RESEARCH ARTICLE

Hierarchical metapopulation structure in a highly mobile marine predator: the southern Australian coastal bottlenose dolphin (*Tursiops* cf. *australis*)

Eleanor A. L. Pratt[1,2] · Luciano B. Beheregaray[1] · Kerstin Bilgmann[1,2,3] · Nikki Zanardo[1,2] · Fernando Diaz-Aguirre[1,2] · Luciana M. Möller[1,2]

Abstract

Little is known about the population ecology of the recently described bottlenose dolphin species *Tursiops australis*. The classification of this species is still under debate, but this putative species is thought to be comprised of small and genetically distinct populations (including sub-populations under increasing anthropogenic threats) and is likely endemic to coastal southern Australia. Mitochondrial DNA (mtDNA) control region sequences and microsatellite loci were used to assess genetic variation and hierarchical population structure of coastal *T*. cf. *australis* across a range of spatial scales and environmental discontinuities between southern Western Australia (WA) and central South Australia (SA). Overall, genetic diversity was similar to that typically found for bottlenose dolphins, although very low mtDNA diversity was found in Gulf St. Vincent (GSV) dolphins. We found historical genetic subdivision and likely differences in colonisation between GSV and Spencer Gulf, outer- and inner-gulf locations, and SA/WA and previously identified Victorian/Tasmanian populations. A hierarchical metapopulation structure was revealed along southern Australia, with at least six genetic populations occurring between Esperance, WA and southern Tasmania. In addition, fine-scale genetic subdivision was observed within each SA/WA population. In general, contemporary migration was limited throughout southern Australia, but an important gene flow pathway was identified eastward along the Great Australian Bight. Management strategies that promote gene flow among populations should be implemented to assist with the maintenance of the inferred metapopulation structure. Further research into the population ecology of this species is needed to facilitate well-informed management decisions.

Keywords *Tursiops australis* · Conservation genetics · Phylogeography · Management units · Gene flow · Cetacean

✉ Luciana M. Möller
luciana.moller@flinders.edu.au

[1] Molecular Ecology Laboratory, College of Science and Engineering, Flinders University, Bedford Park, SA 5042, Australia

[2] Cetacean Ecology, Behaviour and Evolution Laboratory, College of Science and Engineering, Flinders University, Bedford Park, SA 5042, Australia

[3] Department of Biological Sciences, Faculty of Science and Engineering, Macquarie University, Sydney, NSW 2109, Australia

Introduction

Worldwide, populations of large mammals are experiencing major declines, with an estimated 25% of mammal species threatened with extinction, and a further 836 species classified as 'data deficient' (Schipper et al. 2008). Marine mammals, particularly cetaceans, are amongst the most endangered taxa due to anthropogenic threats and several life-history characteristics that restrict their adaptation to changing environments and human-induced impacts (Schipper et al. 2008; Magera et al. 2013). Informed management decisions are crucial for the conservation of these animals. Population genetics plays a central role in improving conservation efforts, allowing important population parameters to be estimated, such as genetic diversity and rates of migration between populations (Hedrick 2001). By gaining a better understanding of threats affecting particular populations,

management bodies can improve the efficacy of conservation strategies.

Cetaceans are highly mobile marine mammals with the ability to disperse over vast distances in search of suitable foraging and nursery grounds (Boyd 2004). Despite this, many cetaceans exhibit considerably higher levels of population genetic structure than expected (e.g. Bilgmann et al. 2007a; Möller et al. 2011; Perez-Alvarez et al. 2015). Physical barriers to the dispersal of cetaceans in the oceans are not common, but gene flow among dolphin populations can be affected by other several factors, such as oceanographic features (e.g. Natoli et al. 2005; Bilgmann et al. 2008; Mendez et al. 2010), complex social structures and dispersal patterns (reviewed in Möller 2011), and discontinuous prey distributions (e.g. Dowling and Brown 1993; Bilgmann et al. 2007a). These factors impact on dolphin species to varying degrees, and often the level of genetic structuring among populations within species can differ dramatically (e.g. *D. delphis*, Bilgmann et al. 2008; Querouil et al. 2010; Moura et al. 2013; Amaral et al. 2012; *Stenella frontalis*; Caballero et al. 2013; Viricel and Rosel 2014).

Globally, bottlenose dolphins (*Tursiops* spp.) exhibit complex patterns of population genetic structure. Coastal bottlenose dolphins often exhibit fine-scale population genetic structure (e.g. Möller et al. 2007; Fruet et al. 2014; Charlton-Robb et al. 2015), while oceanic populations typically maintain higher gene flow levels (Querouil et al. 2007; Silva et al. 2008). In addition, adjacent coastal and oceanic populations often differ both genetically and morphologically (Mead and Potter 1995; Hoelzel et al. 1998; Lowther-Thieleking et al. 2015). Genetic breaks in *Tursiops* populations are typically associated with differences in oceanographic and ecological features (e.g. Hoelzel et al. 1998; Natoli et al. 2005; Bilgmann et al. 2007a). Differential dispersal patterns between sexes are also thought to impact substantially on bottlenose dolphin population structure, particularly in coastal populations where female philopatry is common (Möller and Beheregaray 2004; Wiszniewski et al. 2010).

Clarifying dolphin metapopulation structure and dynamics helps to identify small and localised biological units potentially at risk of extinction through demographic and genetic stochasticity. It has been suggested that a pattern of partly-isolated and distinct genetic populations is typical of the recently described bottlenose dolphin species (*Tursiops australis)*, which appears to be endemic to coastal southern Australian waters (Möller et al. 2008; Charlton-Robb et al. 2011, 2015). The recognition of *T. australis* as a separate species is still under debate among marine mammal scientists. As such, the populations from coastal southern Australia are referred herein as *T.* cf. *australis*. Charlton-Robb et al. (2015) described two genetically distinct populations in the eastern region of the species range [i.e. Victoria (VIC) and Tasmania (TAS)], while Bilgmann et al. (2007a)

documented two additional populations in the central range of the species [i.e. around Spencer Gulf (SG) in South Australia (SA)]. Those in SA are thought to be separated by environmental differences between coastal habitats within SG and adjacent waters outside the gulf (Bilgmann et al. 2007a). Southern Australian bottlenose dolphin populations often reside in inshore and nearshore waters in close proximity to areas highly impacted by human activities, such as shipping, commercial and recreational fishing, aquaculture, tourism, and pollution (Bilgmann et al. 2007a; Charlton-Robb et al. 2015; Zanardo et al. 2016), as well as potential upcoming oil mining areas in the Great Australian Bight (see Chevron Australia 2016). Ongoing threats increase the vulnerability of these bottlenose dolphins to population disturbances, declines and/or extinction, and highlight the importance of well-informed conservation strategies.

In this study, we elucidate the metapopulation structure of coastal bottlenose dolphins (*T.* cf. *australis)* in southern Australia by carrying out complementary phylogeographic and population genetic analyses using mitochondrial DNA (mtDNA) and nuclear datasets. For the purposes of this study, a genetic population can be defined in a similar manner to a 'management unit (MU)', being "demographically independent populations" based on statistically significant genetic differentiation (and thus low gene flow) at the nuclear level (see Palsbøll et al. 2007). We test for hierarchical population structure and investigate if population connectivity is influenced by spatial distance between demes, by major environmental discontinuities, or by sex-biased dispersal. This was achieved by analysing samples from putative populations between southern Western Australia (WA) and central SA, including nested sampling within two gulfs and one embayment. Additionally, we compared the mtDNA of dolphins from our study region to those of samples collected from the eastern range of the species in VIC and TAS (Charlton-Robb et al. 2015), therefore covering most of the species' range. Our findings provide timely information that is currently lacking on patterns of connectivity in a top predator across the marine park networks along the southern Australia coastline. We report on the metapopulation connectivity and on the number of population units for *T.* cf. *australis* for over 2000 km of southern Australia's coast, providing novel information for conservation management of this species.

Materials and methods

Study sites and sample collection

Biopsy samples from free-ranging bottlenose dolphins (*T.* cf. *australis*) were collected from various vessels between 2004 and 2015 at 11 locations in southern Australian waters

from inner-gulf (inside Gulf St. Vincent or Spencer Gulf) and open-coast (outside of these gulfs) habitats (Fig. 1; Table S1). Our study substantially extends the geographic coverage of population genetics work done with this species (Bilgmann et al. 2007a; Charlton-Robb et al. 2015). The locations sampled include, for the first time, several sites representing the two SA gulfs and samples from southwestern Australia. Skin and blubber samples were collected from individuals using either a hand-held biopsy pole for bow-riding dolphins (Bilgmann et al. 2007b) or a remote biopsy gun system (Krützen et al. 2002). Resampling of individuals was minimised by visually checking for biopsy wound marks on the animal's body and through identification of recognisable dorsal fin characteristics. No samples were obtained from dependent calves. Biopsy samples were preserved in either 90% ethanol or a salt-saturated solution of 20% dimethyl sulphoxide (DMSO), and later stored at −80 °C.

Genetic methods

DNA extraction and molecular sexing

DNA was extracted from biopsy samples using the salting-out protocol (Sunnucks and Hales 1996) and quantified using a ND-1000 spectrophotometer (NanoDrop). The sex of individual dolphins was genetically determined by using the polymerase chain reaction (PCR) to amplify fragments of the ZFX and SRY genes on the X and Y chromosomes respectively, following a protocol originally developed by Gilson et al. (1998), and performed as per conditions reported in Möller et al. (2001).

mtDNA sequencing and comparison with published data from the eastern range of the species

A mtDNA control region fragment of approximately 450 base pairs (bp) in length was amplified for 134 samples (as per supplementary material). Purified PCR products were sequenced via capillary electrophoresis conducted on an Applied Biosystems ABI 3730xl DNA analyser. Ninety-two control region sequences of samples collected in 2004/05 were previously available from Bilgmann et al. (2007a). We also compared our mtDNA results with 159 published *T. australis* control region sequences (GenBank accession numbers JN571464 to JN571469 and JN571481; trimmed to 418 bp) of samples collected from the eastern-most known range of the species in Victoria (VIC) and Tasmania (TAS) (Charlton-Robb et al. 2015).

Microsatellite genotyping

A total of 175 individuals were genotyped using 11 polymorphic cetacean nuclear microsatellite loci (as per supplementary material). Although many of the individuals genotyped were the same as those sequenced for the mtDNA control region, sample size differences exist between the two datasets due to a number of poor quality mtDNA control region sequences. We also had mtDNA control region sequences for a number of individuals for which tissue was no longer available, and consequently microsatellite analysis could not be completed. Samples were mixed with an internal size standard and run on an ABI 3130 Genetic Analyser. Allele fragment sizes were scored using GENEMAPPER v.4.1 (Applied Biosystems), and checked individually.

Statistical analyses

mtDNA analysis

A total of 134 mtDNA control region sequences were cleaned and 226 sequences [134 from this study and 92 from Bilgmann et al. (2007a)] were aligned using SEQUENCER v5.2.4 (Gene Codes Corporation, Ann Arbor, MI, USA) resulting in a 437 bp fragment. ARLEQUIN v3.5.2.2 (Excoffier and Lischer 2010) was used to estimate nucleotide and haplotypic diversity for each putative population based on sampling location. Pairwise genetic differentiation between putative populations, and the associated statistical significance was calculated in ARLEQUIN based on 10,000 permutations. Genetic differentiation was estimated by F_{ST}, which takes only haplotype frequency into account, and Φ_{ST}, which also incorporates a genetic distance [Tamura and Nei (1993) with gamma correction, $\alpha = 0.5$ as previously used for *T.* cf. *australis* (Bilgmann et al. 2007a)]. To balance the risks of Type 1 and 2 errors significance levels for all multiple tests (including microsatellite analyses) were corrected using Benjamini and Yekutieli's (2001) method (B–Y correction) (see Narum 2006). A median-joining network of haplotypes was constructed in NETWORK v.4.6.1.3 with default settings (Bandelt et al. 1999) to investigate genealogical relationships among mtDNA control region haplotypes. Pairwise genetic differentiation and the median-joining haplotype network were then re-analysed with the addition of 159 *T.* cf. *australis* sequences (418 bp) from VIC and TAS (Charlton-Robb et al. 2015) to gauge maternally-derived patterns of population structure on a larger geographic scale.

Microsatellite analysis

The microsatellite dataset was screened for potential scoring errors, presence of null alleles, stuttering and large allelic dropout using MICROCHECKER v2.2.3 (Van Oosterhout et al. 2004). Samples of the same sex, and with identical mtDNA haplotypes and microsatellite genotypes [identified using GenAlEx v6.5 (Peakall and Smouse 2006, 2012)], were considered to be the same individual and were included
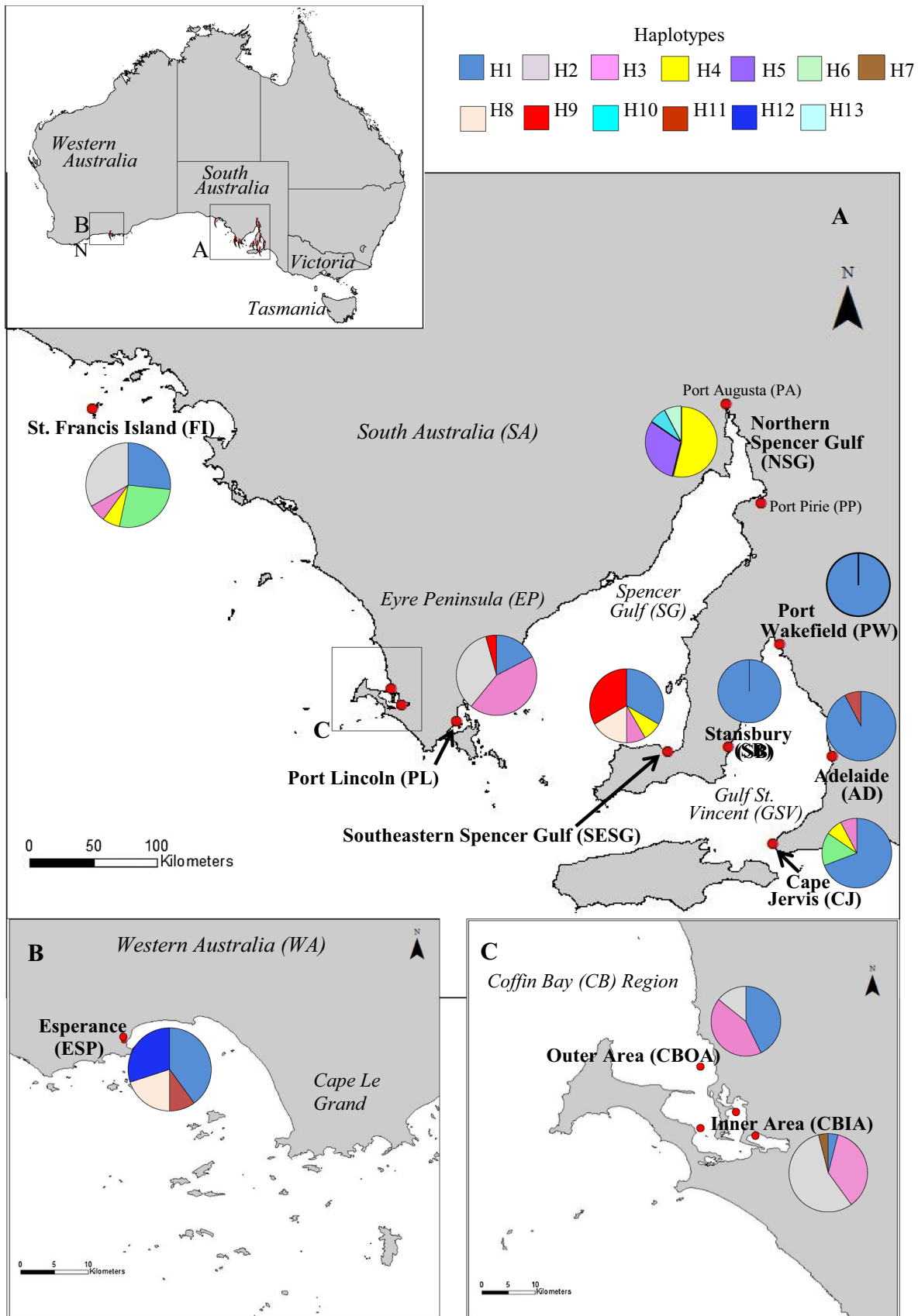
◄**Fig. 1** Map of southern Australia, illustrating *Tursiops* cf. *australis* biopsy sampling locations, and mitochondrial DNA (mtDNA) control region haplotype distribution. Pie charts lie adjacent to the respective sampling locations. Coloured sectors are proportional to the number of individuals bearing a given haplotype in each location. (Color figure online)

only once in the dataset. Relatedness estimates were calculated in GenAlEx based on the Queller and Goodnight (1989) estimator. Estimates of ≥ 0.5 indicate likely first-order relatives, as a mean relatedness value of 0.5 is expected for parent-offspring pairs and full siblings (DeWoody et al. 2010). Twelve likely first-order relative pairs were found, none of which had individuals from different putative populations, and as such, one of each pair was removed from the original dataset to avoid analytical biases.

Tests for linkage disequilibrium (B–Y corrected $\alpha = 0.0108$) and exact tests for departures from Hardy–Weinberg equilibrium (HWE) (B–Y corrected $\alpha = 0.0165$) were conducted for each putative population in GENEPOP v.4.2 (Raymond and Rousset 1995; Rousset 2008) based on the Markov chain method and 1000 iterations. ARLEQUIN was used to calculate the mean number of alleles per locus, and mean observed and expected heterozygosity for each sampling location. Allelic richness for each sampling location was calculated in FSTAT v.2.9.3.2 (Goudet 2001).

F_{ST} values were calculated in ARLEQUIN to determine genetic differentiation levels and corresponding statistical significance among pairs of sampling sites, based on 10,000 permutations. F_{ST} was chosen as it is a relatively conservative measure for estimation of population differentiation when sample sizes and the number of loci are relatively small (Gaggiotti et al. 1999). Confidence intervals were calculated for F_{ST} estimates using the R package 'diveRsity' (Keenan et al. 2013). Coffin Bay (CB) area samples were collected in both 2005 and in 2014/2015, providing a temporal comparison of genetic differentiation in this area. Based on microsatellite F_{ST} values, no significant genetic differentiation was found between the two CB datasets (Table S3). We thus removed the 2005 samples from the dataset in order to retain a similar sample size among all localities [CBIA n = 25/28 (mtDNA/microsatellites) compared to n = 10–26 for each other site]. Samples from different embayments in the inner area of CB (known to belong to different social communities of dolphins (Diaz-Aguirre et al. unpublished data)] exhibited no significant genetic differentiation (Table S3) and were combined to putatively form the inner CB population. Port Augusta (PA) and Port Pirie (PP) samples, and northern and southern Adelaide social communities (Zanardo et al. unpublished data) also demonstrated no significant differentiation between respective location pairs and were subsequently merged to represent northern Spencer Gulf (NSG) and the Adelaide metropolitan

coast, respectively (Table S3). While we acknowledge that sample sizes in some cases, particularly northern SG, were too low to return reliable F_{ST} estimates, using these estimates to group individuals from different sampling locations that were not significantly genetically differentiated from one another was necessary to improve sample sizes for these locations for further analyses. Further sampling in northern SG is needed to better elucidate the population genetic structure in that region. Jost's D (Jost 2008) was also calculated to determine pairwise genetic differentiation among sampling locations, based on 10,000 permutations in GenAlEx. Jost's D is independent of genetic variation, allowing it to be used when there is high genetic variation within populations, a situation where F_{ST} may underestimate differentiation (Jost 2008; Bird et al. 2011).

The Bayesian clustering method employed in STRUCTURE v.2.3.4 (Hubisz et al. 2009) was used to test for the presence of population structure and identify the most likely number of genetic clusters (K) in the dataset. This method was implemented with, and then again without, prior sampling location information provided. The initial burn-in period of 200,000 iterations was followed by 10^6 Markov chain Monte Carlo (MCMC) repetitions, for K values one to 14 [K_{max} = number of sampling locations + number of known social communities in CB and Adelaide metropolitan coast based on photo-identification studies (Diaz-Aguirre et al. unpublished data; Zanardo et al. unpublished data)] using both the admixture and correlated allele frequency models (P(X/K)), and 20 iterations for each K value. Based on the results, the dataset was then separated into sites to the east and west of Eyre Peninsula (EP) to investigate the potential presence of hierarchical genetic structure. Values of K between one and ten, and one and seven, were used for the eastern and western sites respectively, along with the same initial parameter settings. The dataset was further split into four genetic populations, and STRUCTURE re-run with the same initial parameter settings and K values between one and four for both the CBIA/CBOA and SG datasets, between one and three for the ESP/FI dataset, and between one and five for the GSV/CJ dataset. STRUCTURE HARVESTER (Earl and vonHoldt 2012) was used to estimate the most likely K from the STRUCTURE results using both the Evanno and log-likelihood (L(K)) methods (described in Evanno et al. 2005). CLUMPAK (Kompelman et al. 2015) was implemented to combine the graphs created from the iterations of each K value. A discriminant analysis of principal components (DAPC) using the R package 'adegenet' (Jombart et al. 2010; Jombart and Ahmed 2011) was then run to further test for the presence of hierarchical structure as inferred by STRUCTURE, by assigning sites to the east and west of EP to two separate clusters and testing for significant divergence between them. The 'find.

clusters' function in adegenet was also used to determine the most likely number of genetic clusters in the dataset. One hundred principal components were retained, as was the first discriminant function. Finally, ARLEQUIN was used to perform a hierarchical analysis of molecular variance (AMOVA) grouping locations based on the STRUCTURE results to better assess the distribution of genetic variation in regard to hierarchical structure. Significance was tested with 10,000 permutations.

Isolation by distance (IBD) was tested using IBDWS v.3.23 (Jensen et al. 2005) to assess the relationship between genetic [linearised F_{ST} ($F_{ST}/(1−F_{ST})$)] and seascape geographical distance. Tests were done both including and excluding Esperance (WA), as this was the most geographically separated sampling location. A stratified Mantel test using linearised F_{ST} was run in GENODIVE v2.0b27 (Meirmans and Van Tienderen 2004) due to the potential presence of hierarchical structure (see STRUCTURE results). This test has been shown to distinguish between patterns resulting from clustering compared to those from IBD (Meirmans 2012). Statistical significance was evaluated using 10,000 permutations. The geographical distance matrix was calculated using Google Earth (2012) following the shortest nearshore distance between each sampling location. This is the most likely path of travel for *T.* cf. *australis* moving between areas [confirmed from aerial survey sightings throughout the sampling region (Bilgmann et al. unpublished data)].

The magnitude and direction of contemporary gene flow (over the last few generations) among the four identified genetic populations (see STRUCTURE results) was estimated using the Bayesian multilocus approach implemented in BAYESASS v.3.0 (Wilson and Rannala 2003). Four independent runs were performed using 10^6 burn-in and 10^7 MCMC repetitions, and a sampling interval of 100. The mixing parameters (migration rates, allele frequencies and inbreeding coefficients) were adjusted to 0.20 in order to obtain acceptance rates of 20–60%, as suggested by Rannala (2007). Convergence was examined by conducting four independent runs initialised with different seeds, and then comparing the posterior mean parameter estimates for concordance among runs.

The potential for sex-biased dispersal was investigated using GenAlEx to calculate corrected assignment indices (*AIc*) for both sexes in the four identified genetic populations (see STRUCTURE results). Under the method utilised by GenAlEx, assignment indices (*AI*) are corrected for population effects by subtracting population means after log-transformation. Significance was tested with a two-tailed U-test. To test the reliability of these results, FSTAT was also used to establish mean relatedness (*R*) between same-sex pairs, using 100 randomisations.

Results

Genetic variation

Mitochondrial DNA

A 437 bp fragment of the mtDNA control region was analysed for 178 *T.* cf. *australis* samples (excludes CB 2005 samples, likely first-order relatives and duplicate samples). This revealed the presence of 13 haplotypes in the sampled putative populations, including three novel haplotypes for the species (H11, H12, H13; Fig. 2 and Fig. S1). Between one and five haplotypes were identified at each sampling location. Gulf St. Vincent (GSV) dolphins had considerably lower haplotypic and nucleotide diversity compared to all other locations, while SG communities showed diversity levels more consistent with open-coast dolphins (Table 1). VIC and TAS populations (based on a 418 bp fragment) displayed a similar pattern of variability in nucleotide and haplotypic diversity among locations (Table S2).

Microsatellite data

Nuclear DNA diversity varied little among locations, but was in general slightly lower for embayment and gulf populations (Table 1). Levels of observed and expected heterozygosities were similar across all putative populations (Table 1). There was no evidence for linkage disequilibrium, or significant deviations from HWE that were consistent across loci and populations (Table 1).

Genetic differentiation

Mitochondrial DNA

In general, pairwise mtDNA control region genetic differentiation using F_{ST} and Φ_{ST} estimated similar levels of differentiation, revealing contrasting patterns in the two SA gulfs. While all SG sample locations were found to be highly differentiated from one another ($F_{ST} = 0.206–0.463$), GSV locations were not significantly different from each other ($F_{ST} = 0.000–0.006$; Table 2). Similarly, samples from the outer (CBOA) and inner (CBIA) CB areas were not significantly differentiated (Table 2). There was little haplotype sharing (Fig. 1) and a variable pattern of moderate differentiation (Table 2) between gulfs, and inner-gulf and open-coast communities.

The haplotype network proposed haplotype 1 (H1) as the ancestral haplotype [in agreement with Bilgmann et al. (2007a)]. The shape of the network suggests recent matrilineal diversification in SA and WA (Fig. 2; Fig. S1)
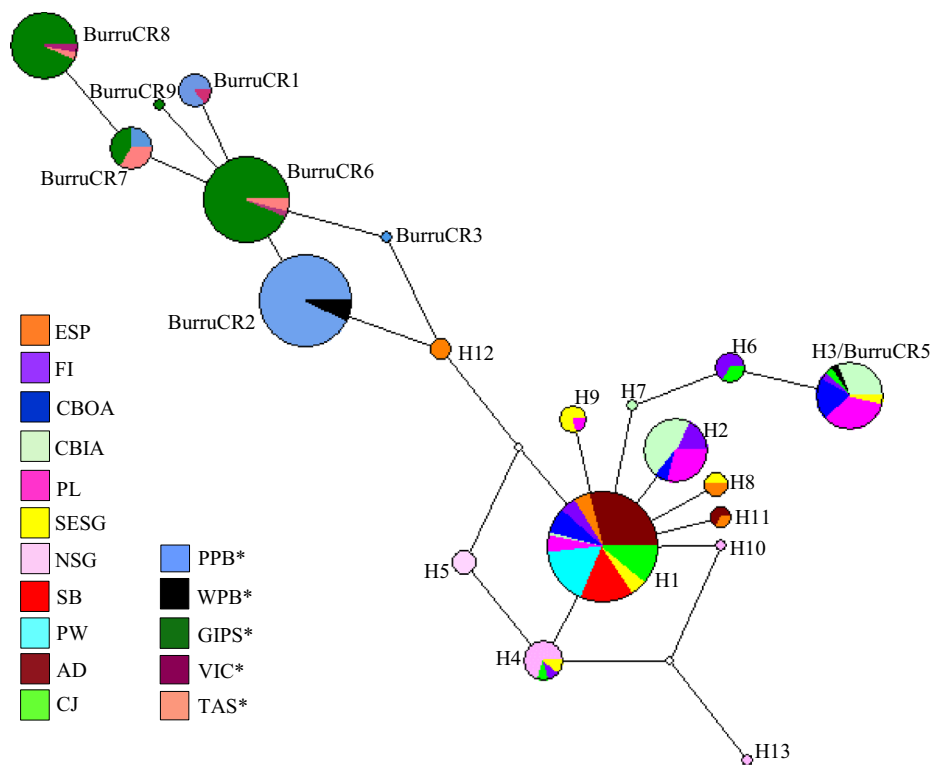
Fig. 2 Median-joining network of 178 *Tursiops* cf. *australis* mtDNA control region haplotypes (437 bp) from southern Australia (haplotypes beginning with 'H'), and 159 *T. australis* control region haplotypes (418 bp) from southeastern Australia (see Charlton-Robb et al. 2015 for geographic locations; locations marked with an asterisk (*), haplotypes beginning with "BurruCR"). The size of the circles is proportional to the total number of individuals bearing that haplotype; black connecting lines represent one mutational step between haplotypes; small white circles represent missing haplotypes; coloured sectors in circles are proportional to the number of individuals bearing a given haplotype at each sampled location. Location abbreviation explanations are given in Fig. 1 and Table 1, or for locations marked with an asterisk in Table S1. Haplotypes are named in line with those published by Bilgmann et al. (2007a) (GenBank accession numbers EF192140 to EF192149) and Charlton-Robb et al. (2015) (GenBank accession numbers JN571464 to JN571469 and JN571481). (Color figure online)

demonstrated by sampled haplotypes being a maximum of three mutational steps from H1. This is consistent with the low levels of nucleotide diversity found, particularly in GSV (Table 2). GSV dolphins had an almost uniform distribution of H1, with only 3.5% of sampled individuals having another haplotype (H11). Conversely, nine haplotypes were found in SG dolphins, with four unique to this gulf (Fig. 1). A 418 bp fragment of the mtDNA control region was then used to compare samples from our study region to VIC and TAS populations. There was only one haplotype (H3/BurruCR5) that was represented in both the VIC and TAS, and SA and WA populations. This haplotype was reported in one individual from Westernport Bay in VIC, and 27 individuals throughout central and western southern Australia (Fig. 2). All other sampled haplotypes from VIC and TAS were three to six mutational steps from H1 (Fig. 2), suggesting a relatively longer period of isolation between than within dolphins from these two regions (central/western vs eastern southern Australia). MtDNA differentiation estimates supported this, showing that samples from VIC and TAS were

generally highly differentiated from all populations in SA and WA (Table 2).

Microsatellite data

While the two microsatellite fixation indices showed a similar pattern of differentiation among sampling sites, overall Jost's D estimated higher levels of divergence. This indicates that F_{ST} may have underestimated population differentiation due to high levels of genetic variation within populations (Jost 2008; Bird et al. 2011). The highest levels of divergence were found between gulf and open-coast localities ($F_{ST} = 0.023$–0.182; Table 3). GSV sample locations exhibited low levels of differentiation from one another ($F_{ST} = 0.014$–0.026), while SG locations demonstrated considerably higher differentiation ($F_{ST} = 0.037$–0.074; Table 3), although there was some overlap in the confidence intervals for F_{ST} estimates among sites from the two gulfs (Table S4). Significant differentiation was revealed between CBOA and CBIA populations (Table 3), which attests for the power

Table 1 Summary of genetic variability for *Tursiops* cf. *australis* in southern Australia based on 178 mitochondrial DNA (mtDNA) control region sequences (437 bp) and 11 microsatellite loci for 175 samples

Location (abbreviation)	Mitochondrial DNA					Microsatellites						
	n	M/F	NH	h	π	n	M/F	NA	AR	H_E	H_O	HWE
Esperance (ESP)	10	6/4	4	0.778 (0.091)	0.0035 (0.0026)	10	6/4	4.73	4.59	0.667 (0.118)	0.664 (0.201)	0.824
St. Francis Island (FI)	15	7/6*	5	0.791 (0.059)	0.0039 (0.0027)	13	7/6	5.00	4.60	0.699 (0.097)	0.719 (0.190)	0.253
Coffin Bay—Outer Area (CBOA)	14	9/4	3	0.659 (0.072)	0.0044 (0.0029)	15	10/4	4.27	3.85	0.602 (0.157)	0.552 (0.202)	0.103
Coffin Bay—Inner Area (CBIA)	25	6/19	4	0.577 (0.066)	0.0047 (0.0030)	28	7/21	4.64	3.82	0.619 (0.141)	0.610 (0.174)	0.706
Port Lincoln (PL)	23	6/16*	4	0.688 (0.055)	0.0049 (0.0032)	17	5/12	4.27	3.87	0.649 (0.121)	0.647 (0.174)	0.148
Northern Spencer Gulf (NSG)	13	9/4	4	0.654 (0.106)	0.0025 (0.0019)	11	9/2	4.00	3.81	0.541 (0.155)	0.526 (0.197)	0.896
Southeastern Spencer Gulf (SESG)	12	5/7	5	0.803 (0.078)	0.0034 (0.0025)	10	3/7	4.73	4.59	0.699 (0.064)	0.646 (0.144)	0.209
Stansbury (SB)	13	10/3	1	0.000 (0.000)	0.0000 (0.0000)	16	13/3	4.27	3.79	0.619 (0.139)	0.642 (0.173)	0.999
Port Wakefield (PW)	14	7/7	1	0.000 (0.000)	0.0000 (0.0000)	15	8/7	3.90	3.59	0.620 (0.140)	0.648 (0.246)	0.495
Adelaide (AD)	26	12/14	2	0.148 (0.089)	0.0003 (0.0005)	26	12/14	4.55	3.97	0.650 (0.103)	0.626 (0.113)	0.190
Cape Jervis (CJ)	13	6/7	5	0.526 (0.153)	0.0025 (0.0019)	14	7/7	4.55	4.21	0.692 (0.087)	0.678 (0.101)	0.884

Locations are ordered by geographic position from west to east

n sample size [likely first-order relatives removed (Queller and Goodnight index (1989), r ≥ 0.5)], *M/F* number of males/females, *NH* number of haplotypes, *h* haplotypic diversity, *π* nucleotide diversity, *NA* mean number of alleles per locus, *AR* allelic richness, H_E mean expected heterozygosity, H_O mean observed heterozygosity, *HWE* Hardy–Weinberg equilibrium, *2 FI, and 1 PL sample/s of unidentified sex used for mtDNA analysis. Standard errors shown in parentheses. *Note* sample size differences exist in mtDNA and microsatellite datasets due to a number of poor quality mtDNA control region sequences, and the availability of mtDNA control region sequences for a number of individuals for which tissue was no longer available and consequently microsatellite analysis could not be completed

Table 2 Pairwise fixation indices between 11 sampling locations in southern Australia based on 178 *Tursiops* cf. *australis* mitochondrial DNA (mtDNA) control regions sequences (437 bp)

	ESP	FI	CBOA	CBIA	PL	NSG	SESG	SB	PW	AD	CJ	PPB*	WPB*	GIPS*	VIC*	TAS*
ESP (10)		**0.215**	**0.280**	**0.313**	**0.290**	**0.423**	0.114	0.208	0.220	0.266	0.158	**0.748**	0.478	**0.766**	**0.663**	**0.746**
FI (15)	0.213		0.038	0.025	0.028	**0.430**	0.139	0.229	0.239	0.304	0.020	**0.772**	0.500	**0.757**	**0.643**	**0.713**
CBOA (14)	0.278	0.037		0.038	−0.037	**0.489**	0.195	0.342	0.353	0.425	0.075	**0.774**	0.454	**0.776**	**0.652**	**0.722**
CBIA (25)	0.312	0.025	0.038		−0.013	**0.486**	0.250	0.329	0.337	0.398	0.170	**0.745**	0.473	**0.725**	**0.589**	**0.652**
PL (23)	0.289	0.028	−0.037	−0.013		0.468	0.208	0.306	0.314	0.378	0.118	**0.740**	0.440	**0.741**	**0.601**	**0.664**
NSG (13)	0.424	0.428	0.484	0.483	0.463		0.416	0.639	0.650	0.684	0.442	**0.841**	0.694	**0.828**	**0.796**	**0.839**
SESG (12)	0.117	0.139	0.192	0.249	0.206	0.413		0.138	0.141	0.197	0.062	**0.812**	0.583	**0.809**	**0.729**	**0.789**
SB (13)	0.214	0.233	0.343	0.333	0.309	0.640	0.138		0.000	0.002	0.123	**0.864**	0.851	**0.837**	**0.939**	**0.948**
PW (14)	0.226	0.243	0.354	0.341	0.317	0.650	0.147	0.000		0.006	0.132	**0.865**	0.858	**0.839**	**0.943**	**0.951**
AD (26)	0.270	0.307	0.424	0.401	0.380	0.685	0.203	0.002	0.006		0.179	**0.872**	0.870	**0.850**	**0.940**	**0.946**
CJ (13)	0.159	0.022	0.074	0.172	0.119	0.440	0.061	0.125	0.134	0.180		**0.805**	0.589	**0.803**	**0.763**	**0.813**
PPB* (64)	**0.589**	**0.561**	**0.610**	**0.611**	**0.574**	**0.615**	**0.570**	**0.783**	**0.785**	**0.763**	**0.654**		0.178	**0.554**	**0.586**	**0.664**
WPB* (5)	**0.371**	**0.341**	**0.380**	**0.427**	**0.350**	**0.436**	**0.339**	**0.892**	**0.898**	**0.804**	**0.510**	−0.016		**0.481**	0.379	**0.450**
GIPS* (73)	**0.373**	**0.361**	**0.410**	**0.433**	**0.395**	**0.412**	**0.360**	**0.594**	**0.597**	**0.585**	**0.454**	**0.572**	**0.581**		−0.056	0.054
VIC* (3)	0.146	0.141	0.236	0.303	0.222	0.239	0.130	**0.817**	**0.828**	**0.725**	0.338	**0.594**	0.366	−0.025		0.074
TAS* (7)	**0.273**	**0.261**	**0.338**	**0.385**	**0.320**	**0.341**	**0.257**	**0.756**	**0.767**	**0.714**	**0.417**	**0.625**	**0.584**	0.209	0.036	

Locations marked with an asterisk (*) were published in Charlton-Robb et al. (2015); 159 samples were compared to our samples using a 418 bp control region fragment. Locations are ordered by geographic position from west to east. Mitochondrial F_{ST} values are given below the diagonal and Φ_{ST} values (Tamura and Nei distance measure) above the diagonal. Significant results are indicated by bold text (B–Y corrected critical value α = 0.0108, and samples from *locations α = 0.0093)

Samples sizes are given in parentheses after sampling location. Location abbreviation explanations are given in Fig. 1 and Tables 1 and S1

Table 3 Pairwise fixation indices between 11 sampling locations in southern Australia based on 11 microsatellite loci across 175 *Tursiops* cf. *australis* samples

	ESP	FI	CBOA	CBIA	PL	NSG	SESG	SB	PW	AD	CJ
ESP (10)		0.133	0.129	0.097	0.203	0.331	0.191	0.254	0.248	0.179	0.127
FI (13)	0.060		0.124	0.162	0.191	0.222	0.109	0.175	0.156	0.156	0.161
CBOA (15)	0.072	0.062		0.078	0.118	0.162	0.065	0.165	0.124	0.087	0.154
CBIA (28)	0.053	0.079	0.048		0.201	0.167	0.095	0.180	0.154	0.131	0.120
PL (17)	0.096	0.084	0.063	0.103		0.123	0.073	0.170	0.151	0.099	0.129
NSG (11)	0.182	0.122	0.111	0.103	0.074		0.075	0.153	0.122	0.108	0.205
SESG (10)	0.083	0.047	0.036	0.049	0.037	0.046		0.126	0.123	0.083	0.095
SB (16)	0.125	0.084	0.093	0.099	0.089	0.096	0.064		0.045	0.044	0.044
PW (15)	0.121	0.073	0.070	0.085	0.079	0.078	0.062	0.026		0.026	0.105
AD (26)	0.086	0.071	0.047	0.069	0.051	0.064	0.042	0.024	0.014		0.031
CJ (14)	0.058	0.068	0.078	0.060	0.061	0.114	0.043	0.023	0.053	0.017	

Locations are ordered by geographic position from west to east. Microsatellite F_{ST} values are given below the diagonal, and Jost's D above the diagonal. Significant results are indicated by bold text (B–Y corrected critical value $\alpha = 0.0108$)

Samples sizes are given in parentheses after sampling location. Location abbreviation explanations are given in Fig. 1 and Tables 1 and S1

of microsatellite markers to disclose fine-scale patterns of genetic structure.

As STRUCTURE results were similar for models with and without location-prior, only results of the latter are provided here. Hierarchical metapopulation structure was revealed by STRUCTURE modelling, with a strong first division between sites to the east and west of EP in SA (Fig. 3a). Analysis of only the sites east of EP showed clear separation between gulfs indicating that SG and GSV/Cape Jervis (CJ) belong to two genetically distinct populations (Fig. 3b). This interpretation was supported by both the log-likelihood (L(K)) and Evanno methods (DeltaK) estimating that two genetic populations with potential further sub-division was the most well supported

number of populations for this sub-analysis (Fig. S2A and B). Within the GSV/CJ genetic population statistical support was given for a further two sub-populations, with dolphins from Port Wakefield (PW) (top of GSV) and CJ (open-coast at the opening of GSV) being genetically differentiated, while Stansbury (SB) and Adelaide (AD) dolphins (mid-Gulf positions on western and eastern side, respectively) showed admixture with both (Fig. S3A, Fig. S5A and B). Similarly, the SG genetic population was found to be further differentiated, with NSG and southeast SG (SESG) dolphins forming a separate sub-population from individuals sampled around the more open location of Port Lincoln (PL) at the opening of SG (Fig. S3B, Fig. S5C and D).
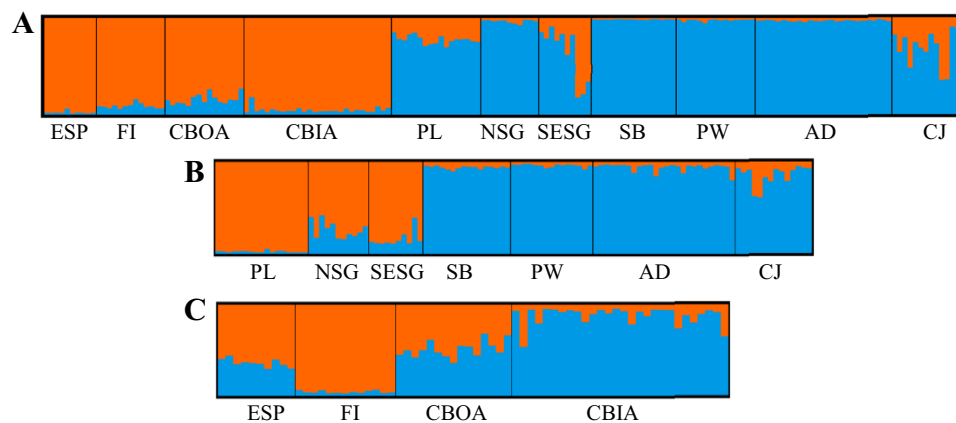

Fig. 3 *Tursiops* cf. *australis* STRUCTURE results with locational prior for **a** all 11 sampling locations in southern Australia (175 individuals); and **b** localities east of Eyre Peninsula only (66 individuals), **c** localities west of Eyre Peninsula only (109 individuals) to test for hierarchical population structure. Each vertical column represents an individual dolphin, and separation of the columns into orange/blue represents the probability of that individual belonging to a given population. Locations are ordered by geographic position from west to east for all analyses. Location abbreviation explanations are given in Fig. 1 and Tables 1 and S1. (Color figure online)

Both Evanno and log-likelihood methods also estimated that the most likely number of populations to the west of EP was two (Fig. S2C and D), suggesting that although Esperance (ESP) dolphins show some level of admixture with the CBIA population, they belong to a separate genetic population alongside St. Francis Island (FI) individuals (Fig. 3c). The CBIA and CBOA communities represent another genetic population, with CBOA dolphins potentially facilitating contemporary gene flow with the ESP/FI population and/or additional(s) unsampled "ghost population(s)" (see Beerli 2004; Slatkin 2005) (Fig. 3c). While K = 2 was the most statistically supported number of genetic populations for the dolphins to the west of EP (Fig. S2B), further clarification emerges when considering K = 3 in this sub-analysis. The CBOA dolphins emerge as a separate sub-population, but FI and ESP individuals still cluster together (Fig. S4). When considering the CBOA/CBIA population separately further genetic structuring was revealed with the sub-population split into further sub-populations (Fig. S3C). This may relate to the presence of kin-biased social communities within CB (Diaz-Aguirre, et al. in prep.). However, additional analysis of the ESP/FI population displayed no further genetic structuring between dolphins from the two locations (Fig. S3D). Hierarchical structure was further supported by the DAPC method, with significant divergence between dolphins sampled at sites east and west of EP (Fig. S6), and further subdivision into four genetic clusters (Fig. S7). The AMOVA also supported hierarchical structure, with significant differentiation between sites east and west of EP, and among sampling locations (Table S5). Although a Mantel test did reveal significant IBD (data not shown), due to the likely presence of hierarchical genetic structure, a stratified Mantel test was preferred and this revealed that IBD was not significant (Mantel's r = 0.0446, p = 0.856).

Contemporary migration and sex-biased dispersal

Four independent runs performed in BAYESASS for initial migration analysis returned similar results, and therefore, results from only the first run are reported. Despite an overall pattern of limited gene flow among populations, a noteworthy pathway for migration of bottlenose dolphins in southern Australia appears to be occurring eastward along the Great Australian Bight, from the ESP/FI population to CB (Fig. 4; Table S6). Additionally, a low level of migration was revealed from SG to the neighbouring CB and GSV populations (Fig. 4; Table S6). This is consistent with the population structure indicated by STRUCTURE. The proportion of non-migrants in each population was higher for sub-populations associated with gulf or embayment habitats (91–96%) than the open-coast (73%).

As no substantial differences between the mean relatedness method and corrected assignment index (*AIc*) were found only results of the latter are shown. Dispersal in the CB and GSV/CJ populations appears to be dominated by males, while in the ESP/FI and SG populations it appears to be female-biased. These differences were however, not statistically significant overall (Table 4), and therefore sex-biased dispersal appears not to be a major factor influencing population structure in southern Australia.

Fig. 4 Recent migration rate estimates among four genetic populations of *Tursiops* cf. *australis* in southern Australia coastal waters. Percentages within circles represent the proportion of non-migrants in the genetic population. Location abbreviation explanations are given in Fig. 1 and Tables 1 and S1. (Color figure online)
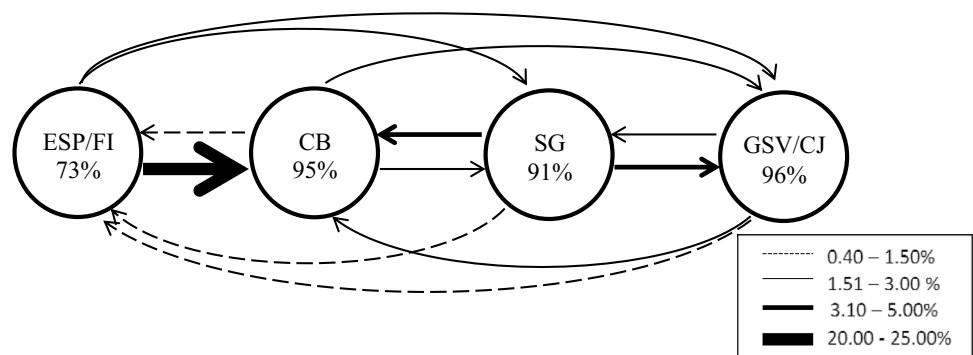

Table 4 Sex-biased dispersal analysis for the four estimated genetic populations of *Tursiops* cf. *australis* in coastal southern Australia

	Male mean *AIc*	Female mean *AIc*	Z	Probability
ESP/FI	0.334	− 0.434	− 1.674	0.094
CB (IA and OA)	− 0.315	0.197	− 1.126	0.260
SG	0.377	− 0.323	1.014	0.310
GSV/CJ	− 0.152	0.184	1.022	0.307

Locations are ordered by geographic position from west to east

Location abbreviation explanations are given in Fig. 1 and Tables 1 and S1

Discussion

Our study elucidated the population genetic structure of *T. cf. australis* along the southern Australia coastline. MtDNA diversity was considerably lower in GSV than in SG and open-coast populations, while nuclear DNA diversity was similar across populations. It appears that this species has a relatively shallow evolutionary history in southern Australia, with likely differences in colonisation between the two SA gulfs, open-coast regions and southeastern Australia. Hierarchical metapopulation structure in central and western southern Australia was revealed, with four genetically distinct populations and a genetic break at EP. Contemporary migration is limited across this region, and occurs mostly eastward from around the Great Australian Bight. MtDNA comparisons with the two *T. australis* populations previously identified in southeastern Australia (Charlton-Robb et al. 2015) showed little historical connectivity with the populations identified in our study region.

Genetic variation

While low mtDNA diversity appears to be typical of coastal bottlenose dolphin populations (e.g. Rosel et al. 2009; Wiszniewski et al. 2010; Louis et al. 2014; Charlton-Robb et al. 2015), to the best of our knowledge populations in GSV displayed considerably lower mtDNA diversity than any other studied bottlenose dolphin population in Australia (Krützen et al. 2004; Bilgmann et al. 2007a; Möller et al. 2007; Wiszniewski et al. 2010; Ansmann et al. 2012; Charlton-Robb et al. 2015). Negligible mtDNA diversity has however, been found in nearshore *T. truncatus* populations off the eastern South American coast, and could be associated with founding events (Fruet et al. 2014). Nuclear DNA diversity in our study was found to be, on average, lower for populations in embayment areas than open-coast locations highlighting how different habitats (see Harvey 2006; Möller et al. 2007; Kämpf et al. 2010) and historical processes, such as colonization, can potentially generate highly distinct patterns of genealogical structure and differentiation for bottlenose dolphins over relatively small geographical scales (Möller et al. 2007). Although care should be taken when directly comparing studies utilising different microsatellite markers, Charlton-Robb et al. (2015) found on average lower nuclear DNA diversity for *T. australis* in southeastern Australia.

Genetic differentiation

Analyses based on mtDNA and microsatellite datasets highlighted likely differences in historical and contemporary connectivity among populations. Present-day hierarchical metapopulation structure of bottlenose dolphins was revealed in central and western regions of southern Australia. A hierarchical metapopulation is a large population consisting of several smaller local populations that maintain a low level of gene flow among them (adapted from Hanski and Gilpin 1991). The formation of this pattern likely stems from a larger source population that over time diverged into a number of semi-isolated populations through local adaptation to heterogeneous environments (Hanski and Gilpin 1991). A genetic division between sites to the east and west of EP represents the highest level of this hierarchy, and has been previously documented for bottlenose dolphins in this region using a small subset of the samples used in this study (Bilgmann et al. 2007a). This division also mirrors a genetic break previously found for common dolphins (*D. delphis*) in SA (Bilgmann et al. 2014). This potential barrier to the dispersal of small cetaceans is perhaps related to differences in oceanography and/or prey assemblages (Bilgmann et al. 2014; also see; Middleton and Bye 2007), as has been previously suggested to impact upon gene flow in bottlenose dolphins (e.g. Natoli et al. 2005; Bilgmann et al. 2007a; Möller et al. 2007; Fruet et al. 2014). Genetic and geographical distances were not significantly correlated when cluster structure was accounted for, demonstrating that geographical distance are unlikely to have a major impact on the levels of gene flow among the studied populations (Meirmans 2012).

Inner-gulf locations

Bottlenose dolphins from the two SA gulfs appear to be genetically distinct from each another, and from all open-coast locations. This may be related to differences in historical colonisation of the two gulfs, with ongoing genetic division potentially maintained by differing physical characteristics of the two gulfs (see Harvey 2006; Kämpf et al. 2010; Scientific Working Group 2011). Populations within GSV showed a lack of genetic subdivision for both markers, indicating both historic and contemporary gene flow throughout the gulf, which is potentially facilitated by a relatively homogenous environment within GSV (DEH 2006). Conversely, relatively recent separation appears to exist between the southern and northern SG locations, with mtDNA haplotypes found in northern SG only one to two mutational steps from more ancestral haplotypes found in the south. Stable isotope and stomach content analyses also revealed differences in diet between dolphins in northern and southern SG, likely reflecting variation in habitat and prey assemblages between the two regions (Gibbs et al. 2011). Giant cuttlefish (*Sepia apama;* Payne et al. 2013) and western king prawns (*Penaeus latisulcatus;* Roberts et al. 2012) also exhibit north–south genetic subdivision in SG, thought

to be related to physically divergent environments (Kämpf et al. 2010).

Open-coast locations

Historic connectivity among dolphins from open-coast locations potentially reflects the movement of these dolphins across the seascape as they colonised new habitats. There appears to be a degree of contemporary separation among these populations, perhaps suggesting current adaptation to local environments. As the open-coast populations sampled in this study are separated by substantial geographical distance (~2600 km of coastline), genetic differentiation among these populations is not unexpected. Coastal bottlenose dolphins worldwide have been shown to demonstrate genetic population structure over relatively small distances, despite their physical capacity to travel much further (Sellas et al. 2005; Wiszniewski et al. 2010; Fruet et al. 2014). However, despite being over 1000 kilometres apart, ESP and FI dolphins appear to belong to the same genetic population, being more similar to one another than to the dolphins from CBIA and CBOA. While little is known about the distribution and abundance of bottlenose dolphins across the Great Australian Bight, largely due to difficult sampling conditions in that remote region, this study suggests that there is a moderate level of contemporary migration occurring across the region, potentially facilitated by southern Australia's Coastal Current (Cirano and Middleton 2004; Middleton and Bye 2007). The lower level of nuclear DNA differentiation between ESP and FI indicated by F_{ST} estimates provides evidence for a hierarchical metapopulation structure not immediately recognised by STRUCTURE, potentially due to relatively small sample sizes for these locations and putative social structure within populations.

The inner and outer regions of CB are likely to have differentiated relatively recently, a possibility supported and potentially strongly influenced by social structuring (Diaz-Aguirre et al. unpublished data). Low emigration rates have been documented for this population (Passadore et al. 2017), supporting our finding of limited gene flow and significant genetic differentiation between CBIA and all other populations. CBOA bottlenose dolphins have a much more fluid social (Diaz-Aguirre et al. unpublished data) and population structure than in CBIA, and likely interbreed with the ESP/FI and CBIA populations to some extent, as well as potentially additional "ghost populations" (see Beerli 2004; Slatkin 2005) inhabiting the coastline between FI and CBOA. Although dolphins from CBIA and CBOA appear to be biologically distinct entities we conservatively suggest that these two genetic sub-populations be considered as a single population for conservation management purposes due to their low level of contemporary genetic differentiation, very close geographical proximity and connectivity through

a narrow ocean opening, and potential for social interactions between the two. Splitting them into two separate management units without further clarification of the patterns of gene flow would likely be more detrimental to the long-term persistence of these sub-populations than managing them together. Changes to the management of one sub-population would likely impact on the other sub-population, and could potentially have considerable effects if both regions are not considered together in management decisions.. This could be particularly harmful for CBIA dolphins due to the small size and resident nature of this sub-population (Passadore et al. 2017), and its connectivity to CBOA through a narrow ocean opening. While, dolphins from the inner and outer areas of CB should be managed together, caution must be taken as some threats to dolphins in the inner area likely differ to those in the outer area. Further sampling is required along the coastline between CBOA and FI to clarify the potential for additional populations and further population structuring existing in this region.

Inner-gulf versus open-coast locations

The haplotype network suggests a relatively recent pattern of matrilineal diversification for *T.* cf. *australis* in central and western regions of southern Australia. Marine transgression began in both SA gulfs approximately 10,000 years ago, and reached present-day sea levels 6000–7000 years ago (Cann et al. 1988; Belperio et al. 2002; Harvey 2006). It is likely that bottlenose dolphins moved into the region, particularly SG and GSV, during this period of marine transgression, and underwent differing levels of matrilineal diversification within the gulfs and open-coast areas, potentially related to differences in habitat features. Non-significant mtDNA differentiation between PL and SESG dolphins and those from sites to the west of EP may be reflective of high levels of historical gene flow between these populations as SG flooded 6000–10,000 years ago (Belperio et al. 2002). At the nuclear level on the other hand, these sites were significantly differentiated, suggesting contemporary separation between these populations. This pattern, as well as the observed genetic divergence between ESP/FI dolphins and all inner-gulf demes may be as a result of contemporary local adaptation and/or the barrier to gene flow that appears to exist in the waters around EP.

With a high percentage of individuals carrying H1 in the CJ community, it may be suggested that individuals with this haplotype dispersed from CJ and adjacencies into GSV, perhaps with the postglacial marine transgression (Harvey 2006), while individuals that remained out of the gulf underwent matrilineal diversification and migrated in an eastward direction. This suggestion is supported by the mtDNA haplotype network comparing VIC and TAS to SA and WA dolphins. Populations from these two regions of southern

Australia are significantly differentiated based on mtDNA, with this genetic break corresponding to proposed marine biogeographical provinces (see Waters and Roy 2003) that have previously been suggested to be associated with genetic breaks in bottlenose dolphins (Charlton et al. 2006; Charlton-Robb et al. 2015).

While sample sizes for many locations in this study may appear limited to a small number, we believe this is likely to be a good representation of the genetic variation in coastal bottlenose dolphins of this region. Nearshore and inshore bottlenose dolphins typically exist in small populations, and as such relatively small sample sizes are generally sufficient to achieve a representative sample of the larger population. Bottlenose dolphin abundance estimates are not available for all sampled locations, but the GSV putative population is estimated to be between approximately 700 and 1,200 individuals (Bilgmann et al. unpublished data), and in Adelaide's metropolitan waters to vary between approximately 90 and 240 individuals seasonally (Zanardo et al. 2016). Spencer Gulf, on the other hand, is reported to have between approximately 1900 and 2400 individuals (Bilgmann et al. unpublished data), while an estimated 306 individuals occur in Coffin Bay (Passadore et al. 2017). Abundance estimates for the open-coast locations (ESP and FI) are also suggested to be relatively small (Bilgmann, personal observations), although this has not been scientifically tested. This study is an important first step in elucidating the metapopulation structure of coastal bottlenose dolphins in southern Australia, and further work should be done to increase sample sizes for some areas, particularly in Spencer Gulf, to allow for more robust conclusions to be drawn. The inclusion of additional sampling sites to cover some geographical gaps would also be beneficial to maximise reliability and resolution of the results.

Contemporary migration and sex-biased dispersal

While migration estimates indicated generally limited contemporary gene flow between southern Australia's coastal bottlenose dolphin populations, some key pathways for migration were revealed. In the western-most region a high level of contemporary migration appears to be occurring along the Great Australian Bight, from the ESP/FI population eastward to CB. This could potentially be influenced by the Coastal Current moving eastward during winter (Middleton and Bye 2007), and highlights an important area for gene flow among populations along ~ 1500 km of southern Australia's coastline. Bottlenose dolphins in southeastern Australia have also been shown to disperse over relatively large expanses of water, with a high level of gene flow across Bass Strait, although fine-scale population structure over relatively small distances was also documented (Charlton-Robb et al. 2015). These

patterns of both large- and fine-scale population structure highlights the role that ecological conditions and potential local adaptation may have on the species. While dolphins from the two SA gulfs do appear to be largely separated from one another and from open-coast locations, there is a low level of contemporary migration maintaining a hierarchical metapopulation structure among these populations. Specifically, there appears to be some gene flow from the larger SG population to the smaller GSV and CB populations (Holmes 2011; Passadore et al. 2017), potentially highlighting an important source-sink dynamic.

The overriding pattern of limited bottlenose dolphin movement across parts of the southern Australian coastline despite relatively negligible geographical separation, has been also observed in other inshore bottlenose dolphin populations (*T. truncatus*, Sellas et al. 2005; Fruet et al. 2014; *T. aduncus*; Wiszniewski et al. 2010). One potential factor reinforcing this is the complex social system exhibited by bottlenose dolphins (reviewed in Möller 2011), and in particular the potential for natal philopatry (Möller and Beheregaray 2004; Tsai and Mann 2012). This is particularly common in inshore and protected coastal habitats due to greater resource predictability and availability compared to open oceans (reviewed in Möller 2011). This supports our finding of populations most-closely associated with embayment habitats demonstrating higher rates of non-migrants than open-coast habitats, suggesting stronger philopatry in the former. While a number of bottlenose dolphin populations exhibit a female-bias in philopatry (male-dominated dispersal) (Krützen et al. 2004; Möller and Beheregaray 2004; Wiszniewski et al. 2010), this does not appear to be the general pattern in southern Australia with both sexes showing an overall relatively equal probability of dispersal. The presence of limited haplotype sharing between inner-gulf and open-coast regions and between gulfs does however, suggest that sex-biased dispersal may have historically, or presently be having an effect on the population structure of bottlenose dolphins in this region.

Overall movements of this species appears to be largely associated with the Coastal Current that moves along the southern Australian coast, and potentially the Zeehan Current which curves south-easterly around the southern edge of TAS (Cirano and Middleton 2004; Middleton and Bye 2007). Australian east-coast Indo-Pacific bottlenose dolphins (*T. aduncus*) on the other hand, have been suggested to be associated with the East Australian Current (EAC) (Möller et al. 2008), which moves southward and deflects away from the mainland as it approaches the southern border of New South Wales (Cirano and Middleton 2004). This corresponds to the proposed southern-most limit to *T. aduncus* distribution on the east-coast, suggesting that the EAC may have a role in the transition from *T. aduncus* to *T.* cf. *australis* populations throughout this region (see Möller et al. 2008).

Conservation implications

With ongoing anthropogenic impacts in southern Australian waters, including shipping, commercial and recreational fishing, tourism, and pollution (Svane 2005; Seuront and Cribb 2011; Filby et al. 2014; Monk et al. 2014), as well as breakouts of infectious diseases such as morbillivirus (Kemper et al. 2016), *T.* cf. *australis* populations are at increasing risk of decline and/or extinction. This is further exacerbated by the presence of relatively small (e.g. Zanardo et al. 2016), genetically distinct *T.* cf. *australis* populations as identified in this study. We found a minimum of four genetically distinct *T.* cf. *australis* populations in central and western regions of southern Australia: (1) ESP/FI; (2) CB (inner and outer areas); (3) SG; (4) GSV/CJ, with an additional two populations previously found in southeastern Australia: (5) Port Phillip Bay; and (6) Gippsland Lakes (GIPS)/TAS. These six genetic populations have been identified as per our original definition of a genetic population, based on statistically significant genetic differentiation among populations. Due to the hierarchical metapopulation structure found in this system it is difficult to conclusively say whether these populations are truly "demographically independent", and therefore further research must be done to establish the degree to which these populations are demographically separated. We suggest these six genetic populations be managed independently, but due to the presence of a number of subpopulations that appear to be acting as important genetic links between regions, it is important that for conservation purposes connectivity among locations be promoted. While typical metapopulations are more robust to potential species extinction through the "rescue-effect" (Hanski and Gilpin 1991), the hierarchical nature of this metapopulation suggests that populations are not equally connected and may be diverging through adaptation to local conditions. Marine park networks are thus an important tool to protect these populations and ensure that connectivity among them is maintained. The current network of marine parks in southern Australia does not appear to be sufficient to encompass the range of bottlenose dolphin genetic populations in WA, SA, VIC or TAS (see Parks and Wildlife 2017; DEWNR 2014; ELWP 2016a, b for marine park network maps). In GSV, for example, the Upper Gulf St. Vincent Marine Park covers approximately 25% of the northern end of the gulf (DEWNR 2012), while the bottlenose dolphin population shows movement throughout the gulf (although further work needs to be done on the home ranges of individual dolphins to evaluate this further). Similarly, the network of marine national parks and sanctuaries (no-take) in VIC and TAS does not provide protection to those populations with relatively large-scale movements, as seen between GIPS and TAS (Charlton-Robb et al. 2015; ELWP 2016a, b). This implies that issues affecting bottlenose dolphin populations in the area, such as overfishing of prey species, habitat degradation and destruction, and pollution will still have an impact on these dolphins. A more comprehensive marine park network taking into account the movement of this species throughout coastal southern Australia would facilitate maintenance of the hierarchical metapopulation structure and enhance gene flow among, and genetic variability within populations, thus decreasing the potential risk of population declines and extinctions (Frankham 1995).

Conclusions

This study clarified the population genetic structure of coastal bottlenose dolphins (*T.* cf. *australis*) across much of the species' range in southern Australia. We revealed the presence of a hierarchical metapopulation structure, with a major genetic division between sites to the east and west of EP, and at least four genetically distinct populations in central and western southern Australia: (1) ESP/FI; (2) CB (inner and outer areas); (3) SG; and (4) GSV/CJ. A further two previously identified genetic populations exist in southeastern Australia: (5) PPB; and (6) GIPS/TAS (Charlton-Robb et al. 2015). Historical genetic divergence and differences in colonisation of GSV, SG, and open-coast populations is likely, with GSV dolphins having considerably lower mtDNA diversity than dolphins from other locations. Historical genetic separation is also evident between dolphins from SA and WA and those in VIC and TAS. Overall, there was limited migration among locations, although notable gene flow occurs along the Great Australian Bight, from the ESP/FI population to CB, demonstrating an important area for connectivity along a large stretch of the southern Australian coast. Marine park networks in southern Australia should be managed so as to maximise gene flow among the six identified genetic populations in order to promote the persistence of the species in these waters. Ongoing research into *T.* cf. *australis* is required to gain a better understanding of the population ecology of this species, and to identify the range and population sizes of these dolphins in order to facilitate more informed conservation strategies.

from the Department of Environment, Water and Natural Resources (DEWNR), South Australia, and with permit from the Department of Environment and Conservation, WA (#SF008961). Animal ethics approvals were acquired from the Flinders University Animal Welfare Committee, projects #E310, #E375 and #E326. The present article is publication #65 of the Molecular Ecology Group for Marine Research (MEGMAR).

References

Amaral AR, Beheregaray LB, Bilgmann K, Boutov D, Freitas L, Robertson KM, Sequeira M, Stockin KA, Coelho MM, Möller LM (2012) Seascape genetics of a globally distributed, highly mobile marine mammal: the short-beaked common dolphin (genus *Delphinus*). PLoS ONE 7:e31482

Ansmann IC, Parra GJ, Lanyon JM, Seddon JM (2012) Fine-scale genetic population structure in a mobile marine mammal: inshore bottlenose dolphins in Moreton Bay, Australia. Mol Ecol 21:4472–4485. https://doi.org/10.1111/j.1365-294X.2012.05722.x

Bandelt H-J, Forster P, Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. Mol Biol Evol 16:37–48

Beerli P (2004) Effect of unsampled populations on the estimation of population sizes and migration rates between sampled populations. Mol Ecol 13:827–836

Belperio A, Harvey N, Bourman R (2002) Spatial and temporal variability in the Holocene sea-level record of the South Australian coastline. Sediment Geol 150:153–169

Benjamini Y, Yekutieli D (2001) The control of the false discovery rate in multiple testing under dependency. Ann Stat 29:1165–1188

Bilgmann K, Möller L, Harcourt R, Gibbs S, Beheregaray L (2007a) Genetic differentiation in bottlenose dolphins from South Australia: association with local oceanography and coastal geography. Mar Ecol Prog Ser 341:265–276

Bilgmann K, Griffiths O, Allen S, Möller L (2007b) A biopsy pole system for bow-riding dolphins: sampling success, behavioral responses, and test for sampling bias. Mar Mam Sci 23:218–225. https://doi.org/10.1111/j.1748-7692.2006.00099.x

Bilgmann K, Möller LM, Harcourt RG, Gales R, Beheregaray LB (2008) Common dolphins subject to fisheries impacts in southern Australia are genetically differentiated: implications for conservation. Anim Conserv 11:518–528. https://doi.org/10.1111/j.1469-1795.2008.00213.x

Bilgmann K, Parra G, Zanardo N, Beheregaray L, Möller L (2014) Multiple management units of short-beaked common dolphins subject to fisheries bycatch off southern and southeastern Australia. Mar Ecol Prog Ser 500:265–279

Bird C, Karl S, Smouse P, Toonen R (2011) Detecting and measuring genetic differentiation. CrustIssues 19(3):31–55

Boyd IL (2004) Migration of marine mammals. Springer, Berlin

Caballero S, Santos MCD, Sanches A, Mignucci-Giannoni AA (2013) Initial description of the phylogeography, population structure and genetic diversity of Atlantic spotted dolphins from Brazil and the Caribbean, inferred from analyses of mitochondrial and nuclear DNA. Biochem Syst Ecol 48:263–270. https://doi.org/10.1016/j.bse.2012.12.016

Cann JH, Belperio AP, Gostin VA, Murraywallace CV (1988) Sea-level history, 45,000 to 30,000 year BP, inferred from benthic foraminifera, Gulf St. Vincent, South Australia. Quat Res 29:153–175. https://doi.org/10.1016/0033-5894(88)90058-0

Charlton K, Taylor A, McKechnie SW (2006) A note on divergent mtDNA lineages of bottlenose dolphins from coastal waters of southern Australia. J Cetacean Res Manag 8:173

Charlton-Robb K, Gershwin L, Thompson R, Austin J, Owen K, McKechnie S (2011) A new dolphin species, the Burrunan dolphin *Tursiops australis* sp. nov., endemic to southern Australian coastal waters. PLoS ONE 6:e24047. https://doi.org/10.1371/journal.pone.0024047

Charlton-Robb K, Taylor A, McKechnie S (2015) Population genetic structure of the Burrunan dolphin (*Tursiops australis*) in coastal waters of south-eastern Australia: conservation implications. Conserv Genet 16:195–207. https://doi.org/10.1007/s10592-014-0652-6

Chevron Australia (2016) Great Australian bight—Chevron's exploration activities (Online). https://www.chevronaustralia.com/our-businesses/exploration/great-australian-bight. Accessed 23rd Nov 2016

Cirano M, Middleton JF (2004) Aspects of the mean wintertime circulation along Australia's southern shelves: Numerical studies. J Phys Oceanogr 34:668–684. https://doi.org/10.1175/2509.1

DEH (Department of Environment and Heritage) (2006) 'Map 2 IMCRA 4.0: Meso-scale Bioregions', Australian Government Data Sources

DEWNR (Department of Environment Water and Natural Resources) (2014) Recreational fishing in SA marine parks. Government of South Australia, Adelaide

DEWNR (Department of Environment, Water and Natural Resources) (2012) Upper Gulf St. Vincent Marine Park Management Plan. Government of South Australia, Adelaide

DeWoody JA, Bickham JW, Michler CH, Nichols KM, Rhodes GE, Woeste KE (2010) Molecular approaches in natural resource conservation and management. Cambridge University Press, New York

Dowling TE, Brown WM (1993) Population structure of the bottlenose dolphin (*Tursiops truncatus*) as determined by restriction endonuclease analysis of mitochondrial DNA. Mar Mam Sci 9:138–155. https://doi.org/10.1111/j.1748-7692.1993.tb00439.x

Earl D, vonHoldt B (2012) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conserv Genet Resour 4:359–361. https://doi.org/10.1007/s12686-011-9548-7

ELWP (Department of Environment, Land, Water and Planning) (2016a) Marine National Parks (Online). Victoria State government. http://www.depi.vic.gov.au/forestry-and-land-use/coasts/marine/marine-national-parks/marine-national-parks. Accessed 19 Jan 2017

ELWP (Department of Environment, Land, Water and Planning) (2016b) Marine sanctuaries (Online). Victoria State government. http://www.depi.vic.gov.au/forestry-and-land-use/coasts/marine/marine-national-parks/marine-sanctuaries. Accessed 19 Jan 2017

Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Mol Ecol 14:2611–2620. https://doi.org/10.1111/j.1365-294X.2005.02553.x

Excoffier L, Lischer H (2010) Arlequin suite ver3.5: a new series of programs to perform population genetics analyses under Linux and Windows. Mol Ecol Res 10:564–567

Filby N, Stockin K, Scarpaci C (2014) Long-term responses of *Burrunan dolphins* (*Tursiops australis*) to swim-with dolphin tourism in Port Phillip Bay, Victoria, Australia: a population at risk. Global Ecol Conserv 2:62–71

Frankham R (1995) Conservation genetics. Annu Rev Genet 29:305–327. https://doi.org/10.1146/annurev.ge.29.120195.001513

Fruet PF, Secchi ER, Daura-Jorge F, Vermeulen E, Flores PA, Simoes-Lopes PC, Genoves RC, Laporta P, Di Tullio JC, Freitas TRO (2014) Remarkably low genetic diversity and strong population structure in common bottlenose dolphins (*Tursiops truncatus*) from coastal waters of the Southwestern Atlantic Ocean. Conserv Genet 15:879–895

Gaggiotti O, Lange O, Rassmann K, Gliddon C (1999) A comparison of two indirect methods for estimating average levels of gene flow using microsatellite data. Mol Ecol 8(9):1513–1520

Gibbs S, Harcourt R, Kemper C (2011) Niche differentiation of bottlenose dolphin species in South Australia revealed by stable isotopes and stomach contents. Wildl Res 38:261–270

Gilson A, Syvanen M, Levine K, Banks J (1998) Deer gender determination by polymerase chain reaction: validation study and application to tissues, bloodstains, and hair forensic samples from California. Calif Fish Game 84(4):159–169

Google Earth 6.2.1.6014 (2012) Southern Australia coastline. Places data layer. http://www.google.com/earth/index.html. Accessed 02 Nov 2015

Goudet J (2001) FSTAT, a program to estimate and test gene diversities and fixation indices, Ver 2.9.3. http://www.unil.ch/popgen/softwares/fstat.html

Hanski I (1998) Metapopulation dynamics. Nature 396:41–49

Hanski I, Gilpin M (1991) Metapopulation dynamics: brief histroy and conceptual domain. Biol J Linnean Soc 42:3–16

Harvey N (2006) Holocene coastal evolution: barriers, beach ridges, and tidal flats of South Australia. J Coast Res 22:90–99. https://doi.org/10.2112/05a-0008.1

Hedrick PW (2001) Conservation genetics: where are we now? Trends Ecol Evol 16:629–636. https://doi.org/10.1016/s0169-5347(01)02282-0

Hoelzel A, Potter C, Best P (1998) Genetic differentiation between parapatric 'nearshore' and 'offshore' populations of the bottlenose dolphins. J R Soc 265:1177–1183

Holmes L (2011) Relative abundance of the southern Australian bottlenose dolphin *Tursiops australis* within the South Australian Gulfs. Honours thesis, Flinders University, Adelaide

Hubisz MJ, Falush D, Stephens M, Pritchard JK (2009) Inferring weak population structure with the assistance of sample group information. Mol Ecol Resour 9:1322–1332. https://doi.org/10.1111/j.1755-0998.2009.02591.x

Jensen J, Bohonak A, Kelley S (2005) Isolation by distance, web service v.3.23. BMC Genet 6:13

Jombart T, Ahmed I (2011) Adegenet 1.3-1: new tools for the analysis of genome-wide SNP data. Bioinformatics 27:3070–3071

Jombart T, Devillard S, Balloux F (2010) Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genet 11:94

Jost L (2008) G(ST) and its relatives do not measure differentiation. Mol Ecol 17:4015–4026. https://doi.org/10.1111/j.1365-294X.2008.03887.x

Kämpf J, Payne N, Malthouse P (2010) Marine connectivity in a large inverse estuary. J Coast Res 26:1047–1056. https://doi.org/10.2112/jcoastres-d-10-00043.1

Keenan K, McGinnity P, Cross TF, Crozier WW, Prodöhl PA (2013) Diversity: an R package for the estimation and exploration of population genetics parameters and their associated errors. Methods Ecol Evol 4:782–788. https://doi.org/10.1111/2041-210X.12067

Kemper C, Tomo I, Bingham J, Bastianello S, Wang J, Gibbs S, Woolford L, Dickason C, Kelly D (2016) Morbillivirus-associated unusual mortality event in South Australian bottlenose dolphins is largest reported for the Southern Hemisphere. R Soc Open Sci 3:160838

Kompelman N, Mayzel J, Jakobsson M, Rosenberg N, Maryrose I (2015) CLUMPAK: a program for identifying clustering models and packaging population structure inferences across K. Mol Ecol Resour 15:1179–1191. https://doi.org/10.1111/1755-0998.12387

Krützen M, Barre L, Möller L, Heithaus M, Simms C, Sherwin W (2002) A biopsy system for small cetaceans: darting success and wound healing in *Tursiops* spp. Mar Mam Sci 18:863–878

Krützen M, Sherwin W, Berggren P, Gales N (2004) Population structure in an inshore cetacean revealed by microsatellite and mtDNA analysis: bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. Mar Mam Sci 20:28–47. https://doi.org/10.1016/j.quascirev.2012.09.006

Louis M, Viricel A, Lucas T, Peltier H, Alfonsi E, Berrow S, Brownlow A, Covelo P, Dabin W, Deaville R (2014) Habitat-driven population structure of bottlenose dolphins, *Tursiops truncatus*, in the North-East Atlantic. Mol Ecol 23(4):857–874

Lowther-Thieleking J, Archer F, Lang A, Weller D (2015) Genetic differentiation among coastal and offshore common bottlenose dolphins, *Tursiops truncatus*, in the eastern North Pacific Ocean. Mar Mam Sci 31:1–20

Magera AM, Flemming JEM, Kaschner K, Christensen LB, Lotze HK (2013) Recovery trends in marine mammal populations. PLoS ONE 8:12. https://doi.org/10.1371/journal.pone.0077908

Mead J, Potter C (1995) Recognizing two populations of the bottlenose dolphin (*Tursiops truncatus*) off the coast of North America: morphologic and ecological considerations. IBI Rep 5:3144

Meirmans P (2012) The trouble with isolation by distance. 21:2839–2846

Meirmans PG, Van Tienderen PH (2004) GENOTYPE and GENODIVE: two programs for the analysis of genetic diversity of asexual organisms. Mol Ecol Notes 4:792–794. https://doi.org/10.1111/j.1471-8286.2004.00770.x

Mendez M, Rosenbaum HC, Subramaniam A, Yackulic C, Bordino P (2010) Isolation by environmental distance in mobile marine species: molecular ecology of Franciscana dolphins at their southern range. Mol Ecol 19:2212–2228

Middleton JF, Bye JAT (2007) A review of the shelf-slope circulation along Australia's southern shelves: Cape Leeuwin to Portland. Prog Oceanogr 75:1–41. https://doi.org/10.1016/j.pocean.2007.07.001

Möller L (2011) Sociogenetic structure, kin associations and bonding in delphinids. Mol Ecol 21:745–764. https://doi.org/10.1111/j.1365-294X.2011.05405.x

Möller LM, Beheregaray LB (2004) Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). Mol Ecol 13:1607–1612. https://doi.org/10.1111/j.1365-294X.2004.02137.x

Möller L, Beheregaray L, Harcourt R, Krützen M (2001) Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) southeastern Australia. J R Soc 268:1941–1947

Möller L, Wiszniewski J, Allen S, Beheregaray L (2007) Habitat type promotes rapid and extremely localised genetic differentiation in dolphins. Mar Freshw Res 58:640–648

Möller L, Bilgmann K, Charlton-Robb K, Beheregaray L (2008) Multi-gene evidence for a new bottlenose dolphin species in southern Australia. Mol Phylogenet Evol 49:674–681

Möller L, Valdez F, Allen S, Bilgmann K, Corrigan S, Beheregaray L (2011) Fine-scale genetic structure in short-beaked common dolphins (*Delphinus delphis*) along the East Australian Current. Mar Biol 158:113–126

Monk A, Charlton-Robb K, Buddhadasa S, Thompson RM (2014) Comparison of mercury contamination in live and dead dolphins from a newly described species, *Tursiops australis*. PLoS ONE 9:6. https://doi.org/10.1371/journal.pone.0104887

Moura AE, Natoli A, Rogan E, Hoelzel AR (2013) Atypical panmixia in a European dolphin species (*Delphinus delphis*): implications for the evolution of diversity across oceanic boundaries. J Evol Biol 26:63–75. https://doi.org/10.1111/jeb.12032

Narum SR (2006) Beyond Bonferroni: less conservative analyses for conservation genetics. Conserv Genet 7:783–787

Natoli A, Birkun A, Lopez A, Hoelzel A (2005) Habitat structure and the dispersal of male and female bottlenose dolphins (*Tursiops truncatus*). J R Soc 272:1217–1226

Palsbøll PJ, Berube M, Allendorf FW (2007) Identification of management units using population genetic data. Trends Ecol Evol 22:11–16

Parks and Wildlife (2017) Marine parks and reserves (Online). Government of Western Australia. https://www.dpaw.wa.gov.au/management/marine/marine-parks-and-reserves. Accessed 19 Jan 2017

Passadore C, Möller L, Diaz-Aguirre F, Parra GJ (2017) Demography of southern Australian bottlenose dolphins living in a protected inverse estuary. Aquat Conserv 1:1–12

Payne NL, Snelling EP, Semmens JM, Gillanders BM (2013) Mechanisms of population structuring in giant Australian cuttlefish *Sepia apama*. PLoS ONE 8:7. https://doi.org/10.1371/journal.pone.0058694

Peakall R, Smouse P (2006) GENALEX 6: gentic analysis in Excel. Population genetic software for teaching and research. Mol Ecol Notes 6:288–295

Peakall R, Smouse P (2012) GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. Bioinformatics 28:2537–2539

Perez-Alvarez MJ, Olavarria C, Moraga R, Baker CS, Hamner RM, Poulin E (2015) Microsatellite markers reveal strong genetic structure in the endemic Chilean dolphin. PLoS ONE 10:e0123956. https://doi.org/10.1371/journal.pone.0123956

Queller DC, Goodnight KF (1989) Estimating relatedness using genetic markers. Evolution 43:258–275

Querouil S, Silva MA, Freitas L, Prieto R, Magalhaes S, Dinis A, Alves F, Matos JA, Mendonca D, Hammond PS, Santos RS (2007) High gene flow in oceanic bottlenose dolphins (*Tursiops truncatus*) of the North Atlantic. Conserv Genet 8:1405–1419. https://doi.org/10.1007/s10592-007-9291-5

Querouil S, Freitas L, Cascao I, Alves F, Dinis A, Almeida JR, Prieto R, Borras S, Matos JA, Mendonca D, Santos RS (2010) Molecular insight into the population structure of common and spotted dolphins inhabiting the pelagic waters of the Northeast Atlantic. Mar Biol 157:2567–2580. https://doi.org/10.1007/s00227-010-1519-0

Rannala B (2007) BayesAss esition 3.0 user's manual. University of California, Davis

Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism1. J Hered 86:248–249

Roberts S, Dixon C, Andreacchio L (2012) Temperature dependent larval duration and survival of the western king prawn, *Penaeus (Melicertus) latisulcatus* Kishinouye, from Spencer Gulf, South Australia. J Exp Mar Biol Ecol 411:14–22. https://doi.org/10.1016/j.jembe.2011.10.022

Rosel PE, Hansen L, Hohn AA (2009) Restricted dispersal in a continuously distributed marine species: common bottlenose dolphins *Tursiops truncatus* in coastal waters of the western North Atlantic. Mol Ecol 18(24):5030–5045

Rousset F (2008) Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. Mol Ecol Resour 8:103–106

Schipper J, Chanson JS, Chiozza F, Cox NA, Hoffmann M, Katariya V, Lamoreux J, Rodrigues ASL, Stuart SN, Temple HJ, Baillie J, Boitani L, Lacher TE, Mittermeier RA, Smith AT, Absolon D, Aguiar JM, Amori G, Bakkour N, Baldi R, Berridge RJ, Bielby J, Black PA, Blanc JJ, Brooks TM, Burton JA, Butynski TM, Catullo G, Chapman R, Cokeliss Z, Collen B, Conroy J, Cooke JG, da Fonseca GAB, Derocher AE, Dublin HT, Duckworth JW, Emmons L, Emslie RH, Festa-Bianchet M, Foster M, Foster S, Garshelis DL, Gates C, Gimenez-Dixon M, Gonzalez S, Gonzalez-Maya JF, Good TC, Hammerson G, Hammond PS, Happold D, Happold M, Hare J, Harris RB, Hawkins CE, Haywood M, Heaney LR, Hedges S, Helgen KM, Hilton-Taylor C, Hussain SA, Ishii N, Jefferson TA, Jenkins RKB, Johnston CH, Keith M, Kingdon J, Knox DH, Kovacs KM, Langhammer P, Leus K, Lewison R, Lichtenstein G, Lowry LF, Macavoy Z, Mace GM, Mallon DP, Masi M, McKnight MW, Medellin RA, Medici P, Mills G, Moehlman PD, Molur S, Mora A, Nowell K, Oates JF, Olech W, Oliver WRL, Oprea M, Patterson BD, Perrin WF, Polidoro BA, Pollock C, Powel A, Protas Y, Racey P, Ragle J, Ramani P, Rathbun G, Reeves RR, Reilly SB, Reynolds JE, Rondinini C, Rosell-Ambal RG, Rulli M, Rylands AB, Savini S, Schank CJ, Sechrest W, Self-Sullivan C, Shoemaker A, Sillero-Zubiri C, De Silva N, Smith DE, Srinivasulu C, Stephenson PJ, van Strien N, Talukdar BK, Taylor BL, Timmins R, Tirira DG, Tognelli MF, Tsytsulina K, Veiga LM, Vie JC, Williamson EA, Wyatt SA, Xie Y, Young BE (2008) The status of the world's land and marine mammals: diversity, threat, and knowledge. Science 322:225–230. https://doi.org/10.1126/science.1165115

Scientific Working Group (2011) The vulnerability of coastal and marine habitats in South Australia. Marine Parks: Department of Environment, Water and Natural Resources, Government of South Australia, Adelaide

Sellas AB, Wells RS, Rosel PE (2005) Mitochondrial and nuclear DNA analyses reveal fine scale geographic structure in bottlenose dolphins (*Tursiops truncatus*) in the Gulf of Mexico. Conserv Genet 6:715–728. https://doi.org/10.1007/s10592-005-9031-7

Seuront L, Cribb N (2011) Fractal analysis reveals pernicious stress levels related to boat presence and type in the Indo-Pacific bottlenose dolphin, *Tursiops aduncus*. Phys A 390:2333–2339. https://doi.org/10.1016/j.physa.2011.02.015

Silva MA, Prieto R, Magalhaes S, Seabra M, Santos R, Hammond P (2008) Ranging patterns of bottlenose dolphins living in oceanic waters: implications for population structure. Mar Biol 156:179–192. https://doi.org/10.1007/s00227-008-1075-z

Slatkin M (2005) Seeing ghosts: the effect of unsampled populations on migration rates estimated for sampled populations. Mol Ecol 14:67–73

Sunnucks P, Hales DF (1996) Numerous transposed sequences of mitochondrial cytochrome oxidase I–II in aphids of the genus *Sitobion* (Hemiptera: Aphididae). Mol Biol Evol 13:510–524

Svane I (2005) Occurrence of dolphins and seabirds and their consumption of by-catch during prawn trawling in Spencer Gulf, South Australia. Fish Res 76:317–327. https://doi.org/10.1016/j.fishres.2005.07.012

Tamura K, Nei M (1993) Estimation of the number of nucleotide substitutions in the control region of mitochondrial-DNA in humans and chimpanzees. Mol Biol Evol 10:512–526

Tsai Y, Mann J (2012) Dispersal, philopatry, and the role of fission-fusion dynamics in bottlenose dolphins. Mar Mam Sci. https://doi.org/10.1111/j.1748-7692.2011.00559.x

Van Oosterhout C, Hutchinson W, Wills D, Shipley P (2004) MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Mol Ecol Notes 4:535–538

Viricel A, Rosel PE (2014) Hierarchical population structure and habitat differences in a highly mobile marine species: the Atlantic spotted dolphin. Mol Ecol 23:5018–5035. https://doi.org/10.1111/mec.12923

Waters JM, Roy MS (2003) Marine biogeography of southern Australia: phylogeographical structure in a temperate sea-star. J Biogeogr 30:1787–1796

Wilson G, Rannala B (2003) Bayesian inference of recent migration rates using multilocus genotypes. Genetics 163:1177–1191

Wiszniewski J, Beheregaray L, Allen S, Möller L (2010) Environmental and social influences on the genetic structure of bottlenose dolphins (*Tursiops aduncus*) in southeastern Australia. Conserv Genet 11:1405–1419

Zanardo N, Parra GJ, Möller LM (2016) Site fidelity, residency, and abundance of bottlenose dolphins (*Tursiops* sp.) in Adelaide's coastal waters, South Australia. Mar Mam Sci 32(4):1381–1401