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RESEARCH ARTICLE

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Australian sperm whales from different whaling stocks belong to the same population

Joanna Day[1,2,3] | David Power[3,4] | Rosemary Gales[5] | John Bannister[6†] | Maxine P. Piggott[3] | Kerstin Bilgmann[1,3] | Robert Harcourt[3] | Luciano B. Beheregaray[1] | Luciana M. Möller[1,7]

[1]Molecular Ecology Lab, College of Science and Engineering, Flinders University, Adelaide, South Australia, Australia

[2]Taronga Institute of Science and Learning, Taronga Conservation Society Australia, Mosman, New South Wales, Australia

[3]Department of Biological Sciences, Macquarie University, North Ryde, New South Wales, Australia

[4]Australian Fisheries Management Authority, Canberra, Australian Capital Territory, Australia

[5]Department of Primary Industries, Parks, Water and Environment, Tasmania, Australia

[6]Western Australian Museum, Perth, Western Australia, Australia

[7]Cetacean Ecology, Behaviour and Evolution Lab, College of Science and Engineering, Flinders University, Adelaide, South Australia, Australia

Correspondence
Joanna Day, Taronga Institute of Science and Learning, Taronga Conservation Society Australia, PO Box 20, Mosman NSW 2088, Australia.
Email: jday@zoo.nsw.gov.au

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Abstract

1. Understanding the factors driving population structure in marine mammals is needed to evaluate the impacts of previous exploitation, current anthropogenic threats, conservation status, and success of population recovery efforts.
2. Sperm whales are characterized by a worldwide distribution, low genetic diversity, complex patterns of social and genetic structure that differ significantly within and between ocean basins, and a long history of being commercially whaled. In Australia, sperm whales from the (International Whaling Commission assigned) southern hemisphere 'Division 5' stock were very heavily exploited by whaling.
3. The present study assessed the potential effects of whaling on the genetic diversity of sperm whales in Australia and the population genetic structure of these whales within a global context. A combination of historical and contemporary sperm whale samples (n = 157) were analysed across six regions, from south-eastern Australia ('Division 6' stock in the Pacific Ocean) to south-western Australia ('Division 5' stock in the Indian Ocean).
4. Sperm whales sampled from the 'Division 5' and 'Division 6' stocks belong to the same population based on nuclear and mitochondrial DNA (mtDNA) analyses. Four novel sperm whale mtDNA haplotypes were identified in animals from Australian waters. Levels of genetic diversity were low in Australian sperm whales but were similar to those previously reported for populations in the Indian and Pacific Oceans.
5. Given the genetic distinctiveness of sperm whales in Australian waters from other regions in the Pacific and Indian Oceans, and the lack of recovery in population numbers, further scientific studies are needed to increase our understanding of population dynamics and the effectiveness of threat management strategies in this species.

KEYWORDS
historical DNA, *Physeter macrocephalus*, population genetics, sperm whale, whaling

† Deceased.

1 | INTRODUCTION

An intricate combination of social, life-history, and environmental factors often contribute to creating genetic structure in social species. These may include high philopatry by one or both sexes, low dispersal capability, preferential associations among kin, dominance hierarchies, nonrandom mating patterns, habitat discontinuities, local habitat adaptation, and differential resource use (e.g. Chesser, 1991; Hoelzel, 1998; Dobson et al., 2004; Archie et al., 2008). Thus, patterns of population structure and dispersal can vary substantially within and between closely related species, and fine-scale structure may occur even in species characterized by high dispersal capabilities and/or among populations living in continuous environments (Hazlitt, Goldizen & Eldridge, 2006; Neaves et al., 2009; Wiszniewski et al., 2010; Bilgmann et al., 2014). This is especially evident in the marine environment, where genetic boundaries occur in species that exhibit habitat and resource affinities (Beheregaray & Sunnucks, 2001; Banks et al., 2007; Bilgmann et al., 2007; Fontaine et al., 2007). Understanding the demographic history of populations, and their current patterns of distribution, dispersal, genetic diversity, and population structure, is particularly important for threatened and vulnerable species (Dalén et al., 2006; Okello et al., 2008). This information is needed to develop effective conservation management strategies by assessing the adaptive potential of species, and identifying how they may respond to the impacts of key threatening processes such as habitat loss, the over-exploitation of natural resources, or climate change (Frankham, Bradshaw & Brook, 2014; Weeks, Stoklosa & Hoffmann, 2016).

Marine mammals have been significantly impacted by unsustainable harvesting worldwide and populations of many species do not appear to be recovering, despite long-term conservation efforts (Magera et al., 2013). Moreover, the degree to which whaling has impacted levels of genetic diversity and patterns of population and social structure is largely unknown. With the wide distribution of cetaceans and difficulties in studying them in the field, studies often rely on limited genetic samples to infer population boundaries and dispersal patterns. Historical samples and ancient DNA, combined with new analytical techniques in molecular ecology, provide greater power to investigate population dynamics, ecology, and the impacts of historical exploitation of cetacean species, including loss of genetic diversity, bottlenecks, and changes to the distribution or abundance of animals (reviewed in Foote, Hofreiter & Morin, 2012).

Sperm whales, *Physeter macrocephalus*, were heavily whaled and are currently listed as Vulnerable by the International Union for the Conservation of Nature (IUCN). Whaling differentially targeted males (Whitehead, 2002). Adult males typically travel alone (Whitehead, Brennan & Grover, 1992; Whitehead, 1993; Lettevall et al., 2002); however, subadult males disperse and form apparent bachelor groups with other young males (Gaskin, 1970; Richard et al., 1996; Lyrholm et al., 1999). In contrast, females live in social groups of adult females, subadults, and calves of both sexes (Whitehead, 1996). Sperm whale groups are often composed of closely associating kin (Gero, Engelhaupt & Whitehead, 2008; Pinela et al., 2009), but these groups are not strictly matrilineal and instead are composed of multiple matrilines (Richard et al., 1996). Despite the cosmopolitan distribution of the species (Rice, 1998), significant variation has been observed in ranging patterns, social structure, and patterns of genetic variation of sperm whales living in different ocean basins (Jaquet, Gendron & Coakes, 2003; Rendell & Whitehead, 2003; Whitehead et al., 2008; Gero et al., 2009; Jaquet & Gendron, 2009; Antunes et al., 2011; Ortega-Oritz et al., 2012; Mizroch & Rice, 2013; Alexander et al., 2016). Possible drivers of these differences could include differences between ocean basins in oceanography, predation pressure, prey distribution, prior whaling, and culture (Jaquet & Gendron, 2009; Whitehead et al., 2012).

Given the extensive range of sperm whales and the large global population size of approximately 360,000 today, and 1,100,000 before whaling (based on the latest population estimate of Whitehead, 2002), sperm whales have remarkably low levels of mtDNA diversity compared with most cetacean species (Engelhaupt et al., 2009; Alexander et al., 2013; Morin et al., 2018). Regional and global analyses of sperm whale population structure using nuclear DNA suggest low differentiation among ocean basins and little subdivision within ocean basins (Lyrholm & Gyllensten, 1998; Lyrholm et al., 1999). For example, Mesnick et al. (2011) detected low but significant levels of genetic differentiation within the eastern and central North Pacific using both mitochondrial DNA (mtDNA) and nuclear DNA (nDNA) markers. Other studies have documented hierarchical genetic structure, with social groups within populations showing subdivision, thus supporting strong kin-based social structure (Engelhaupt et al., 2009; Pinela et al., 2009; Alexander et al., 2016).

Until recently, the lack of a good model of sperm whale population structure had hampered efforts to assess their conservation status, their role in pelagic ecosystems, and the impact of historical whaling (Mesnick et al., 2011). The International Whaling Commission (IWC) split sperm whales in the southern hemisphere into nine stocks along the meridians of longitude, extending from the equator to the pack ice in Antarctica. The delineations were based on discontinuities in sperm whale distributions, were tightly linked to whaling grounds, and are still recognized by the IWC for management purposes (Donovan, 1991). In Australian waters, sperm whales are divided into two stocks: 'Division 5' (from 90°E to 130°E) in the Indian Ocean and 'Division 6' (from 130°E to 160°E) in the Pacific Ocean (Figure 1). Sperm whales were heavily exploited in whaling operations off Albany, Western Australia, between 1955 and 1978. The 'Albany stock' underwent a major decline, with an estimated 91% of males and 26% of females killed (Kirkwood, Allen & Bannister, 1980; Kirkwood & Bannister, 1980). Recent abundance estimates of sperm whale bulls off Albany indicate that the numbers in this region have not recovered since whaling ceased in 1978 (Carroll et al., 2014), even though the theoretical population growth rate for this species is 1.0–1.1% (Whitehead, 2003; Chiquet et al., 2013). In contrast, other great whale populations around Australia that were also hunted to near extinction have steadily recovered, particularly humpback whales, *Megaptera novaeangliae* (Noad et al., 2011; Pirotta et al., 2020) and southern right whales, *Eubalaena australis*

(Harcourt et al., 2019). Extremely low abundance and calf recruitment rates have been observed across several sperm whale stocks (Whitehead, Christal & Dufault, 1997; Reeves & Notarbartolo Di Sciara, 2006; Magera et al., 2013), suggesting a lack of recovery of sperm whale populations around the world.

Given the complex matrilineal social structure of sperm whales and the high degree of polygyny exhibited in extant populations, the depletion during whaling is likely to have had a disproportionate impact upon genetic diversity. Moreover, whether there is any genetic discontinuity within or between the previously defined 'Division 5' and Division 6' sperm whale stocks in the southern hemisphere is uncertain. The aims of this study were to: (i) investigate geographical population structure and levels of genetic diversity of sperm whales in south-eastern and south-western Australian waters using nuclear microsatellite and mtDNA control region markers; and (ii) compare levels of genetic diversity between historical and contemporary samples in Australian waters, and integrate these samples into a global analysis of population structure using published mtDNA data. For this study, a combination of historical and contemporary samples was examined from six geographical regions that span over 7,000 km and two ocean basins: the Pacific and the Indian Oceans.

2 | METHODS

2.1 | Study site and sample collection

A total of 176 sperm whale samples, including museum specimens, historical collections from commercial whaling operations, recent strandings, and biopsies of live animals, were collected from animals of Australian waters (Figure 1). Historical sperm whale tooth samples were collected from two sites on the coast of the Indian Ocean in south-western Australia (SW AUS): (i) Carnarvon (CN; *n* = 14) on the west coast of Western Australia (WA); and (ii) Albany (ALB; *n* = 66) on the south WA coast. Sperm whales hunted from these two sites were part of the 'Division 5' stock of the southern hemisphere. The tooth samples were collected as part of the scientific observer programme during commercial whaling and were obtained between 1962 and 1966. Contemporary tissue samples were obtained from the Pacific Ocean ('Division 6' stock) in south-eastern Australia (SE AUS). The majority of samples from New South Wales (NSW) were collected using the PAXARMS biopsy rifle (Paxarms NZ Ltd, Timaru, New Zealand, Krützen et al., 2002) from Eden (*n* = 21) on the south NSW coast in 2005. Samples were obtained from different sperm whale groups distributed over an area of a few kilometres. Samples of skin tissue from the whales were preserved in 100% ethanol. Another four samples were obtained from sperm whale strandings at different locations on the NSW coast. All 51 samples from Tasmania (TAS) were collected from stranded animals between 2002 and 2007 by the Department of Primary Industries, Parks, Water and Environment, mostly from its north and west coasts. Many of these were mass strandings, with up to 19 animals stranded at one time. Skin samples were shipped preserved in dimethyl sulfoxide (DMSO). A combination of contemporary and historical samples from SE AUS were also collected from animals stranded on the Victorian coast (VIC; *n* = 11) between 1956 and 1982 and the South Australian coast (SA; *n* = 9) coast between 1987 and 2007, and stored in Museums Victoria and South Australian Museum, respectively.

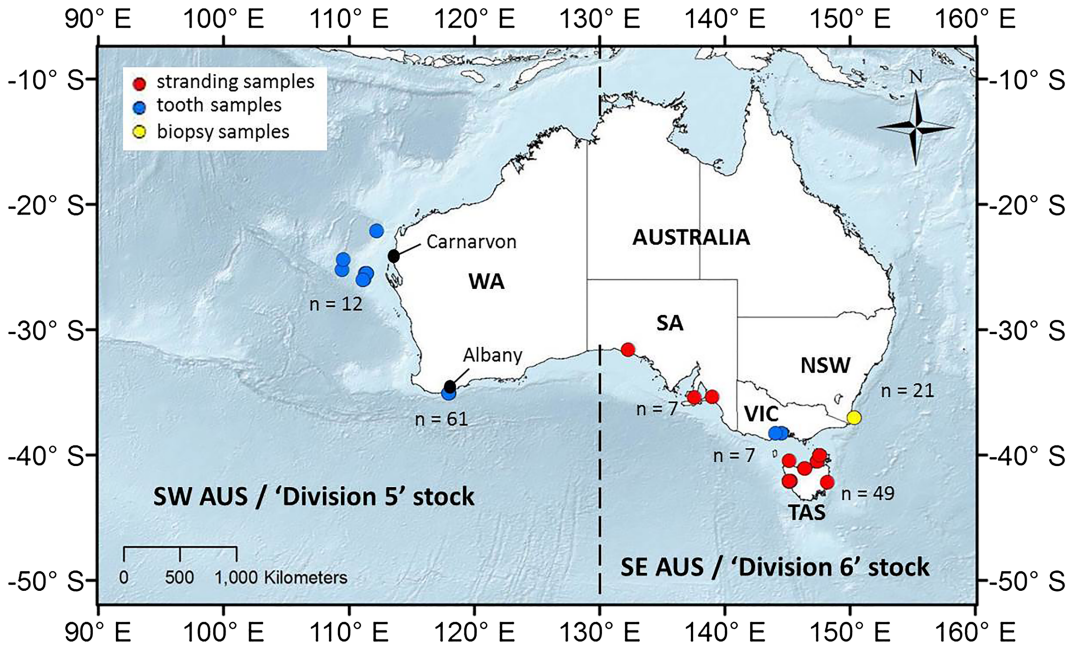

FIGURE 1 Geographic distribution and number of sperm whale (*Physeter macrocephalus*) samples that were analysed after passing quality control (*n* = 157) from New South Wales (NSW), South Australia (SA), Tasmania (TAS), Victoria (VIC), and two sites off Western Australia (WA): Albany (ALB) and Carnarvon (CN). The dashed line represents the stock boundary of sperm whale 'Division 5' stock in south-western Australia (SW AUS) and 'Division 6' stock in south-eastern Australia (SE AUS), as defined by the International Whaling Commission

2.2 | Genetic methods

DNA was extracted from tissue samples using a salting-out protocol (Sunnucks & Hales, 1996) and from tooth samples using the Qiagen DNeasy tissue kit (Qiagen, Hilden, Germany), following the modified protocol described in Data S1. Biopsy samples collected from sperm whales in Eden (NSW) were genetically sexed by amplifying a fragment of the *SRY* and *ZFX* genes following the protocol outlined in Gilson et al. (1998). Samples collected from stranded animals in TAS, NSW, VIC, and SA were also genetically sexed using this method if reliable stranding data on sex were not available. The sex of whales from tooth and degraded museum samples was assessed by the amplification of a fragment from the *SRY* gene (approx. 150 bp) on the Y chromosome (Richard, McCarrey & Wright, 1994), and one nuclear gene, *SPTBN1* (approx. 86 bp), developed for single nucleotide polymorphism (SNP) analysis (Morin et al., 2007), following the protocol described in Data S1. The nuclear gene was used as a control for the identification of females. This method was validated by independently sexing samples with known sex from stranding data (TAS) and historical records of commercially caught animals (WA).

Thirteen cetacean microsatellite loci were amplified: BMY11 (Huebinger et al., 2008); D22 (Shinohara, Domingo-Roura & Takenaka, 1997); DDE70 (Coughlan et al., 2006); EV1, EV5, EV94, EV104 (Valsecchi & Amos, 1996); FCB14 (Buchanan et al., 1996); GT23 (Bérubé et al., 2000); and SW2, SW10, SW13, SW19 (Richard et al., 1996). The amplification of microsatellite loci was conducted in multiplex reactions following the polymerase chain reaction (PCR) methods outlined in Data S1 and S2. Microsatellite genotyping was conducted using the ABI 3130 Genetic Analyzer (Applied Biosystems, Foster City, CA). Genotypic data were scored using GENEMAPPER 4.0 (Applied Biosystems), with peaks scored manually (Data S1). A subset of samples was scored by two people and both contemporary and historical samples were randomly selected for replicate genotyping to check genotyping accuracy. Samples that amplified for less than eight microsatellite loci were removed from the dataset prior to data analysis (following the quality control methods outlined in Morin et al., 2010; Alexander et al., 2016).

A 330-bp fragment of the mtDNA control region fragment was amplified by PCR with primers SWCR-F and SWCR-R following the protocol described in Data S1. These primers were developed specifically by Möller, Bannister & Harcourt (2005) so that DNA from contemporary tissue samples and degraded DNA from tooth and museum samples could be amplified, and the fragment includes most of the mtDNA control region variation known to define haplotypes in sperm whales (Data S3). A larger mtDNA control region fragment of around 700 bp was also amplified by PCR (Data S1) for a subset of tissue samples collected from SE AUS (NSW, n = 8; TAS, n = 8) using primers ThrDlp and TL12R (Lyrholm & Gyllensten, 1998). The purified PCR products were sequenced using the ABI 377 or ABI 3130 sequencer (Applied Biosystems). The mtDNA sequences were aligned and edited using SEQUENCHER 3.0 (Gene Codes Corporation, Ann Arbor, MI). Approximately 10% of all tissue and tooth samples were re-sequenced to ensure the accuracy of the mtDNA haplotypes.

2.3 | Data analysis

2.3.1 | Genetic variation

The average probability of identity (Paetkau & Strobeck, 1994) was calculated across the microsatellite dataset and genotypes were screened for duplicate sampling using GENALEX 6.503 (Peakall & Smouse, 2006; Peakall & Smouse, 2012). To account for genotyping errors, if samples were mismatched at up to four microsatellite loci, but matched for both sex and mtDNA haplotype, the samples were also considered as matching (following Alexander et al., 2016). When a perfect or near match was identified, one individual from the match was retained for subsequent analyses. Genotype comparisons were not conducted between contemporary and historical samples given the impossibility of duplicate sampling. Genotypic errors were assessed using MICRO-CHECKER 2.2.3 (Van Oosterhout et al., 2004). Two datasets were initially compiled for population genetic analyses: (i) the 'full' dataset; and (ii) the 'kin-restricted' dataset. The 'kin-restricted' dataset was created because the presence of relatives within populations can overestimate the level of genetic differentiation between populations. Anderson & Dunham (2008) and Rodriguez-Ramilo & Wang (2012) found that family groups may be incorrectly identified as distinct populations by Bayesian clustering methods such as STRUCTURE (Pritchard, Stephens & Donnelly, 2000). If populations are sampled randomly, however, keeping close relatives in the dataset is not always problematic for other population genetic analyses (Waples & Anderson, 2017). Only potential first-order relatives were identified in this study (i.e. no full or half siblings), as removing too many individuals can impact the statistical power because of the reduced sample size (Hendricks et al., 2018). Therefore, following Mesnick et al. (2011), the maximum-likelihood method implemented in ML-RELATE (Kalinowski, Wagner & Taper, 2006) was used to identify potential first-order relatives within each general location (waters off NSW, TAS, VIC/SA, Albany, WA and Carnarvon, WA). Samples collected from Victoria and South Australia were pooled because of the proximity of the sampling locations and the small sample sizes from each area. For each pair identified as a first-order relative, individuals with the most complete genetic data were retained. Tests for significant deviations from linkage disequilibrium were conducted in GENEPOP 4.2 (Raymond & Rousset, 1995). Tests for significant deviations from Hardy–Weinberg equilibrium (HWE) were conducted in GENEPOP using Fisher's exact test and the Markov chain method with 1,000 iterations for each sampling location and locus. Significance values for all multiple comparisons were adjusted by Bonferroni correction (Rice, 1989). Genetic variation within sampling locations was assessed by calculating allelic richness and inbreeding coefficients (F_{IS}) using FSTAT 2.9.3 (Goudet, 2001), the number of unique alleles in GENALEX, and the levels of observed and expected heterozygosity in ARLEQUIN 3.5.2.2 (Excoffier & Lischer, 2010).

Two mtDNA datasets were created based on fragment size: (i) a smaller 283-bp mtDNA control region fragment that was sequenced for both historical and contemporary samples; and (ii) a larger 563-bp mtDNA control region fragment that was sequenced for

16 contemporary tissue samples obtained from SE AUS. All 16 samples in the second mtDNA dataset were also included in the first dataset. Haplotypic (h) and nucleotide (π) diversity for mtDNA data were calculated for each general location (i.e. putative population) using ARLEQUIN with the Tamura & Nei (1993) correction. To examine genealogical relationships among the mtDNA control region haplotypes, the TCS 1.21 (Clement, Posada & Crandall, 2000) was used to construct a haplotype network using the maximum-parsimony method (Templeton, Crandall & Sing, 1992).

2.3.2 | Genetic differentiation

Genetic differentiation among the five putative populations was assessed by calculating Jost's D (Jost, 2008), based on 10,000 permutations in GENALEX. Jost's D is independent of within population genetic variation, and thus may be more suitable in this situation where genetic variation is high and the fixation index (F_{ST}) may underestimate differentiation (Jost, 2008; Bird et al., 2011). The 95% confidence intervals around Jost's D values were calculated using 1,000 bootstraps in GENALEX. The statistical power to detect genetic heterogeneity for hypothetical levels of true differentiation (quantified as F_{ST}) was estimated using POWSIM 4.1 (Ryman & Palm, 2006). For each dataset, the present sample sizes, number of loci and allele frequencies were used. Analyses were conducted using an effective population size (N_e) of 2,000, 1,000 dememorizations, 100 batches, 1,000 iterations per batch, and 1,000 runs, with significance assessed using the chi-square and Fisher's exact tests. For mtDNA, both F_{ST} and Φ_{ST} (with Tamura & Nei, 1993 correction) were estimated to examine differentiation based on haplotype frequencies and molecular distance (Slatkin, 1995). The significance of all pairwise comparisons was assessed with 10,000 permutations in ARLEQUIN.

To estimate the number of genetically distinct clusters or populations of sperm whales around Australia, a Bayesian model-based clustering method implemented in STRUCTURE 2.3.4 was used (Pritchard et al., 2000). Using the admixture and correlated allele frequency models, Markov chain Monte Carlo (MCMC) runs were conducted for K values ranging from one to five (based on the number of sampling locations) using a burn-in period of 500,000 iterations followed by runs of 10^6. Twenty independent runs were conducted for each value of K (as recommended by Gilbert et al., 2012). The analysis was first performed without sampling location information, followed by runs with sampling locations provided as prior information using the models developed by Hubisz et al. (2009). The latter approach can improve the probability that genetic structure is detected when levels of genetic differentiation among sampling locations are low (Hubisz et al., 2009). To determine the best-supported number of populations, both the highest mean log-likelihood of the data, ln $P(D)$ (Pritchard et al., 2000), and the highest second-order rate of change of ln $P(D)$, ΔK (Evanno, Regnaut & Goudet, 2005), were assessed using STUCTURE HARVESTER 0.6.94 (Earl & von Holdt, 2012). Population structure was also visualized with a discriminant analysis of principal components (DAPC; Jombart, Devillard & Balloux, 2010), with means imputed for missing data, within ADEGENET 2.1.1 (Jombart, 2008) in RSTUDIO 3.5.

To examine patterns of genetic variation and population structure of sperm whales in a global context, mtDNA sequences from this study were compared with the 394-bp mtDNA control region sequences obtained from Alexander et al. (2016), which had been compiled from published studies conducted on sperm whales worldwide. For this analysis, first, the 563-bp sequences amplified from 16 contemporary SE AUS samples were reduced to 394 bp and compared with haplotypes found in Alexander et al. (2016). At this point, levels of genetic differentiation were assessed among 17 locations in the Pacific, Indian, and Atlantic oceans. Following this step, the 394-bp haplotypes from Alexander et al. (2016) were reduced and aligned with the 283-bp haplotypes sequenced for all Australian sperm whales in this study. This maximized the number of Australian samples in the worldwide analysis of population structure and enabled the examination of any changes in genetic variation between historical (this study) and contemporary (Alexander et al., 2016) SW AUS samples.

3 | RESULTS

3.1 | Quality control and assembly of microsatellite and mtDNA datasets

After the removal of poor-quality samples that failed to amplify (n = 16) and duplicate samples (n = 3), a total of 157 sperm whale samples were available for genetic analyses. For the larger mtDNA fragment dataset, 15 SE AUS samples were analysed after the removal of one duplicate sample. The number of samples that passed quality control and for which there were known sample collection locations are presented in Figure 1. Nine samples from NSW (n = 4), TAS (n = 2), VIC (n = 2), and SA (n = 1) were not included in Figure 1 because only the general locations of the strandings were known. The probability of identity between two different individuals at nine loci (allowing the four loci with potential mismatches) was <1.00E−08, and therefore samples matching at nine or more loci were considered to be from the same individual whale. The microsatellite error rate was 1.7% based on seven out of 416 repeated genotypes that did not match. The mismatched genotypes were checked and corrected by reamplification.

For the microsatellite dataset, there was no evidence for linkage disequilibrium among any pair of nuclear loci or any evidence for scoring error caused by stuttering or large allele dropout at any locus. Potential null alleles were, however, detected in NSW samples for loci EV104 (null allele frequency = 0.254) and DDE70 (frequency = 0.124), in TAS samples for locus SW19 (frequency = 0.075), and in CN samples for locus SW13 (frequency = 0.200). As null alleles were not detected consistently across loci and sampling regions, the loci were not removed from the dataset. For the 'full' dataset, there was no evidence for departures from HWE across eight of the 13 loci. Significant deviation from HWE was found in NSW for loci EV94, DDE70, and EV104, in ALB for loci EV104 and BMY11, and in CN for locus

FCB14. The eight loci in HWE were retained for further analyses. Relatedness analysis identified 21 samples (NSW, *n* = 1; TAS, *n* = 6; VIC/SA, *n* = 1; ALB, *n* = 12; CN, *n* = 1) that possibly represent first-order relatives. One individual from each potential pair of relatives was removed, resulting in a total of 136 samples. These samples were used for the 'kin-restricted' mtDNA analyses; however, sequences could not be obtained for four samples (NSW, *n* = 2; SA, *n* = 2), thereby reducing the number of samples to 132. For microsatellites, significant deviation from HWE was still found for three loci (NSW, EV94 and DDE70; CN, FCB14) even after the removal of these 21 individuals. Consequently, a 'kin-restricted' microsatellite dataset was created for the 10 loci in HWE. For this dataset, 36 potential pairs of first-order relatives were identified, with one individual from each pair removed from the dataset (NSW, *n* = 4; TAS, *n* = 11; VIC/SA, *n* = 1; ALB, *n* = 18; CN, *n* = 2), resulting in a total of 121 samples (Table 1).

3.2 | Genetic variation

Measures of nuclear genetic variation, including allelic richness, heterozygosity and number of unique alleles, were moderately high and similar across all five sampling locations (Table 1). Slightly higher levels of genetic variation were found in TAS and ALB WA, which coincides with a larger sample size from these two locations. Genetic variation was not higher in locations where historical samples from commercial whaling were used (SW AUS: ALB and CN WA) compared with locations where samples were obtained from live or stranded animals (SE AUS: NSW, TAS, and VIC/SA). This pattern, however, was not observed for the mtDNA. Sequence alignment of the 283-bp fragment of the mtDNA control region from 132 samples across five locations revealed 10 polymorphic sites, defining 11 unique haplotypes (Table 2; Data S3). All haplotypes were closely related (Figure 2), and haplotype 1 was identified as the ancestral haplotype present in all sampling locations (Figure 2). Between four and seven haplotypes were found in each sampling area, with VIC/SA, NSW, and TAS displaying the highest levels of haplotypic and nucleotide diversity, compared with ALB and CN WA, where only historical samples were analysed (Figure 2; Table 3).

3.3 | Genetic differentiation

In pairwise comparisons for the 'kin-restricted' microsatellite dataset, low but significant genetic differentiation was observed between VIC/SA and ALB WA using Jost's *D* ($P < 0.05$ and lower 95% confidence intervals > 0), but not between any other sampling locations (Table 3). For the 'full' dataset significant Jost's *D* values were observed for several pairwise comparisons (Data S4), but these results are most likely linked to the presence of first-order relatives in the dataset. Power analyses indicate that both the 'full' and 'kin-restricted' datasets contained sufficient statistical power to detect genetic differentiation based on chi-square and Fisher's exact tests. For example, the probability of detecting an F_{ST} of 0.01 was >99% for the 'full' and 'kin-restricted' datasets. The probability of detecting an F_{ST} values as low as 0.005 was also very high (>85% for 'full' and >81% for

TABLE 1 Genetic variability in Australian sperm whales based on the 'kin-restricted' microsatellite dataset of 121 samples and 10 loci in Hardy–Weinberg equilibrium

Region	*N* (m:f:unknown)	UA	AR (SE)	H_O (SD)	H_E (SD)	F_{IS}
NSW	17 (16:0:1)	3	4.04 (0.37)	0.632 (0.186)	0.685 (0.130)	0.079
TAS	38 (16:22:0)	6	4.34 (0.40)	0.741 (0.142)	0.717 (0.121)	0.004
VIC/SA	13 (6:4:3)	1	4.40 (0.41)	0.669 (0.212)	0.683 (0.177)	0.019
ALB WA	43 (22:20:1)	9	4.45 (0.43)	0.692 (0.135)	0.728 (0.110)	0.051
CN WA	10 (10:0:0)	1	3.99 (0.47)	0.624 (0.243)	0.674 (0.144)	0.078

Note: N, number sampled (m, males; f, females); UA, number of unique alleles; AR, allelic richness ± standard error (SE); H_O, mean observed heterozygosity ± standard deviation (SD); H_E, mean expected heterozygosity ± SD; and F_{IS}, inbreeding coefficient. The sex of five individuals could not be determined.

TABLE 2 Percentage frequency and genetic diversity of Australian sperm whale mtDNA control region haplotypes (283 bp) by region, where N_H is the number of haplotypes and SD is the standard deviation, based on the 'kin-restricted' mtDNA dataset of 132 samples

	Haplotype reference number (283-bp ref.)													
Region	1	2	3	4	5	6	7	8	9	10	12	N_H	Haplotypic diversity (SD)	Nucleotide diversity (SD)
NSW	39	22		17	22							4	0.765 (0.055)	0.0036 (0.0028)
TAS	58	5		16	7		10	2	2			7	0.633 (0.074)	0.0040 (0.0029)
VIC/SA	28			18	18	18				9	9	6	0.891 (0.063)	0.0064 (0.0045)
ALB WA	72	6	2	12	8							5	0.474 (0.081)	0.0025 (0.0021)
CN WA	64	9		9	18							4	0.600 (0.154)	0.0027 (0.0024)

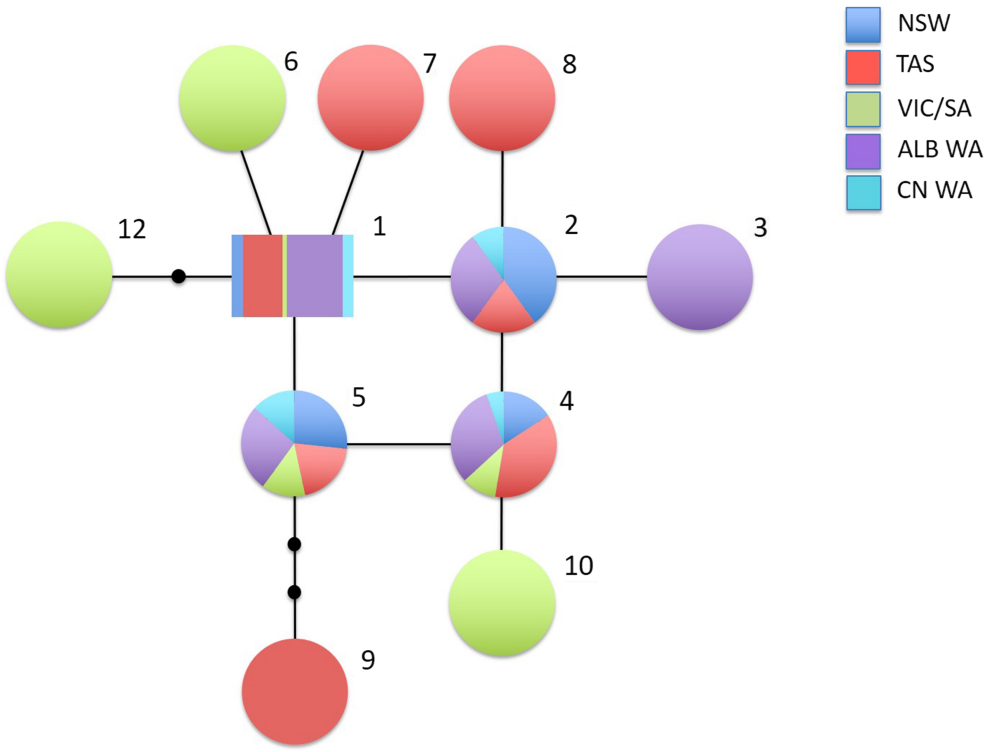

FIGURE 2 Parsimony network of the 283-bp mtDNA control region haplotypes found in Australian sperm whales from the 'kin-restricted' mtDNA dataset of 132 samples. Connections between haplotypes represent 1-bp differences and filled circles represent additional single point mutations. Haplotype 1 was identified as the ancestral lineage based on coalescence theory and is displayed with a rectangle. The colours represent sampling locations: New South Wales (NSW); Tasmania (TAS); Victoria and South Australia (VIC/SA); Albany, Western Australia (ALB WA); and Carnarvon, Western Australia (CN WA)

TABLE 3 Genetic differentiation in Australian sperm whales based on the 'kin-restricted' microsatellite dataset of 121 samples and 10 loci in Hardy–Weinberg equilibrium

Region	NSW	TAS	VIC/SA	ALB WA
TAS	0.022 (−0.003, 0.076)			
VIC/SA	0.047* (−0.015, 0.158)	0.018 (−0.041, 0.083)		
ALB WA	0.002 (−0.019, 0.031)	0.002 (−0.014, 0.028)	0.061** (0.001, 0.153)	
CN WA	0.009 (−0.025, 0.061)	0.027 (−0.013, 0.086)	0.056 (−0.018, 0.164)	0.004 m (−0.016, 0.039)

Note: 95% confidence intervals (95% CIs) for Jost's *D* values given in parentheses (lower 95% CI, upper 95% CI). *$P < 0.05$. **$P < 0.01$.

'kin-restricted' datasets). Similar results were obtained for the 'full' and 'kin-restricted' datasets including loci that significantly deviated from HWE (probability was >91% to detect an F_{ST} of 0.005 for both analyses). The STRUCTURE analyses indicated one single population in the Australian region based on the highest mean log-likelihood of the data observed at $K = 1$ (Data S5) and the assignment probabilities of individuals (Data S6). The result was consistent in the absence of geographical data and with sampling location provided a priori for both the 'full' and 'kin-restricted' datasets (Data S5). The DAPC also found no genetic structure (Figure 3), supporting the results from STRUCTURE. Pairwise tests for genetic differentiation based on the 283-bp mtDNA control region fragment revealed significant structure between ALB WA and the two locations NSW and VIC/SA using F_{ST}, and between ALB WA and VIC/SA using Φ_{ST} (Table 4). All other pairwise comparisons were nonsignificant. The close genealogical relationships among all haplotypes (Figure 2) helps explain the difference observed between the F_{ST} and Φ_{ST} results.

3.4 | Global patterns of genetic differentiation

One thousand and thirteen individuals and 43 unique haplotypes, from seven regions in the Pacific Ocean (including SE AUS, this study), six regions in the Indian Ocean, and four regions in the Atlantic Ocean, were obtained from the 384-bp mtDNA dataset (Alexander et al., 2016, Supplementary Material 10; this study, Data S7). This included two novel 394-bp haplotypes identified in this study (Data S3, GenBank accession numbers MT939514 and MT939515). The reduced Alexander et al. (2016) 283-bp haplotype dataset matched haplotypes found in this study for SE AUS ($n = 72$; NSW, TAS, VIC/SA) and SW AUS ($n = 60$; ALB and CN) (Data S3). Only one variable site from the 394-bp fragment was lost in the 283-bp fragment. The resulting 283-bp dataset contained 28 unique haplotypes, including an additional two novel haplotypes that were identified in this study from SE AUS samples (Data S3, GenBank accession numbers MT939516 and MT939517).

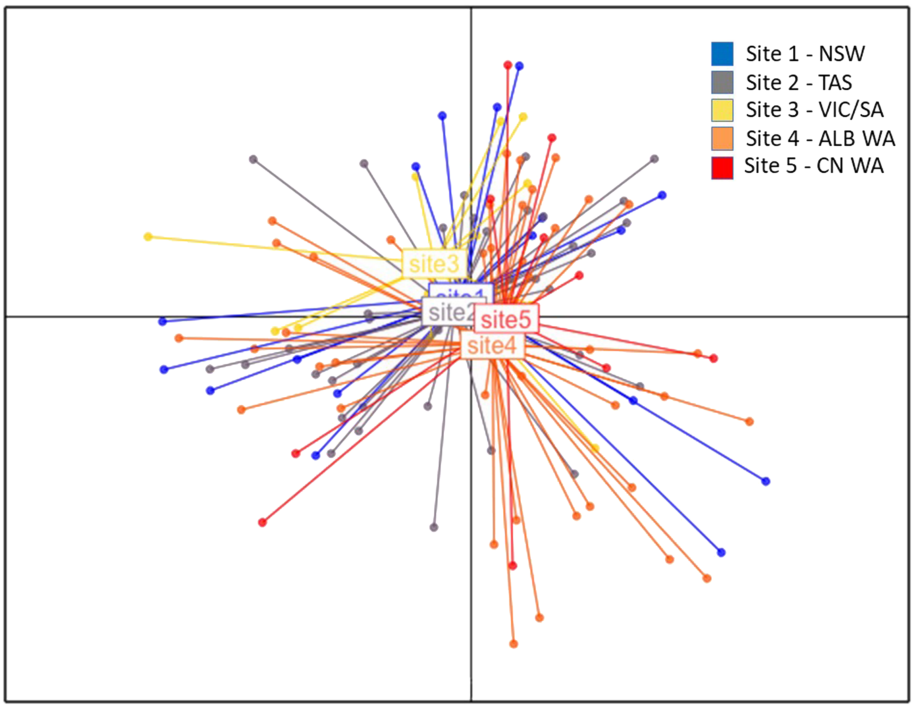

FIGURE 3 Results of the discriminant analysis of principal components performed for Australian sperm whales based on the 'kin-restricted' microsatellite dataset with 10 loci in Hardy–Weinberg equilibrium, with circle colours indicating sampling locations

TABLE 4 Genetic differentiation in Australian sperm whales based on the 283-bp mtDNA control region from the 'kin-restricted' mtDNA dataset of 132 samples

Region	NSW	TAS	VIC/SA	ALB WA	CN WA
NSW		0.035	−0.003	0.093*	−0.012
TAS	0.011		0.063	0.005	−0.032
VIC/SA	−0.003	0.043		0.156*	0.040
ALB WA	0.047	−0.004	0.092*		−0.039
CN WA	−0.012	−0.045	−0.002	−0.050	

Note: Φ_{ST} below the diagonal, F_{ST} above the diagonal.
*$P < 0.05$.
**$P < 0.01$.

Pairwise tests for mtDNA genetic differentiation based on the 394-bp fragment (Data S7) showed significant genetic differentiation between contemporary samples from SE AUS (this study) and SW AUS (Alexander et al., 2016) based on Φ_{ST} (0.1078), but not F_{ST} (0.0216). No significant genetic differentiation was observed between SE AUS and the following regions: Hawaii, Papua New Guinea, Cocos Islands, and Aldabras, and between SW AUS and Papua New Guinea, with either F_{ST} or Φ_{ST}. Significant differentiation was found, however, for all other comparisons with Australian samples (using F_{ST} and/or Φ_{ST}), especially for pairwise comparisons with regions sampled from the Atlantic Ocean (Data S7). Pairwise tests for mtDNA genetic differentiation based on the 283-bp fragment (Data S8) for SE AUS comparisons were similar to those found for the 394-bp fragment. Significant genetic differentiation was observed between historical and contemporary samples from SW AUS (F_{ST} = 0.1848, Φ_{ST} = 0.1587). Pairwise comparisons between historical and contemporary SW AUS samples with other regions in the Pacific and Indian Oceans were similar but not consistent (Data S8). These findings are also reflected in the levels of genetic variation observed among Australian samples (Data S9). For instance, haplotypic and nucleotide diversity were similar for contemporary samples collected from SE AUS and SW AUS, but reduced diversity was seen for SW AUS historical samples compared with contemporary samples (Data S9). The reduced diversity for historical SW AUS samples could be attributed to 70% of sampled individuals sequenced bearing haplotype 1 (Data S3), in contrast to 33% for the contemporary samples collected from the same broad region.

4 | DISCUSSION

This is the first study to examine the fine-scale population structure of sperm whales from south-eastern to south-western Australia and contributes to our understanding of global sperm whale population structure. Although the absence of genetic differentiation among sampling regions in Australia is congruent with the spatial scale of population structure found for this species (Lyrholm et al., 1999; Engelhaupt et al., 2009; Pinela et al., 2009; Mesnick et al., 2011; Alexander et al., 2016), these findings are integral to the future management of sperm whales around Australia as abundance estimates indicate that the population has not yet recovered since the end of whaling (Carroll et al., 2014).

Overall, levels of nDNA and mtDNA variation were similar to those reported by Alexander et al. (2016) for this geographical region, despite smaller sample sizes in their dataset. Levels of mtDNA variation in Australian sperm whales, and in sperm whales sampled from other areas in the Indian and Pacific Oceans were, however, considerably higher than in sperm whales from the Atlantic Ocean. Consistent with the lack of genetic structure, levels of genetic variation were

relatively similar across sampling regions for nDNA, regardless of whether contemporary or historical samples were used. For mtDNA, SW AUS (ALB WA, in particular) had the lowest haplotypic and nucleotide diversity despite samples being collected during the whaling era in the late 1950s and early 1960s. Lower levels of genetic variation were also detected when comparing historical samples from SW AUS (this study) and contemporary samples from this same region (Alexander et al., 2016). Based on the numbers of sperm whales killed during the whaling era, this result was unexpected as it was hypothesized that historical samples would show greater levels of genetic variation compared with contemporary samples from the same or nearby regions. Although the impact of whaling on sperm whale abundance in Australia could be readily detected off Albany in Western Australia (Carroll et al., 2014), the effect of whaling on genetic diversity may not be seen for some time because of the long generation time and complex social system of this species. Nevertheless, genetic diversity in sperm whales is markedly low compared with other cetacean species (Alexander et al., 2013; Morin et al., 2018). Recent population expansion or a selective sweep through adaptive cultural traits being transmitted in parallel with mitochondrial genes (cultural hitchhiking, sensu Whitehead, 1998) had been proposed as the most likely explanations for lower than expected diversity in mtDNA based on population size (Alexander et al., 2016; Whitehead, Vachon & Frasier, 2017). The absence of reduced nuclear genetic diversity in a species displaying strong female philopatry and male-biased dispersal is also consistent with a recent population expansion or cultural hitchhiking (Charlesworth, Charlesworth & Barton, 2003; Whitehead et al., 2017). Recent analysis of the sperm whale mitogenome and nuclear genome, however, suggests instead that demographic processes including a worldwide decline in effective population size prior to the start of the Pleistocene epoch followed by a recent population expansion, is primarily responsible for the low worldwide mtDNA diversity observed in sperm whales (Warren et al., 2017; Morin et al., 2018). Low mtDNA diversity and an absence of distinct lineage sorting between ocean basins on a global scale has largely been attributed to a possible expansion event of one refugial population in the Pacific Ocean that may have occurred approximately 80,000 years ago (Alexander et al., 2016; Morin et al., 2018).

Previous studies detected significant mtDNA genetic differentiation between the Atlantic, Pacific, and Indian oceans (including sperm whale samples from Australia), but not with microsatellites, suggesting limited female dispersal between ocean basins and gene flow mediated by roving adult males (Lyrholm & Gyllensten, 1998; Lyrholm et al., 1999; Alexander et al., 2016). There is evidence for bisexual philopatry of sperm whales within the eastern and central North Pacific (Mesnick et al., 2011), however, based on significant genetic differentiation detected using mtDNA and nDNA markers. At the regional level, there are higher levels of genetic differentiation in mtDNA within the Atlantic and Indian oceans compared with the Pacific Ocean, and these ocean basin differences are attributed to differences in ranging patterns, habitats, culture, and demographic history (Alexander et al., 2016). This study, however, detected little genetic structure between sperm whales sampled in the Indian (SW AUS) and Pacific (SE AUS) Oceans for either mtDNA or nDNA, nor between Australia and some nearby regions in the Indian and Pacific Oceans (e.g., Papua New Guinea, Hawaii, and Cocos Island) for mtDNA. Thus, although many studies focus on between- and within-ocean genetic differentiation, genetic discontinuities at ocean basin boundaries cannot always be assumed for this species.

Genetic distinction of populations (or stocks) has also been observed in Australian waters for other whale species. For instance, humpback whale breeding stocks on the east and west coasts of Australia were significantly differentiated from each other, as well as from all other southern hemisphere stocks, including those found nearby in the Western South Pacific islands of Oceania (Anderson, 2013; Rosenbaum et al., 2017). Carroll et al. (2011) determined that south-west and south-east Australian stocks of southern right whales were genetically distinct based on mtDNA, and both were genetically differentiated from the New Zealand stock based on mtDNA and microsatellites. Similar patterns have been observed in other highly mobile or migratory marine species found in Australian waters, including many shark species (Castro et al., 2007; Ovenden et al., 2009; Corrigan et al., 2018) As found in these studies, population structure cannot simply be explained by spatial distance and oceanographic features such as ocean boundaries, current systems, and bathymetry. Instead, a multitude of other factors may influence patterns of genetic variation and population structure in sperm whales, including the social system, culturally determined vocalizations and movement patterns, predation pressure, prey distribution, impact of human exploitation, and prior population expansion or bottleneck events (Jaquet & Gendron, 2009; Rendell et al., 2012; Whitehead et al., 2012; Alexander et al., 2016). Understanding the relative influence of each of these factors on patterns of population structure will require further sampling, more in-depth genomic analysis using SNPs or whole-genome sequencing, and a greater understanding of the movement patterns and social structure of sperm whales in the South Pacific and Indian Oceans.

4.1 | Recovery and management of sperm whales in Australia

The current management recommendations for sperm whales in Australian waters are based on the IWC's 'Division 5' and 'Division 6' stock boundaries. This study, however, showed little evidence of genetic structuring, suggesting that sperm whales from south-eastern to south-western Australia should be managed as a single population. A lack of female samples from NSW and CN WA may have hampered our ability to detect genetic differentiation, especially considering the complex social structure and male-biased dispersal system that is characteristic of this species. Sampling sperm whale aggregations from other locations in Australian waters and generating genomic data, including samples from nearby regions in the South Pacific and Indian oceans, may provide more precise estimates of genetic divergence and migration rates.

Our ability to monitor sperm whale population abundance and trends in Australian waters is hampered by a paucity of knowledge of movement patterns and contemporary rates of breeding and mortality. The finding that the 'Division 5' and 'Division 6' stocks belong to the same genetic population suggests that different anthropogenic threats in different regions of Australia may negatively affect the entire population (Attard et al., 2018). At the same time, genetic differentiation between sperm whales in Australian waters and other populations in the Indian and Pacific Oceans may increase their susceptibility to further population decline because of increasing anthropogenic impacts. Given that we identified distinct maternal lineages in different Australian regions, knowledge of where aggregations display biologically important behaviour, such as breeding, foraging, and resting (i.e. biologically important areas, BIAs), could help inform regional conservation priorities. Identifying and minimizing threats in BIAs could reduce mortality, improve reproductive fitness, and preserve cultural knowledge. This would in turn minimize further loss of genetic diversity and maximize the species evolutionary potential to adapt to changing climatic conditions and oceanographic processes. Potential causes for the lack of recovery of sperm whale numbers worldwide include: long-term demographic consequences from whaling, such as a reduction in female reproductive rates (Whitehead, 2003; Rankin & Kokko, 2007; Chiquet et al., 2013); marine pollution (de Swart et al., 1996; Symons et al., 2003; Evans, Hindell & Hince, 2004; Roos et al., 2012); environmental noise, fishing gear entanglements, and ship strikes (Mate, Stafford & Ljungblad, 1994; Reeves & Notarbartolo Di Sciara, 2006; Chiquet et al., 2013; Gero & Whitehead, 2016); and climate change (Sousa et al., 2019).

Currently, sperm whales are listed as Vulnerable by the IUCN and by some Australian state legislative authorities. They are protected legally in Australia and by IWC regulations and other international agreements throughout their range, including the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). A conservation management plan (CMP), similar to the CMPs implemented for southern right and blue whales, however, has not been developed under Australian legislation or by the IWC. General policies and regulations managing some threats, such as interactions with fishing gear, seismic activities, and whale watching, are in force, which may benefit cetacean species in general, including sperm whales (Australian Fisheries Management Authority (AFMA), 2017; Woinarski, Burbidge & Harrison, 2014). Goals in future sperm whale recovery plans should include measuring and monitoring population size and trends in Australian waters, strengthening national and international legislation and agreements to protect sperm whales, and implementing adaptive management regimes to reduce anthropogenic causes of mortality in Australian waters. Furthermore, given the extensive home ranges of sperm whales, multinational collaborative efforts to reduce the impact of anthropogenic threats and the coordination of population monitoring should be included in the recovery goals.

In conclusion, considering the results indicating a single population of sperm whales in Australian waters, and genetic distinctiveness to other southern hemisphere stocks, a precautionary approach to population management that is cross-jurisdictional and addresses the primary anthropogenic threats to sperm whales is required. Combined with further research to understand population movements, abundance trends, the impact of anthropogenic threats, and the effectiveness of threat mitigation strategies for this species will help to assist in the recovery of sperm whales worldwide.

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ORCID

Joanna Day https://orcid.org/0000-0001-9390-7506
Maxine P. Piggott https://orcid.org/0000-0002-7307-708X
Kerstin Bilgmann https://orcid.org/0000-0003-0681-2301
Robert Harcourt https://orcid.org/0000-0003-4666-2934
Luciano B. Beheregaray https://orcid.org/0000-0003-0944-3003
Luciana M. Möller https://orcid.org/0000-0002-7293-5847

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SUPPORTING INFORMATION

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