-SOUTH_GAB) samples appearing to be connected more to Western Australia rather than to South Australia; however, larger samples sizes are still required to measure the full extent of connectivity between those regions. From the perspective of fisheries management, *C. brachyurus* from the major fisheries regions in South Australia and New Zealand are panmictic and, therefore, represent a single management stock. Interestingly, *C. brachyurus* showed an overall higher genetic diversity compared to *C. obscurus* across the sampling areas we investigated. More samples from the western and eastern regions for *C. brachyurus* would contribute to an understanding of any underlying biological relevance, but unfortunately, few samples were available from those areas.

For *C. obscurus*, our confirmation of a seemingly shared stock across the Timor Trench also has important implications for management. The Australian *C. obscurus* samples seem to form some part of the Indonesian fishery and vice versa, which is not unexpected given the reported overlap in areas of the shark fisheries (Blaber et al. 2009). This could affect the management of the cross-jurisdictional stock of mature dusky sharks that is protected from fishing in Western Australia. The largest Australian catches of *C. obscurus* occur in Western Australia, where management relies on effort control, spatial closures, gear restrictions, and size limits designed to direct fishing-related mortality on the youngest age classes and protect large juveniles and adults. No such size limits exist in other regions (e.g., New South Wales and South Australia), where large juveniles and/or adults can be caught (Geraghty et al. 2015; Rogers et al. 2013a). However, to restrict what was considered unsustainable catches during 2007, New South Wales implemented a total allowable catch (Macbeth et al. 2009). Given that our findings and various tagging studies indicate that stocks are shared across jurisdictional boundaries (Huveneers et al. 2014; Rogers et al. 2013a, b), catches in Indonesia, eastern Australia, and South Australia would affect the stock of *C. obscurus* in Western Australia, and vice versa, if these populations are also demographically linked. Fisheries catching *C. obscurus* should therefore consider the cumulative effects of each fishery and the potential need for cross-jurisdiction fishery assessments and management.

We had access to only seven Indonesian samples, of which the exact origin was uncertain. However, the fish market from where the samples came and the size of boats landing sharks suggest that sharks were most likely caught in Indonesia. The samples also came from the same region/market as described in Geraghty et al. (2014), and described as Indonesian as well. More samples from Indonesia would help clarify structure between Indonesia and Australia.

Using genetics to manage shark fisheries is plagued with vagueness in the eyes of managers (Waples et al. 2008). Managers are primarily interested in determining whether there are demographically independent units that can be modelled separately; however, it is still unknown how much migration is required to produce demographic coupling. Populations linked by a 10% permanent immigration rate between them can be considered 'demographically coupled' (*sensu* Hastings 1993); regardless, immigration rates lower than this could still mean that populations are demographically 'linked'. However, genetic methods

struggle to distinguish the degree of connectivity requiring separate stock management if migration rates are high (Waples et al. 2008), because demographically linked populations might still be connected genetically over many generations (Ovenden 2013). Nevertheless, genetic assessments are the gold standard for determining stock structure, because they allow enduring patterns of connectivity to be captured by measuring it across multiple generations (Dichmont et al. 2012; Flood et al. 2014); however, they are most powerful in conjunction with other stock-differentiation methods.

A recent study from Bailleul et al. (2018) on blue sharks proposed the concept of a "population grey zone" for similarly mobile species and scenarios, explaining that such widespread genetic interdependence could in fact camouflage a wide range of demographic situations. They point to a common problem highly relevant to managers, which refers to the inferences that can be made about genetic and demographic independence if differentiation is found, and how on the other hand, a lack thereof (panmixia) does not necessarily imply demographic unity. In such cases, the authors suggest a conservative and global management strategy until demographic homogeneity is either confirmed or can be ruled out.

Both dusky sharks and bronze whalers, seem largely panmictic across the areas we sampled. However, recreational catch records, conventional tagging, and preliminary acoustic data (Huveneers et al. 2014; Huveneers, unpublished data; Izzo et al. 2016; Rogers et al. 2013b) suggest some residency and site fidelity [defined by Chapman et al. (2015)]. Accurately scaled stock assessments are therefore needed to ensure that the effect of each local fishery is considered (Bradshaw et al. 2018). We also recommend more studies examining residency, site fidelity, and potential philopatry to determine the requirement for and effectiveness of protective legislation (e.g., spatial closures) intended to prevent local extirpation (Chapman et al. 2015). A logical next step would also be to collect more samples from difficult to access, but nevertheless important areas, like the western parts of Australia for *C. brachyurus,* and to include a seascape genomic approach with a balanced sample design integrating genomic and oceanographic data.

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Compliance with ethical standards

No sharks were sacrificed for this study. All tissue samples were approximately 2×2 cm and were taken from pectoral fins (unless otherwise indicated). All samples were obtained legally (see Electronic Supplementary Material 10).

Conflict of interest All authors declare that they have no conflict of interest and all applicable international, national and/or institutional guidelines for the care and use of animals were followed.

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Affiliations

Claudia Junge[1,2,3] · Stephen C. Donnellan[4,5] · Charlie Huveneers[6,7] · Corey J. A. Bradshaw[8] · Alexis Simon[1,9] · Michael Drew[7] · Clinton Duffy[10] · Grant Johnson[11] · Geremy Cliff[12] · Matias Braccini[13] · Scott C. Cutmore[14] · Paul Butcher[15] · Rory McAuley[13] · Vic Peddemors[16] · Paul Rogers[6] · Bronwyn M. Gillanders[1,2]

[1] Southern Seas Ecology Laboratories, School of Biological Sciences, The University of Adelaide, Adelaide, SA 5005, Australia

[2] The Environment Institute and School of Biological Sciences, The University of Adelaide, Adelaide, SA 5005, Australia

[3] Havforskningsinstituttet (Institute of Marine Research, IMR), Postboks 6606, Framsenteret, Langnes, 9296 Tromsö, Norway

[4] Australian Centre for Evolutionary Biology and Biodiversity, The University of Adelaide, Adelaide, SA 5005, Australia

[5] South Australian Museum, North Terrace, Adelaide, SA 5000, Australia

[6] South Australian Research and Development Institute, Adelaide, SA 5024, Australia

[7] Southern Shark Ecology Group, College of Science and Engineering, Flinders University, Adelaide, SA 5001, Australia

[8] Global Ecology, College of Science and Engineering, Flinders University, Adelaide, SA 5001, Australia

[9] École Normale Supérieure, Formation Interuniversitaire de Biologie, 75230 Paris Cedex 05, France

[10] Aquatic and Reporting Unit, Department of Conservation, Auckland 1010, New Zealand

[11] Department of Primary Industry and Fisheries, Aquatic Resource Research Unit, GPO Box 3000, Darwin, NT 0801, Australia

[12] KwaZulu-Natal Sharks Board, Umhlanga Rocks, South Africa and Biomedical Resource Unit, University of KwaZulu-Natal, Durban, South Africa

[13] Western Australian Fisheries and Marine Research Laboratories, PO Box 20, North Beach, WA 6920, Australia

[14] School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia

[15] New South Wales Department of Industry, Department of Primary Industries, DPI Fisheries, Coffs Harbour, NSW 2450, Australia

[16] New South Wales of Department of Primary Industries, Sydney Institute of Marine Science, 19 Chowder Bay Road, Mosman, NSW 2088, Australia