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Socio-genetic structure of short-beaked common dolphins in southern Australia

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Abstract

Delphinids show a wide range of social structures. However, studies investigating the influence of genetic relatedness and maternal kinship on school associations are limited to a small number of relatively well-studied delphinid species. This study investigated biparental genetic relatedness and potential maternal kinship structure in schools of short-beaked common dolphins *Delphinus delphis* from southern Australian waters. A total of 128 biopsy samples were obtained from free-ranging individuals within 62 schools of common dolphins. Each sample was genotyped at 13 nuclear microsatellite markers, sequenced at 438 bp of the mitochondrial DNA control region, and used for genetic sexing. Pairwise analyses within and between schools showed that the average genetic relatedness between males was greater within schools than between schools. Pairs of individuals within schools were also more likely to share mtDNA haplotypes, for both pairs of males and of females. The results suggest that both biparental relatedness and potentially maternal kinship have an impact on school associations of short-beaked common dolphins in southern Australia, similar to social traits reported of other dolphin species inhabiting shallow coastal environments. The information provided by this study contributes to our understanding of social evolution in delphinids. It also suggests that dolphin bycatch and deaths in fisheries from this region could lead to a reduction in the genetic diversity of this population, particularly if related individuals are simultaneously killed in the nets.

Introduction

Group living is widespread and highly variable among mammals (Krause & Ruxton, 2002; Silk, 2007). Ecological and social factors are major underlying forces shaping social structure in these animals. The main ecological factors that influence group associations include predation risk and food availability, while the main social factors include reproductive strategies and investment in parental care (Clutton-Brock, 2007; Gowans, Würsig & Karczmarski, 2008; Möller, 2012). For example, studies of various mammals have shown that by associating in groups individuals may increase their ability to detect predators, reduce the probability that they will be preyed upon, or deter predators from attacking (Krause & Ruxton, 2002). Group association can also aid in increasing food intake through more efficient prey capture and by the defence of localized food sources (Krause & Ruxton, 2002). These benefits, however, can also be influenced by the composition, group size and stability of groups (Majolo, de Bortoli Vizioli & Schino, 2008; Meldrum & Ruckstuhl, 2009).

The segregation of individuals into different groups can affect the genetic structure within and between demes and populations (Hoelzel, 1994; Sugg *et al.*, 1996). Genetic structure is particularly impacted upon when there is a tendency for individuals to associate preferentially in groups containing kin. Close associations between kin potentially benefit individuals through inclusive fitness gains; where individuals may increase their own fitness by positive effects on the reproduction of their relatives (Hamilton, 1964). Increased fitness can be achieved through cooperative foraging, protection from predators or by helping to rear young.

Delphinids show a wide range of social structures (Wells, Scott & Irvine, 1987; Gowans *et al.*, 2008; Möller, 2012), however, studies investigating the influence of genetic relatedness and maternal kinship on associations are limited to a number of relatively well-studied delphinid species (reviewed in Möller, 2012). Gowans *et al.* (2008) proposed an ecological framework which suggests that delphinid social structures are highly influenced by the risk of predation and availability of food resources, which are in turn associated with habitat and ecological factors. Inshore environments are more likely to be associated with predictable resources, promoting site fidelity and small group sizes, which allows individuals to form close and, potentially, kin associations (Gowans *et al.*, 2008). Alternatively, offshore environments are more likely to be associated with unpredictable resources, prompting larger dispersal and the formation of larger groups required for predator avoidance and increased foraging efficiency (Gowans *et al.*, 2008).

The short-beaked common dolphin (*Delphinus delphis*, hereafter referred to as 'common dolphin'), is typically found to inhabit shelf and pelagic waters of the Atlantic and Pacific Oceans (Perrin, 2009). Common dolphins are considered a social species as they travel in schools ranging from dozens to hundreds, or even thousands of individuals (Forney & Barlow, 1998; Gerrodette *et al.*, 2008; Möller *et al.*, 2011). School sizes of common dolphins are generally assumed to be influenced by predation risk and food requirements, indicative of their habitat and its environmental conditions. As the risk of predation is thought to be higher within pelagic and continental shelf waters than within coastal waters, the ecological framework proposed by Gowans *et al.* (2008) suggests that common dolphins may associate in larger schools in these environments for increased protection. Furthermore, to optimize food intake, specifically on large schools of pelagic fish, common dolphins may benefit most from cooperative foraging in larger schools (Norris & Dohl, 1980; Wells, Irvine & Scott, 1980). Interestingly, in southern Australia, common dolphins have typically been found to associate in small schools (Filby *et al.*, 2010).

Information on the socio-genetic structure of common dolphin schools is limited to one study along the English Channel, France. Here, Viricel *et al.* (2008) analysed samples from one mass stranding, but the results were unsupportive. Furthermore, it has been shown that samples from strandings may not always be reliable indicators of real social structure (Oremus *et al.*, 2013). Studies of the socio-genetic structure of free-ranging common dolphins are therefore needed to better understand potential factors influencing school associations in this species.

In this study, we used skin samples from free-ranging common dolphins from southern Australia to test for the potential influence of biparental genetic relatedness and maternal kinship on school associations. Specifically, we used information from microsatellite DNA markers to test for differences in average relatedness, and mitochondrial DNA (mtDNA) sequences to test for a difference in the number of pairs sharing haplotypes within and between schools, and of the same sex. We focus our study on southern Australia as dolphin bycatch and deaths in fisheries in this area are of major concern (Kemper *et al.*, 2005; Hamer, Ward & McGarvey, 2008). Common dolphins in Australian coastal and continental shelf waters show a higher level of genetic structuring than reported elsewhere (Bilgmann *et al.*, 2008, 2014; Möller *et al.*, 2011), and therefore may be more vulnerable to human-induced reductions in genetic diversity. Understanding the socio-genetic structure of these dolphin populations, and the driving forces behind school associations are essential to better understand the potential cumulative impacts of dolphin–fishery interactions.

Materials and methods

Study area and samples

Biopsy samples of free-ranging common dolphins were collected within southern Australian waters and previously used as part of a larger study of the population genetic structure of this species across southern and south-eastern Australia (Bilgmann *et al.*, 2014). Individuals from the study presented here belong to Population 4 (the widest distributed population described in Bilgmann *et al.*, 2014). Population 4 is distributed in coastal, continental shelf and gulf waters between Eyre Peninsula, in the Australian state of South Australia (SA) to the west (35°12′S 136°29′E), and Wilsons Promontory, in the Australian state of Victoria (VIC) to the east (38°76′S 145°55′E) (Fig. 1) (Bilgmann *et al.*, 2014). Dolphins were defined as part of the same school if they were within a 50 m radius of each other and generally displaying the same behaviour, or bow-riding (Bilgmann *et al.*, 2014). For detailed methodology of the biopsy sampling procedure, see Supporting Information Appendix S1.

DNA extraction and genetic sexing

Genomic DNA was extracted from biopsy samples using a standard salting-out method (Sunnucks & Hales, 1996). The sex of each dolphin was genetically determined by polymerase chain reaction (PCR) using the protocol developed by Banks *et al.* (1995). A *z*-test (Zar, 1996) was used to test whether the sex ratio of sampled dolphins differed significantly from a 1:1 sex ratio.

Microsatellite genotyping

Samples were genotyped for 13 cetacean microsatellite loci (see Bilgmann *et al.*, 2014). Details regarding microsatellite amplification followed Amaral *et al.* (2012). Following amplification, samples were mixed with an internal size standard and analysed on an ABI 3130 Genetic Analyser. The sizes of allele fragments were scored using GENEMAPPER V.4.1 (Applied Biosystems).

Mitochondrial DNA sequencing

A 438 bp fragment of the mtDNA control region was amplified by PCR as described in Möller & Beheregaray (2001). PCR products were purified with the UltraClean 15 DNA Purification Kit (MO BIO, Carlsbad, CA, USA) and sequenced in an ABI 3130 automated DNA sequencer according to manufacturer's instructions.

Microsatellites and genetic relatedness

We used MICRO-CHECKER v. 2.2.3 (Van Oosterhout *et al.*, 2004) to test for genotyping errors, potentially caused by null alleles, stutter peaks and/or allelic dropout. We also used CERVUS v. 3.0 (Marshall *et al.*, 1998) to investigate the presence of potential duplicate samples. All sample pairs that showed up to two differing alleles were rechecked for potential scoring errors. Individuals were considered as resampled (duplicates) if they were of the same sex, had identical microsatellite genotypes, and the same mtDNA haplotype. One sample of each duplicate was removed for data analysis. A total of 20% of samples were also regenotyped to assess reliability.

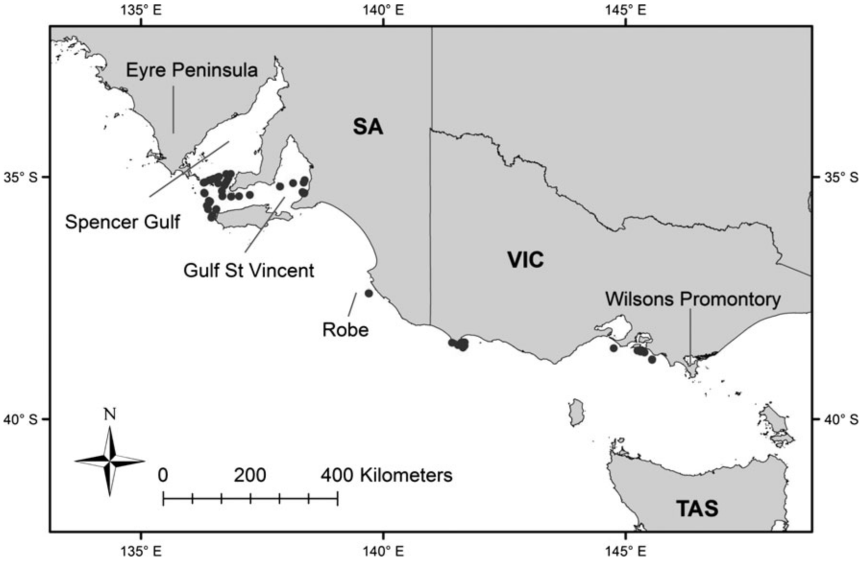

Figure 1 Distribution of biopsy samples collected from short-beaked common dolphins from Population 4 (Bilgmann *et al.*, 2014) in southern Australia. Grey circles represent the location of each individual during sample collection.

Tests for departures from Hardy–Weinberg equilibrium (HWE) and for linkage disequilibrium were conducted in GENEPOP v. 4.0.10 (Raymond & Rousset, 1995) based on a Markov chain method and 10 000 iterations. Bonferroni correction was applied to adjust the significance level (Holm, 1979). Mean number of alleles per locus, allele frequencies, and expected (H_E) and observed (H_O) heterozygosities were calculated in ARLEQUIN v. 3.5.1.2.

In order to determine the best estimator for quantifying genetic relatedness, we simulated a dataset with known allele frequencies in COANCESTRY v. 1.0.1.5 (Wang, 2011). We estimated pairwise genetic relatedness for pairs of individuals with the triadic likelihood estimator (Wang, 2007) as it provided the highest correlation with the true values (Wang, 2011). We assessed whether average relatedness of pairs of individuals within schools was significantly higher than between schools, and whether average relatedness of pairs of individuals of the same sex was significantly higher than between pairs of individuals of different sexes, both within and between schools. Permutation tests were carried out in COANCESTRY, with 10 000 bootstraps. To test for potential bias of including schools where only one individual was sampled (and therefore only contributed to between-school comparisons), we reran these tests with only schools that contained two or more sampled individuals. We found similar results with both datasets, and therefore results presented here include the full dataset. We also inferred sibship relationships using pairwise likelihood methods in COLONY v. 2.0 (Jones & Wang, 2010), and used a randomization test of independence to test if the proportion of relationship types (full-sib, half-sib and non-sib) differed within and between schools.

The average relatedness for each school was also estimated using COANCESTRY and a Pearson's correlation test was used to test for a correlation between school size and average school relatedness using SigmaStat v. 3.0 (SPSS Inc, Chicago, IL, USA).

Mitochondrial DNA and potential maternal kinship

MtDNA control region sequences were aligned in SEQUENCHER v. 4.1.2 (Gene Code Corp., Ann Arbor, MI, USA). A neighbour joining tree of mtDNA haplotypes using total number of base pair differences was constructed in PAUP v. 4 (Swofford 2003) to identify unique mtDNA haplotypes. We assumed that individuals bearing the same mtDNA haplotype were more likely to belong to the same maternal lineage and therefore to be maternal kin. However, we acknowledge that although we have used the most variable part of the mtDNA control region for analysis, some genetic variation outside the fragment analysed may have been missed. Haplotype and nucleotide diversities were estimated using ARLEQUIN v. 3.5.1.2 (Excoffier & Lischer, 2010). A total of 10% of samples were resequenced to check for potential errors.

To test for an association between mtDNA haplotype and school association, a pairwise matrix was constructed using a binary scale for the mtDNA haplotypes, where 0 denoted pairs of individuals carrying different haplotypes, and 1 denoted two individuals sharing the same haplotype (as in Oremus *et al.*, 2013). This matrix was tested against a binary association matrix including the same individuals, where 0 denoted pairs of individuals sampled from different schools, and 1 denoted pairs sampled in the same school. The test was conducted using a mantel matrix randomization procedure in GenAlEx v. 6.41, with 10 000 iterations (Peakall & Smouse, 2006). Tests were performed for all sampled individuals, and then for females and males separately.

Results

Sampling effort

One hundred and twenty-eight common dolphins in 62 schools were biopsied from Population 4 (Bilgmann *et al.*, 2014) (Fig. 1) and included in the socio-genetic analysis. Observed schools in this population ranged in size from one to approximately 50 individuals (Fig. 2). Of the 128 individual dolphins sampled, 67 were genetically identified as males and 61 as females (Supporting Information Table S1). No significant difference from a 1:1 sex ratio ($Z = 0.749$, $P = 0.4$) was observed, supporting previous findings of no sex bias in sampling of bow-riding common dolphins off southern Australia (Bilgmann *et al.*, 2007).

Biparental genetic relatedness and school association

Microsatellite diversity was similar to that reported for samples of common dolphins collected in 2004 and 2005 from the same general region (Bilgmann *et al.*, 2008). For details of the microsatellite diversity, see Supporting Information Appendix S2.

Mean relatedness within schools was significantly greater than the mean relatedness between schools ($P < 0.01$, Table 1). When comparisons were made separately for each sex, males exhibited significantly higher mean relatedness within schools than between schools ($P < 0.05$, Table 1). Females exhibited higher mean relatedness between schools, but the result was not significant ($P > 0.05$, Table 1). Relatedness among males within schools was significantly greater than among females within schools ($P < 0.05$). The proportion of relationship types differed within and between schools; we found a larger proportion of full-sib and half-sib pairs within groups, and a larger proportion of non-sib pairs between groups (Fig. 3), however, results were marginally non-significant ($P = 0.07$). Mean relatedness for each sampled school is provided in Table S4 and interpreted in Appendix S3.

Mitochondrial DNA diversity

MtDNA control region sequences were 438 bp in length and the dataset consisted of a total of 41 unique haplotypes (see Bilgmann *et al.*, 2014). Haplotype and nucleotide diversities were 0.948 (SE ± 0.010) and 0.021 (SE ± 0.011) respectively. Resequenced samples showed no evidence of sequencing errors. Males were represented by 29 different haplotypes while samples from females showed 31 distinct haplotypes (Supporting Information Table S2).

The most common haplotype (H67) was represented by a total of 21 individuals (13 males and eight females) in 16 sampled schools. The greatest number of individuals that shared H67 within schools was five individuals. GenBank Accession Numbers of sequences in the haplotype network are KJ493702–KJ493705, KJ493707–KJ493710, KJ493713, KJ493715, KJ493717, KJ493719, KJ493720, KJ493725, KJ493726, KJ493728–KJ493730, KJ493732–KJ493735, KJ493738, KJ493739, KJ493741–KJ493744, KJ493746, KJ493749, KJ493750, KJ493752, KJ493753, KJ493755-KJ493758, KJ493760, KJ493761, KJ493763 and KJ493764 (Bilgmann *et al.*, 2014).

Mitochondrial DNA haplotype and school association

While acknowledging a discrepancy in sample sizes between the two classes (160 within vs. 7968 between), our results

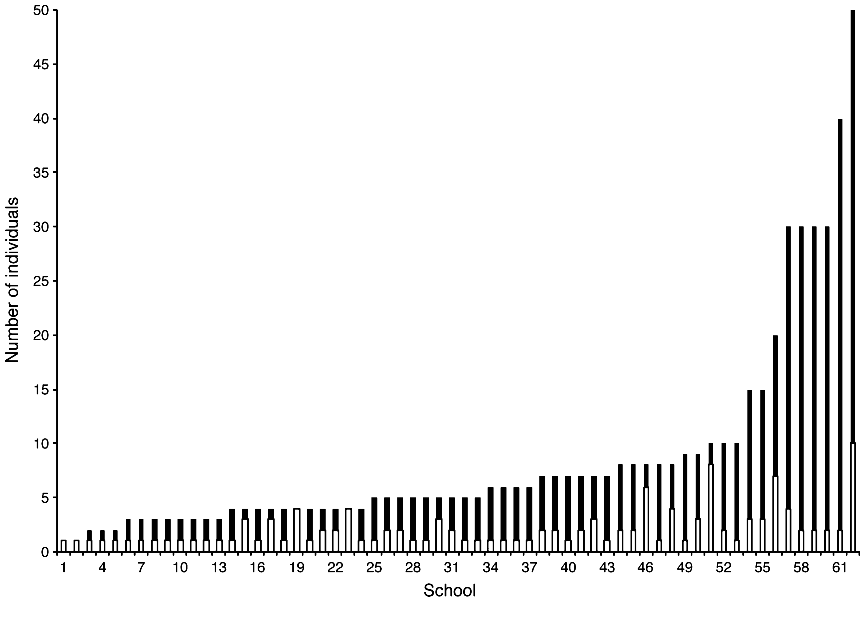

Figure 2 School sizes of short-beaked common dolphins observed in Population 4 (subsample of individuals from MU 4 in Bilgmann *et al.*, 2014) from eastern Eyre Peninsula to western Wilsons Promontory, between years 2009–2012. Unshaded sections represent the total number of samples obtained from a given school.

Table 1 Mean relatedness (*R*) overall, within and between schools of short-beaked common dolphins in southern Australia

	M-F	M-M	F-F
Overall	0.045 (±0.005)	0.041 (±0.005)	0.043 (±0.005)
Within school	0.063 (±0.009)	0.061 (±0.011)	0.033 (±0.001)
Between school	0.044 (±0.005)	0.041 (±0.005)	0.044 (±0.005)

showed that a significant difference was found in the number of pairs of dolphins with the same and different mtDNA haplotypes, within (same haplotype = 32, different haplotype = 128) and between schools (same haplotype = 386, different haplotype = 7582) ($P < 0.001$) (Fig. 4). Our results indicate that individuals with the same haplotype were more likely to be found within the same school. This finding was also significant for same sex pairs (males, $P < 0.001$, Fig. 5a; females, $P < 0.05$, Fig. 5b).

Discussion

Genetic relatedness in common dolphin schools

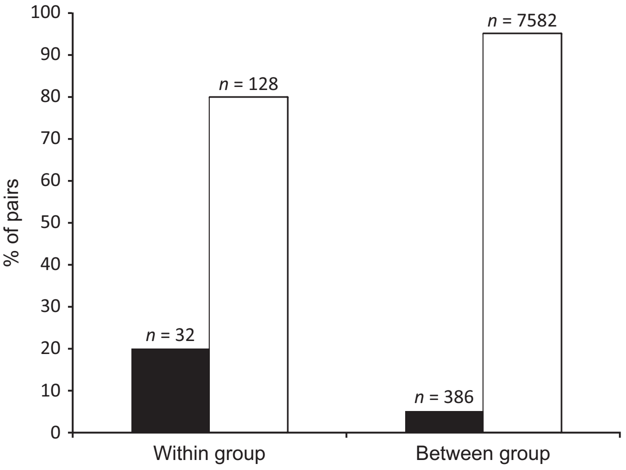

Figure 4 Percentage of short-beaked common dolphin pairs with identical (shaded) and different (unshaded) haplotypes within and between schools in southern Australia. *N*-values are presented above bars.

Our study suggests that biparental genetic relatedness may influence male common dolphin associations, as mean genetic relatedness for males was higher within than between schools, and more full-sib and half-sib relationships were present within schools than between schools. Our results are in contrast to a previous study on common dolphins in the English Channel (Viricel *et al.*, 2008), but are similar to a study of striped dolphins *Stenella coeruleoalba* inhabiting pelagic and continental shelf waters of the Mediterranean, where the average relatedness of the dolphins was larger within than between schools (Gaspari *et al.*, 2007).

Male inshore delphinids are known to associate and form coalitions or alliances to increase the benefits of group living, which include protection from predators or to gain access to females for mating (Möller *et al.*, 2001; Wiszniewski, Brown & Möller, 2012). Where males form alliances for the purposes

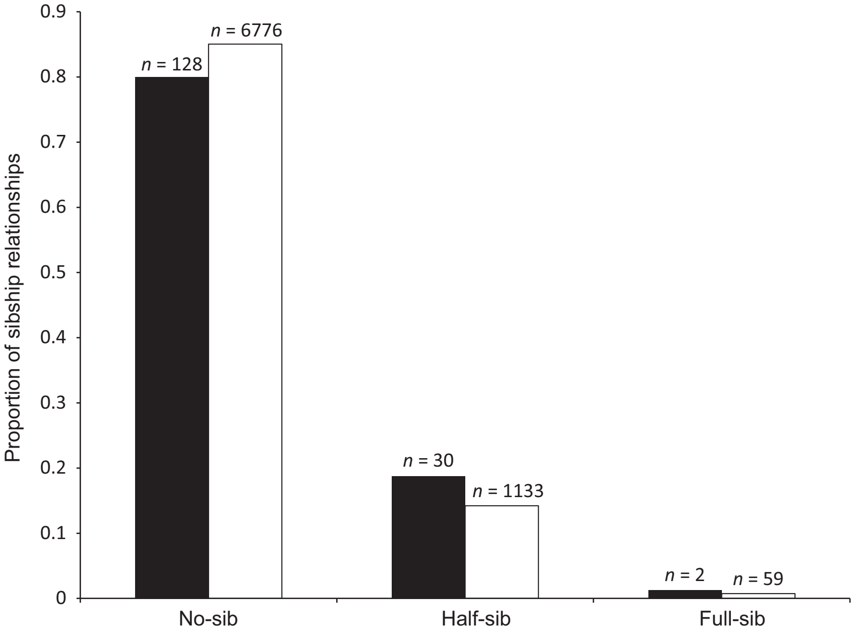

Figure 3 Proportion of sibship relationships between pairs of short-beaked common dolphins within (shaded) and between (unshaded) schools. Relationships were categorized as either 'non-sib', 'half-sib' or 'full-sib' according to the pairwise likelihood method in COLONY (Jones & Wang, 2010). *N*-values are presented above bars.

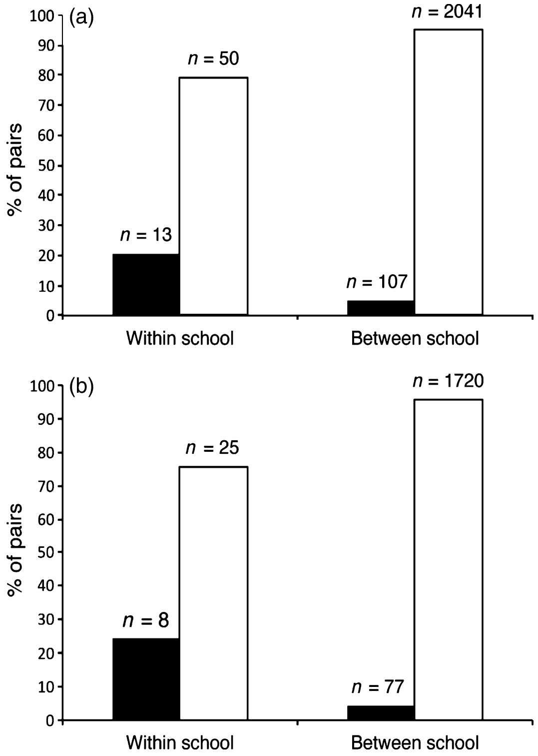

Figure 5 Percentage of short-beaked common dolphin pairs with identical (shaded) and different (unshaded) haplotypes for (a) males and (b) females in southern Australia. *N*-values are presented above bars.

of sexual coercion, individuals may benefit from biparental associations through inclusive fitness gains. Support for male group biparental relatedness has previously been documented in alliances of *Tursiops* sp. in Shark Bay, Western Australia (Krützen *et al.*, 2003) and common bottlenose dolphins *T. truncatus* in Little Bahamas Bank (Parsons *et al.*, 2003). Studies investigating the potential formation of male alliances in common dolphins are needed to assess whether cooperation among males is also leading to associations among kin in this species.

Additionally, our results suggest that other ecological or social factors may be of greater significance in determining school associations among female common dolphins. For example, associating with females of similar reproductive status may provide greater benefits to group living and increased fitness (e.g. Möller & Harcourt, 2008). In coastal bottlenose dolphins, several additional factors have been suggested as impacting upon female associations such as social familiarity, age, calf age and maternal experience (Wells *et al.*, 1980; Möller & Harcourt, 2008), and this may also be the case for common dolphins in southern Australian waters.

Potential maternal kinship in common dolphin schools

Haplotype and nucleotide diversities are similar to results previously reported for these animals in the wider region off southern (Bilgmann *et al.*, 2008, 2014) and eastern Australia (Möller *et al.*, 2011), and elsewhere including New Zealand (Stockin *et al.*, 2008), the English Channel (Viricel *et al.*, 2008) and the North Atlantic (Westgate & Read, 2007; Mirimin *et al.*, 2009).

Results from our study suggest that maternal kinship may also influence associations in common dolphins, with pairs of dolphins with the same mtDNA haplotypes, assumed to belong to the same maternal lineages, more likely co-occurring in the same schools. Previous studies suggested that kinship had no influence on the social structure of short-beaked common dolphins (Natoli *et al.*, 2008; Viricel *et al.*, 2008), although one study showed that some mtDNA haplotypes were shared among females of the same school (Mirimin *et al.*, 2009).

Socio-ecology of common dolphins in southern Australia

Kin associations within pelagic dolphin species are typically less prevalent due to dispersal of both sexes (Mirimin *et al.*, 2011). Philopatry and kin associations, however, appear to be typical of smaller delphinid species inhabiting shallow coastal and inshore environments (Möller, 2012). Our data suggest that common dolphins in southern Australia may show association patterns that more likely resemble those of inshore and coastal dolphins.

Within southern Australian waters, common dolphins are frequently sighted within gulfs and embayments (Mason, 2007; Filby *et al.*, 2010). For example, common dolphins in Gulf St Vincent (GSV), South Australia, utilize the shallower, northern parts of the gulf (Filby *et al.*, 2010). This area has been suggested as an important nursery area for the species as the sheltered gulf waters can provide increased protection from predators (Filby *et al.*, 2010). Individuals that utilize this area may potentially have smaller home ranges and limited dispersal, increasing their opportunity to associate with kin (e.g. Clutton-Brock & Lukas, 2012).

Common dolphin school sizes in GSV were also relatively small, mostly containing ≤10 individuals (Filby *et al.*, 2010). This is in contrast to what is typically reported for common dolphins, a species that is considered to aggregate in large schools, especially when inhabiting neritic and pelagic waters. For example, in the eastern tropical Pacific, they are typically found in schools of approximately 300 individuals (Gerrodette *et al.*, 2008). School sizes of common dolphins found during this study are more comparable to dolphin species that typically inhabit shallow and more protected environments, such as bottlenose and humpback dolphins (Parra *et al.*, 2011), and their social structure in southern Australia may be more similar to these species.

Management implications

Understanding the socio-genetic structure of common dolphins in southern Australia is also important for assessing the potential impacts of dolphin–fishery interactions. School formation in dolphins puts individuals at risk of being entangled simultaneously (Mendez *et al.*, 2010). Given that common dolphins with the same mtDNA haplotypes are more likely to be found in the same schools in this region, bycatch of dolphins from the same school may lead to a reduction of mtDNA diversity in the population. Potential decrease in genetic diversity may also result from simultaneous male entanglements, since biparentally related individuals were more likely to be found in the same schools.

In conclusion, our results suggest an influence of biparental relatedness, particularly on the associations of males, and possibly also an impact of maternal kinship on common dolphin associations in southern Australia. We hypothesize that common dolphins in this region exhibit social traits that are more typically found in other dolphin species inhabiting shallow coastal and inshore environments, and this information should be considered when revising mitigation measures for fishery–dolphin interactions. In particular, the analysis of samples from bycaught dolphins would help in determining if related individuals or those of the same reproductive state, age or sex class are more at risk of simultaneous entanglements and deaths.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Detailed methodology of the biopsy sampling procedure.

Appendix S2 Details of the microsatellite diversity.

Appendix S3 Interpretation of mean relatedness within schools of short-beaked common dolphins in southern Australia.

Table S1 School number (S), sex and haplotype (H) of individual short-beaked common dolphins off southern Australia. Note that duplicate samples were removed.

Table S2 Haplotypes (H) identified in short-beaked common dolphins off southern Australia between eastern Eyre Peninsula and western Wilsons Promontory, the region of Population 4 (Bilgmann *et al.*, 2014).

Table S3 Number of alleles, observed (H_O) and expected (H_E) heterozygosities for each of the 13 microsatellite loci used for data analysis. Mean and standard error (SE) are indicated in bold.

Table S4 Mean relatedness (R) between pairs of individuals of short-beaked common dolphins sampled in the same school (≥2 individuals) in southern Australia.

Figure S1 Median-joining network of 128 mtDNA control region sequences from short-beaked common dolphins, representing a sub sample from dolphins of southern Australia Population 4 (Bilgmann *et al.*, 2014).