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ORIGINAL ARTICLE

Social cohesion and intra-population community structure in southern Australian bottlenose dolphins (*Tursiops* sp.)

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Abstract

Defining intra-population community variation in group living mammals provides insights about the impact of environmental, social, and anthropogenic factors on population sub-structuring. Here, we use generalised affiliation indices (GAIs) and social network analysis to investigate social cohesion and intra-population community structure of southern Australian bottlenose dolphins (*Tursiops* sp.) inhabiting Adelaide's metropolitan coast in South Australia. Information on the sex and site fidelity of photographically identified individuals was used to investigate the potential link between these parameters and preferred affiliations at the population level. Genetic data was also used to investigate genetic relatedness within and between sex and communities. Overall, dolphins showed non-random associations, with preferred associates prominent amongst females and resident individuals. Dolphins were clustered into two social communities that showed little spatial overlap and were associated with different habitats: a northern, shallow-water community (NSWC) and a southern, deep-water community (SDWC). As expected, preferred associations were more prevalent within than between communities, and analyses of genetic relatedness indicated that dolphins, particularly females, were on average more related within than between communities. Social network metrics varied between communities, with the temporal stability of associations for both communities characterised by rapid disassociations and casual acquaintances. We suggest that these two dolphin communities likely arose due to a combination of ecological and socio-genetic factors. This study enhances our understanding of factors shaping social groups in long-lived mammals and our ability to manage human activities that can impact upon their behaviour and social structure.

Significance statement

Determining how and why individual animals interact and form groups is important for understanding the evolution of sociality and designing management strategies for wildlife conservation. We investigated association patterns and social community structure in southern Australian bottlenose dolphins in Gulf waters of South Australia. Within the study area, dolphins were divided into two separate communities associated with different habitat types. Within these two communities, dolphins formed groups with particular individuals and mostly related individuals amongst females. These findings enhance our understanding of the factors shaping mammalian groups and our ability to manage human activities that can impact upon their behaviour and social structure.

Keywords Social structure · Group formation · Lagged association rate · Kinship · Gulf St Vincent · Conservation management

Introduction

The formation of groups is common in a variety of animals, including reptiles (Duffield and Bull 2002), fishes (Balshine et al. 2001), birds (Covas and Griesser 2007), and mammals (Silk 2007). In mammals, a combination of ecological and social factors, demography, and life history traits underpin group living (Kappeler et al. 2013). Animals are more likely to form groups when the benefits of being in a group outweigh the costs (Krause and Ruxton 2002). Benefits of group living may include increased foraging efficiency, protection from

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predators, and mating success, while costs may include increased competition for food resources and space, and increased exposure to pathogens (Rubenstein and Wrangham 1986; Krause and Ruxton 2002). Where individuals associate with kin, they may also benefit from inclusive fitness gains (Hamilton 1964; Seyfarth et al. 2014; VanderWaal et al. 2014a, b). Thus, social structure can influence the survival and reproductive success of individuals and, hence, population persistence. Defining social structure, by determining how and why individuals interact in groups and form social relationships, is therefore important when designing management strategies for conservation of wildlife populations (e.g. Smith et al. 2016).

Communities are groups or clusters of individuals that are behaviourally closed over the relevant time scales so that they interact more frequently amongst themselves than with the rest of the population (Girvan and Newman 2002; Krause and Ruxton 2002; Whitehead 2008). These social communities are common amongst group living mammals such as primates (Goodall 1986), sheep (Coulson et al. 1999), kangaroos (Best et al. 2013), elephants (Wittemyer et al. 2005), and dolphins (Wiszniewski et al. 2009). Social communities typically arise when individuals display site fidelity to an area, which can provide opportunities for social interactions, and accordingly, the development of long-lasting relationships amongst individuals (Hinde 1976; Ramos-Fernández et al. 2006; Wolf and Trillmich 2007). However, the formation and structure of these communities can be influenced by a combination of ecological, social, and anthropogenic factors (Hinde 1976; Caro and Sherman 2011; Blumstein 2012).

Ecological factors that may influence community structure include the surrounding environment and its complexity, resource availability and dispersion, and predation risk (Blumstein 2012). For example, habitat heterogeneity and the quality of food resources have led to the spatial segregation of sheep communities (e.g. Coulson et al. 1999; Wolf et al. 2007; Mourier et al. 2012). Socio-genetic factors that may influence community structure include homophily and/or philopatry, where preferred associations arise amongst individuals of the same sex, age, behavioural attribute, or reproductive status (Hinde 1976). For example, affiliation patterns amongst female rhesus macaques are influenced by age proximity (Widdig et al. 2001). Individuals may also preferentially associate with genetically related individuals, suggesting a role of kin selection on community structure. This has been shown in kangaroos where females had strong social strong social preferences for genetically related individuals within communities, despite significant community overlap (Best et al. 2013). Further, community structure may be influenced by anthropogenic factors that elicit changes to the environment or disrupt natural animal behaviours (Caro and Sherman 2011; Blumstein 2012). For example, in dolphins, trawling efforts that altered food availability have impacted upon the composition of dolphin communities (Chilvers and Corkeron 2001; Ansmann et al. 2012). In addition, in wolves, human hunting of these animals have resulted in low kinship levels, altering their family-based social structure (Rutledge et al. 2010).

Currently, there is a limited understanding of the variation in social structure between communities of the same population (i.e. intra-population community variation) amongst mammals. Information about variation in community structures can provide an understanding of population responses to environmental, social, and anthropogenic factors (Croft et al. 2010), and provide a greater understanding of the evolutionary processes that affect social structure. For example, community-based approaches have been used to compare features of the distribution and abundance of primates, leading to intra-population conservation priorities (Ganzhorn 1999). Intra-population community structure can also be related to small-scale demographic differences (i.e. survival/birth rates) based on their environmental and/or social preferences (Sutherland 1996; Coulson et al. 1999; Ellis et al. 2017), highlighting its importance for conservation management, particularly for long-lived, slow reproducing species. Social network analysis (SNA) has become a powerful tool to investigate social structure and define communities at a range of spatial and temporal scales (Farine and Whitehead 2015), including for giraffes (VanderWaal et al. 2014a, b), bats (Chaverri 2010), marsupials (Best et al. 2013), and delphinids (Titcomb et al. 2015).

Delphinids live in a wide variety of social structures, from strong matrilineal societies to fluid fission-fusion societies (reviewed in Möller 2012). The fluid fission-fusion societies of bottlenose dolphins make them a complex and interesting group to investigate inter- and intra-population community variation. Communities of *Tursiops aduncus* and *T. truncatus* appear to be influenced by habitat type (Rossbach and Herzing 1999; Lusseau et al. 2006; Urian et al. 2009) or are thought to result from a combination of ecological and socio-genetic preferences (Chilvers and Corkeron 2001; Wiszniewski et al. 2009; Louis et al. 2015). Currently, there is no information on the social structure of a third putative species of bottlenose dolphin, the Burrunan dolphin (*T. australis*), likely endemic to coastal waters of southern Australia (Charlton-Robb et al. 2011). As the validity of this species is currently in debate (Perrin et al. 2013), we refer to them here as southern Australian bottlenose dolphins (*Tursiops* sp.).

Adelaide's coastal waters, within the Gulf St Vincent, South Australia, are an important habitat for southern Australian bottlenose dolphins, as up to 239 (SE ± 54.91) individuals occur in the area (Zanardo et al. 2016). Southern Australian bottlenose dolphins in this region appear to show varying degrees of site fidelity, with photo-identified individuals classified as year-round residents, seasonal residents, or occasional visitors (Zanardo et al. 2016). Based on sightings and behavioural observations, it seems that the distribution and movement of these dolphins is likely influenced by seasonal prey availability (Zanardo et al. 2017). As these individuals live adjacent to Australia's fifth largest city, they are at risk from several anthropogenic impacts, such as habitat degradation, recreational fishing, dolphin-swim with tourism, pollution, and harassment (Edyvane 1999; Kemper et al. 2008; Lavery et al. 2008; Peters et al. 2012; Byard et al. 2013). They were also recently subjected to an outbreak of cetacean morbillivirus (Kemper et al. 2016). Information on their social structure is needed to assist mitigation of impacts from anthropogenic stressors and disease spread on this population.

In this study, we use newly developed generalised affiliation indices (Whitehead and James 2015), SNA, ranging patterns, and genetic analysis to investigate population-level and sex-specific association patterns, define intra-population community structure, and assess the potential influence of environmental, social, and genetic factors on intra-population community structure. Overall, we expected the social structure of southern Australian bottlenose dolphins to be representative of a fission-fusion society and resemble those of other coastal bottlenose dolphin populations. The high site fidelity of many individual dolphins to Adelaide's metropolitan coast (Zanardo et al. 2016) could favour preferred associations, the formation of communities, and opportunities to associate with kin. As this is a relatively open coastline with no physical barriers, community structure may arise due to changes in habitat type and/or social preferences, rather than from restricted movement patterns.

Materials and methods

Study site and data collection

Boat-based, photo-identification surveys were conducted between December 2012 and August 2014 along the Adelaide metropolitan coast, in eastern Gulf St Vincent (GSV), a relatively shallow and large inverse estuary in South Australia. Surveys followed predetermined zig-zag line transects, covering approximately 195 km^2 of the metropolitan coastal waters. Once a bottlenose dolphin (hereafter dolphin) group was sighted, they were approached to a distance of approximately 30 m to record data on location (using a hand-held global positioning system), time, group size, and age composition (following Zanardo et al. 2016). It was not possible to record data blindly because our study involved the identification of focal animals in the field. We aimed to photograph all individuals within the group irrespective of their distinctiveness (Zanardo et al. 2016). Photographs of dolphins were categorised (excellent, good, or poor) based on the focus, contrast, angle, and size of the dorsal fin in relation to the photo frame (Urian et al. 1999). Dolphins were then identified based on the unique and natural marks on their dorsal fins (Würsig and Jefferson 1990) and given a measure of distinctiveness. Only excellent- and good-quality images of distinctive individuals were used to identify individuals, ensuring that indivdiuals were correctly identified over time (Würsig and Jefferson 1990; Read et al. 2003). Calves were excluded from analysis as they often lack identifiable marks and are in close association with their mothers. For further details of survey design and photo-identification methods see Zanardo et al. (2016). Biopsy samples of adult animals were collected remotely using the PAXARMS biopsy system (Krützen et al. 2002) or a hand-held biopsy pole for bow-riding dolphins (Bilgmann et al. 2007a). Individuals were recognised at the time of sampling through photo identification to avoid re-sampling. Biopsy samples were preserved in 20% dimethyl sulphoxide (DMSO) saturated with NaCl (Amos and Hoelzel 1991) or 90% ethanol, and later transferred to a − 80 °C freezer.

Genetic analysis

DNA was extracted from samples using a standard salting-out protocol (Sunnucks and Hales 1996). The sex of individuals was genetically determined by amplifying fragments of the ZFX and SRY genes using the polymerase chain reaction (PCR) (conditions as reported in Möller et al. 2001). Females were also identified in situ through repeated presence of a depended calf, and males were identified in situ by visual observation of the genitalia.

Individuals were genotyped at 11 polymorphic cetacean microsatellite loci: eight tetranucleotides (Tur4_80, Tur4_87, Tur4_91, Tur4_105, Tur4_111, Tur4_141, Tur4_142, Tur4_E12) (Nater et al. 2009) and three dinucleotides (MK9 (Krützen et al. 2001), TexVet5 (Rooney et al. 1999), and EV37 (Valsecchi and Amos 1996)). PCR conditions were as reported in Pratt et al. (2018). We used MICRO-CHECKER v 2.2.3 (Van Oosterhout et al. 2004) to test for genotyping errors, presence of null alleles, stutter peaks, and/or allelic dropout. Tests for departures from the Hardy-Weinberg equilibrium and for linkage disequilibrium were conducted in GENEPOP v 4.2 (Raymond and Rousset 1995) based on a Markov chain method with 1000 iterations. Bonferroni correction was applied to adjust significance levels for multiple comparisons (Holm 1979).

One locus (Tur4_142) showed significant deviations from HWE after Bonferroni correction, which was due to heterozygote deficiencies. Heterozygote deficiency in Tur4_142 is unlikely to be due to the presence of null alleles, as other related bottlenose dolphin populations did not show evidence of null alleles (Pratt et al. 2018). Therefore, this locus was retained for analyses. We found no evidence of linkage disequilibrium between any locus pair.

Defining associations

Dolphins were defined as part of the same group if they were within a 100-m radius of each other and heading in the same direction if travelling (Irvine et al. 1981). Dolphins within the same group were assumed to be associated (Whitehead 2008). If an individual or group were sighted more than once during a survey, only the first sighting was included in the analysis. We further restricted our analysis to groups where a minimum of 50% of individuals were identified, based on the visually estimated group size.

The amount of time two individuals are associated can be a result of their true affiliation and preference for one another, but may also be driven by other structural factors such as spatial and/or temporal overlap in habitat use patterns and gregariousness (Whitehead and James 2015). Generalised affiliation indices (GAIs) assess the existence and strength of true affiliations while controlling for structural factors, which can potentially lead to biased indices of association (Whitehead and James 2015). We used program SOCPROG v 2.6 (Whitehead 2009, 2015) to estimate GAIs of dolphins in metropolitan Adelaide. GAIs were calculated as the residuals from a generalised linear model, where half weight association indices were the dependent variable, and the structural predictor variables included gregariousness (tendency to form associations) and home-range overlap.

Gregariousness was calculated within SOCPROG following Whitehead and James (2015), which is the log of the sum of the association indices involving an individual multiplied by the sum of those involving another individual (Whitehead 2015). Areas of home-range overlap between pairs of individuals were calculated in the adehabitatHR package (Calenge 2006) in R v 3.2.3 (R Core Team, 2014), following the kernel-based utilisation distribution overlap index method (Fieberg et al. 2005). This provides a single measure of overlap of the 95% utilisation distribution (UD) between pairs of individuals. Values range from zero (no overlap) to one (uniformly distributed and 100% overlap), but they can be > 1 if both UDs are non-uniformly distributed and have a high degree of overlap. As a minimum of five sightings are required to calculate areas of home-range overlap, we restricted all GAI analysis to only individuals sighted five or more times. To test which structural variables significantly influenced associations, we carried out a multiple regression quadratic assignment procedure (MRQAP) test for each predictor variable and calculated standardised partial correlation coefficients within SOCPROG. Structural variables with a significant correlation were controlled for (as predictor variables) when calculating GAIs (Whitehead and James 2015).

Population-level association patterns

We estimated mean GAI and the standard deviation of the observed associations for all individuals and separately for each sex and site fidelity class (year-round residents, seasonal residents, and occasional visitors as determined by capture rates; see Zanardo et al. 2016 for details). We then used data stream permutation tests (Bejder et al. 1998, modified by Whitehead et al. 2005; Whitehead 2008) to assess whether individuals associate at random, or if they have preferred and/or avoided associates. Estimates for survival and migration are currently not available; however, the variation in site fidelity and abundance across seasons suggest that animals do range beyond the boundaries of the study area (Zanardo et al. 2016) and form part of a larger population within GSV (Pratt et al. 2018). Therefore, in each sampling period, not all individuals are likely to be present, and thus, to account for demographic effects (births, deaths, migration), we permuted groups within sampling periods (one survey day) (Whitehead 2008). We ran multiple tests, increasing the number of permutations until the p value stabilised (Bejder et al. 1998), in our case 2000. Individuals were identified as having preferred or avoided associations when the standard deviation (SD) of the observed associations was significantly higher than the randomly permuted dataset (Whitehead 2009).

Social and spatial segregation of communities

GAIs were then used to create a network of associations between individuals for the whole study period, and assess potential community structuring using the Girvan-Newman algorithm (Girvan and Newman 2002) within SOCPROG. The most parsimonious division is determined by the division that maximises the modularity index, Q, where Q is defined as the difference between associations for all dyads within clusters and the expected value if dyads associated at random, given the summed associations of the different individuals (Newman and Girvan 2004). A value of $Q > 0.3$ indicates a good representation of community separation. We used the spring embedding method in NETDRAW v 2.1.4.1 (Borgatti 2002) to provide a visual representation of community structure.

Although the modularity index, Q, measures the level of clustering in a social network, it does not provide any information on the spatial distribution of the clusters identified. Identifying the space use of all individuals within a cluster can provide additional insights into how space use may shape social network patterns. To identify core areas of use according to community assignment, we calculated kernel density estimates (Worton 1989) using the ‘kernel interpolation with barriers tool’ available within the Geostatistical analyst toolbox in ArcMap (following methods described in MacLeod 2013). These estimates were created using the sighting locations for all individuals assigned to a community. We then extracted kernel ranges of 50 and 95% probability of occurrence for each community. Kernel ranges of 50% were considered core areas of community use, and 95% kernel ranges were considered community representative ranges (Worton 1989).

Community-level association patterns

To examine potential differences in the association patterns between communities identified in the previous analysis, we used three different approaches implemented in SOCPROG: (1) association indices and tests for preferred/avoided associations, (2) network metrics, and (3) lagged association rates. Firstly, we estimated mean GAI and ran permutation tests to assess preferred/avoided associations (see "Materials and methods") within and between communities. Second, we calculated four network metrics for each community to compare patterns of association between communities: strength, eigenvector centrality, clustering coefficient, and affinity (Whitehead 2008). Strength is a measure of gregariousness, representative of the number of social connections an individual has, where high estimates indicate strong associations amongst individuals. Eigenvector centrality is a measure of both how well an individual is associated to its neighbours and how well its neighbours are themselves associated, representing how well connected individuals are within a network. Clustering coefficient is a measure of how well an individual's neighbours are themselves associated, and is high in societies of tight and closed social units. Lastly, affinity is a measure of whether individuals have a strong association to individuals with high strength (Whitehead 2008). These network metrics were compared to the expected values if individuals had no association preferences, using 10,000 data stream permutations (Lusseau et al. 2008). Third, the temporal stability of associations within and between communities was assessed using lagged association rates (LARs) (Whitehead 1995). LARs are the probability that if two individuals are associated within a given time, they will still be associating some time lag later. The LAR for each community was compared to the null association rate, which is the expected value if there are no preferred associations over time (Whitehead 1995). Standard errors were obtained using the jackknife procedure. We fitted eight exponential models of temporal stability to the observed LAR data and used the quasi-Akaike information criterion (QAIC), which corrects for overdispersion, to select the best fit model (Whitehead 2008).

Genetic relatedness and sib-ship relationships

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). The triadic likelihood estimator (Wang 2007) provided the highest correlation with the true values (Wang 2011) (data not shown) and was therefore used to estimate pairwise relatedness between individuals. Genetic analyses were only carried out for those individuals used in the association analysis (i.e. sighted ≥ five times). We used the bootstrap method in COANCESTRY (with 10,000 bootstraps) to test, at the population level, for a significant difference in the average genetic relatedness between all pairs of females, males, and opposite sex. We also used this method to test whether the average relatedness of individuals within communities was significantly higher than between communities, and to test for a difference in the average relatedness of same sex pairs within and between communities. Furthermore, we inferred kinship relationships using pairwise likelihood methods in COLONY v 2.0 (Jones and Wang 2010) and tested for a difference in the proportion of sib-ship relationships (full-sib, half-sib, non-sib) within and between communities using a chi-square test of independence.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Results

A total of 83 survey days were completed between December 2012 and August 2014. During this period, we obtained photographs of 1682 individual dolphins within 228 dolphin groups (median group size 4) and photo-identified 244 distinctly marked individuals (Zanardo et al. 2016). Of these individuals, 127 dolphins were sighted ≥ five times and thus included in the remaining analysis. We obtained biopsy samples from 34 of the 127 individuals, and social analyses included 33 females, 17 males (including 15 and one individual, respectively, sexed in situ), and 77 of unknown sex.

Population-level associations

MRQAP tests indicated a significant correlation of associations with gregariousness ($r = 0.426$, $p < 0.001$) and home-range overlap ($r = 0.181$, $p < 0.001$), and therefore, both structural variables were retained and used to calculate GAIs. The mean GAI for all individuals sighted ≥ five times was − 0.278 (± 0.962). A significantly higher SD of the observed associations compared to random indicated preferred and avoided associations amongst these individuals (observed SD = 0.084, random SD = 0.073, $n = 127$, $p < 0.001$).

The mean GAI was higher amongst females (− 0.135 ± 1.102) than amongst males (− 0.440 ± 1.161) and between-sex associations (− 0.328 ± 0.917). We also found evidence for preferred and/or avoided associations amongst females (observed SD = 0.090, random SD = 0.081, $n = 33$, $p < 0.001$), while marginally non-significant results were obtained for males (observed SD = 0.105, random SD = 0.099, $n = 17$, $p = 0.069$) and between-sex associations (observed SD = 0.071, random SD = 0.069, $n = 50$, $p = 0.052$).

Based on levels of site fidelity, GAI was higher amongst year-round residents (− 0.036 ± 1.442) than seasonal residents (− 0.245 ± 0.935) and occasional visitors (− 0.344 ± 0.479). Preferred and avoided associations were present amongst year-round residents (observed SD = 0.123, random SD = 0.106, $n = 29$, $p < 0.001$) and seasonal residents (observed SD = 0.086, random SD = 0.079, $n = 91$, $p < 0.001$), but were not present amongst occasional visitors (observed SD = 0.060, random SD = 0.060, $n = 7$, $p = 0.241$). We also found a larger proportion of preferred associations amongst year-round residents (preferred = 0.091, avoided = 0.022) than amongst seasonal residents (preferred = 0.029, avoided = 0.006).

Social and spatial segregation of communities

When constructing the network of associations, the modularity index was maximised when individuals were clustered into two communities (Q maxima = 0.36, Fig. 1a). Core and representative kernel ranges indicated that members of the same community had similar geographical ranges, with no overlap in their core ranges and little spatial overlap (9%) between the representative ranges of both communities. This geographical separation between communities appears to coincide with differences in depth ranges in the north and south of the study area, at a depth of approximately 9 m, and therefore, we classed the communities as 'northern shallow-water' and 'southern deep-water' (Fig. 1b). The northern shallow-water community (NSWC) consisted of 57 individuals (including 18 females and 9 males), while the southern deep-water community (SDWC) consisted of 70 individuals (including 15 females and 8 males).

Within communities, the mean GAI was higher for the NSWC (0.16 ± 1.30) than for the SDWC (− 0.05 ± 1.05). Results indicated that preferred and avoided associations were present within and between communities (NSWC: observed SD = 0.113, random SD = 0.105, $n = 57$, $p < 0.001$; SDWC: observed SD = 0.102, random SD = 0.096, $n = 70$, $p < 0.001$; NSWC-SDWC: observed SD = 0.044, random SD = 0.042, $p < 0.05$). As expected, there was a larger proportion of preferred associations within communities (NSWC: preferred = 0.085, avoided = 0.019; SDWC: preferred = 0.042, avoided = 0.005) than between communities (preferred = 0.003; avoided = 0.007).

All four network measures, however, showed no significant differences from random (Table 1). Only eigenvector centrality was significantly lower than expected by chance for the SDWC (observed = 0.09, random 0.10, $p < 0.001$, Table 1), suggesting that members of this community are not well connected.

Lagged association rates within and between communities remained above the null association rate (expected value if there are no preferred associations), indicating non-random associations both within and between communities (Fig. 2). However, associations were stronger within communities, as the LARs remained higher compared to between communities (Fig. 2). We found similar temporal variability in association patterns within and between communities, where the best fitting model for each LAR consisted of 'casual acquaintances and rapid disassociations' (Fig. 2, Supplementary Material Table S2). This model is consistent with social systems in which associations are short-lived, but where individuals still form preferred associations (Whitehead 2008). The SDWC also showed some support for a second model that consisted of 'two levels of casual acquaintances' (see Supplementary Material Table S2). This model is consistent with social systems where individuals form preferred associations that decay over two different time periods. Overall, these models of temporal stability support a fission-fusion social system.

Genetic relatedness and sib-ship relationships within and between communities

Of the 34 biopsy samples, 10 females and 9 males were sampled from the NSWC, and 8 females and 7 males were samples from the SDWC (Supplementary Material Table S1). Overall, the mean pairwise relatedness between females ($n = 18$, $R = 0.081$) was significantly higher than between males ($n = 16$, $R = 0.051$, $p < 0.05$). Further, the mean relatedness of individuals within communities was significantly higher than between communities (within $n = 276$, $R = 0.075$; between $n = 285$, $R = 0.056$, $p < 0.001$, Table 2). When comparisons were made separately for each sex, females exhibited significantly higher mean pairwise relatedness within than between communities (within $n = 83$, $R = 0.097$; between $n = 88$, $R = 0.067$, $p < 0.05$, Table 2). Males exhibited no significant difference in relatedness (within $n = 49$, $R = 0.063$; between $n = 56$, $R = 0.043$, $p = 0.89$) and similarly for between-sex pairs (within $n = 144$, $R = 0.071$; between $n = 141$, $R = 0.053$, $p = 0.93$, Table 2). The proportion of sib-ship relationships also differed within and between communities. We found a significantly larger proportion of half-sib and full-sib pairs within communities than between communities, and a larger proportion of non-sib pairs between communities ($\chi^2 = 11.92$, $df = 2$, $p < 0.05$, Fig. 3).

Discussion

Little is known about intra-population community structure amongst mammals and how ecological and social factors

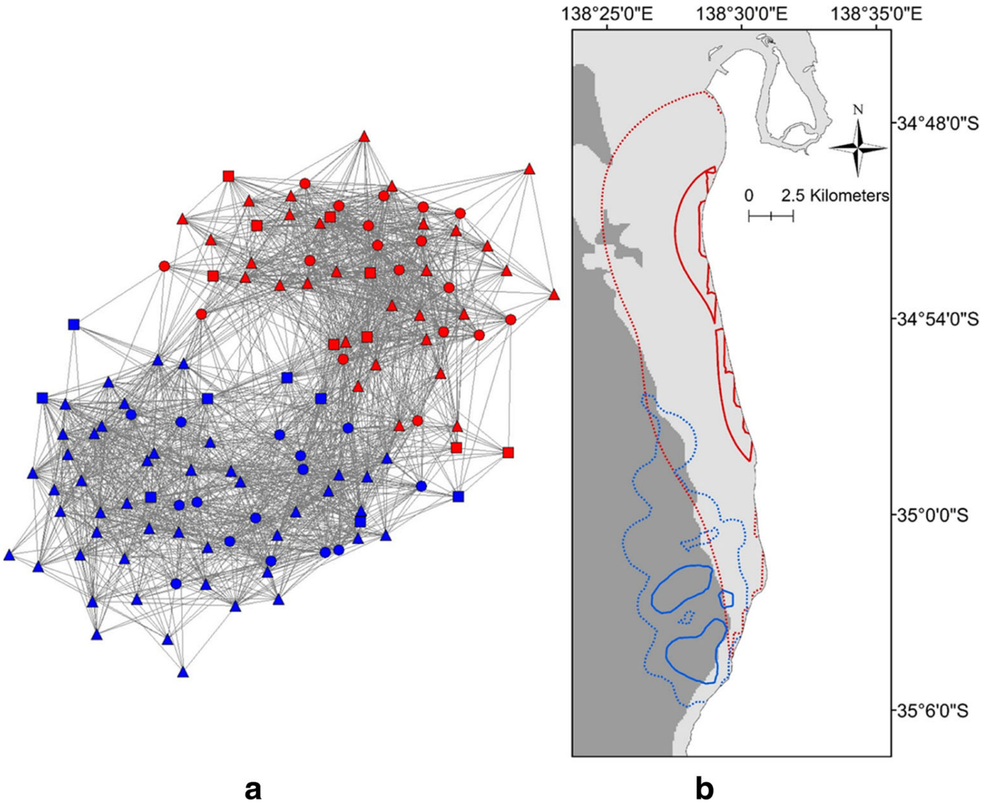

Fig. 1 **a** Social network of southern Australian bottlenose dolphins along Adelaide's metropolitan coast. Each individual is represented by a node, and associations are represented by the black lines. Only individuals sighted five or more times were included. Node colours denote community (red = northern shallow-water community, blue = southern deep-water community), while node shapes denote sex (female = circle, males = square, triangle sex = diamond). **b** Ranges of two communities of southern Australian bottlenose dolphins along Adelaide's metropolitan coast, South Australia. Contours represent 50% core kernel range (solid contour line), 95% representative kernel range (dashed contour line). Red and blue colourations correspond to the northern shallow-water and southern deep-water communities, respectively. Grey shading represents the 9-m depth contour (light grey ≤ 9 m, dark grey ≥ 9 m)

may play a role in the formation of these communities. In this study, we used GAIs and SNA to investigate social cohesion and intra-population community structure in southern Australian bottlenose dolphins along Adelaide's metropolitan coast. Similar to other coastal populations of bottlenose dolphins, individuals along this coast did not associate at random, but had preferred and avoided associates (*T. aduncus*, Wiszniewski et al. 2009; *T. truncatus*, Louis et al. 2015; Titcomb et al. 2015), which were more likely amongst female and year-round residents. Based on these association patterns, the population was divided into two social communities, with little spatial overlap and were associated in different habitats: a NSWC and a SDWC. Associations were higher between NSWC dolphins than between SDWC dolphins. Social network metrics varied between communities, with eigenvector centrality found to be higher in the SDWC than in the NSWC. The temporal stability of associations for both communities was characterised by rapid disassociations and casual acquaintances, suggesting similar fission-fusion social systems at the community level. Genetic relatedness was on average higher within than between communities, particularly for female dolphins. We suggest that these two dolphin communities likely arose from a combination of individual adaptations to ecological conditions, such as depth, benthic habitat type, and prey assemblages, and social factors, such as preferred associates, which likely include close kin.

Ecological and socio-genetic influences on community separation

Our results show that there is little spatial overlap between the two communities of bottlenose dolphins present along the Adelaide metropolitan coast. This spatial separation arises in a relatively open section of the coast that lacks physical barriers to movement, but differs in water depth with one community ranging over shallower waters (< 9 m) to the north of the study area, and the other ranging across deeper waters (9–25 m) to the south. Within this part of the Adelaide coast, the transition from shallow to deep waters also corresponds to changes in benthic habitat. The northern, inshore areas of metropolitan Adelaide lie adjacent to the Port River and Barker Inlet, and consist of estuarine, shallow waters with seagrass meadows and bare sand habitats (Bryars 2003, 2013). In contrast, the southern part of the study area is mostly characterised

Table 1 Network analysis statistics, calculated using generalised affiliation indices (GAI) and averaged for two communities of southern Australian bottlenose dolphins along Adelaide's metropolitan coast. Random values are the mean of values with no individual preferences (expected values from permuted matrices). An asterisk indicates a significant difference from a random network. All data shown as the means ± SD

	Strength	Eigenvector centrality	Clustering coefficient	Affinity
Northern shallow-water				
Class mean	0.07 ± 1.98	0.04 ± 0.02	1.01 ± 3.41	− 0.17 ± 10.87
Random	0.07 ± 1.62	0.03 ± 0.02	2.21 ± 76.95	− 1.01 ± 26.20
Southern deep-water				
Class mean	− 0.04 ± 1.42	0.09 ± 0.06*	0.51 ± 10.48	− 1.62 ± 6.19
Random	− 0.06 ± 1.21	0.10 ± 0.06	− 2.55 ± 80.86	− 2.87 ± 109.33

by temperate reefs and deeper waters that open up to the outer area of Gulf St Vincent (Bryars 2003, 2013). Such community structure linked to habitat features has been observed in other bottlenose dolphin populations. For example, in the Bahamas, a separation of *T. truncatus* communities was found to be associated with changes in water depth and benthic habitat (sandy substrate in deep waters vs. seagrass meadows in shallow waters; Rossbach and Herzing 1999). Similarly, community separation of *T. aduncus* in Port Stephens, New South Wales, corresponded with a change in benthic habitat (sandy substrate vs. muddy substrate; Wiszniewski et al. 2009), while in the northeast Gulf of Mexico, communities of *T. truncatus* were separated by shoals and oyster bars (Tyson et al. 2011). The separation of these two dolphin communities along Adelaide's metropolitan coast may therefore be the result of local adaptation to the different habitat types, water depths, and associated prey assemblages.

Prey movements do appear to influence the distribution of dolphins along the Adelaide metropolitan coast, as dolphins were found to predominately feed in areas with a high probability of dolphin occurrence (Zanardo et al. 2017). The spatial and temporal predictability of resources often found in inshore environments (Gowans et al. 2008) can lead to dolphins developing specific foraging strategies characteristic in particular habitats and/or on types of prey (Sargeant et al. 2007; Torres and Read 2009; Ansmann et al. 2015). These, coupled with local enhancement and social learning of calves from their mothers (Mann and Sargeant 2003; Weiss 2006), could lead to the formation of dolphin communities, later reinforced by intra-population competition for food resources. For example, NSWC individuals may have adapted to foraging amongst shallow seagrass meadows, while individuals in the SDWC may have developed foraging tactics specific to deeper temperate reef environments. Depending on prey availability and the plasticity of feeding strategies, specific feeding strategies may not extend to other areas, habitats, or prey (see Torres and Read 2009) and may help explain the observed community separation. Observations of specific dolphin foraging techniques together with stable isotope analysis and assessment of fish assemblages across habitat types would be necessary to confirm whether these dolphins exhibit community-level differences in feeding ecology.

Further, the site fidelity of individuals may affect community structure and promote differences in community-level social structure (Wolf et al. 2007; Wolf and Trillmich 2007). For example, the level of site fidelity displayed by individuals can regulate opportunities for individuals to interact and form associations (Michod and Sanderson 1985). Individuals within the Adelaide metropolitan coast show varying levels of site fidelity (Zanardo et al. 2016) and results here suggest that preferred associations are more prominent amongst individuals that spend more time within the area (i.e. year-round residents). In addition, a greater proportion of the NSWC dolphins are year-round residents (32%), whereas a greater proportion of seasonal residents (79%) are predominant in the SDWC (Supplementary Material Table S1; Zanardo et al. 2016). Therefore, the higher levels of site fidelity in the NSWC may increase the potential for individuals to associate and form stronger and tighter social connections. Although not significantly different from chance, higher measures of strength, clustering, and affinity were found for NSWC dolphins in comparison to SDWC dolphins. Conversely, lower levels of site fidelity in the SDWC may decrease the potential for individuals to be sighted and to associate with one another and thus may explain the lower network measures. It is important to note that individuals from these communities have been photo-identified in adjacent coastal areas (NZ, personal observations), and it is likely that the home ranges of both of these communities extend to areas outside of the Adelaide metropolitan coast. Therefore, the lower levels of site fidelity and network measures, particularly for the SDWC, may be a reflection on survey effort only encompassing part of their home range.

Associations between kin may also contribute to the observed community separation, as mean genetic relatedness and number of sib-ships were greater within than between communities. The high levels of site fidelity exhibited by individuals along Adelaide's metropolitan coast (Zanardo et al. 2016) also likely provide opportunities for individuals to

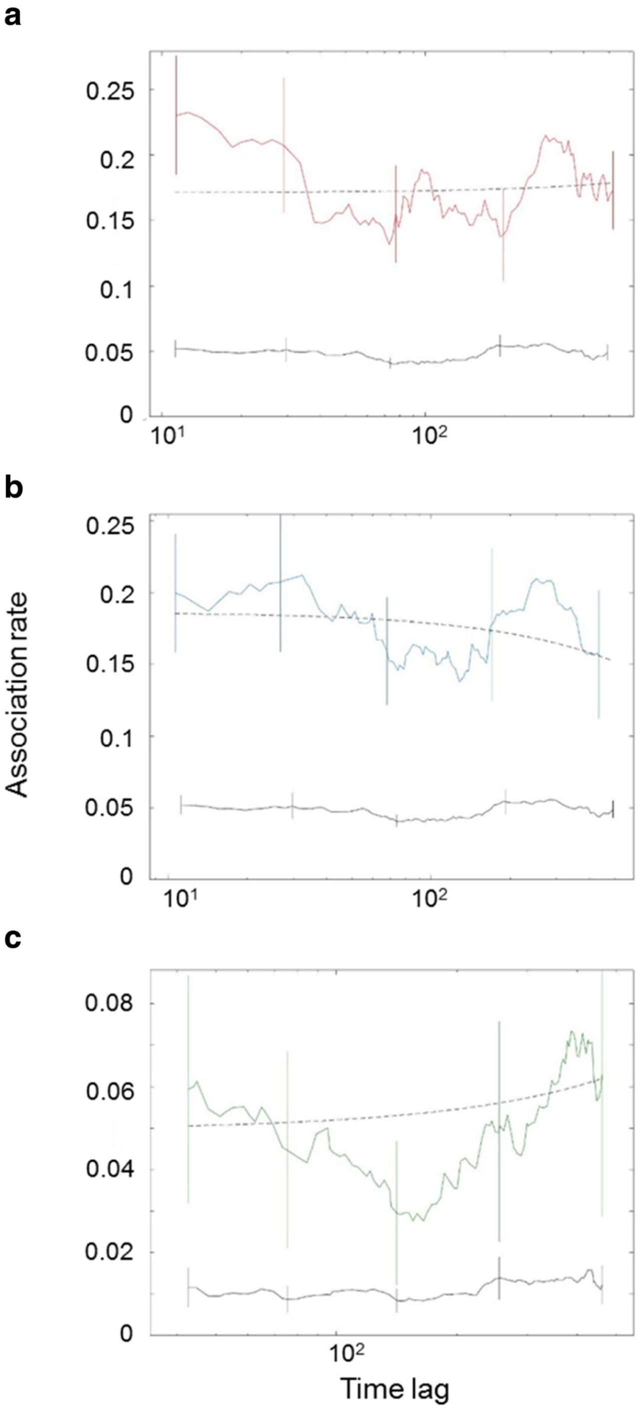

Fig. 2 Lagged association rates (solid coloured line), model of best fit (dotted line), and null association rates (solid black line) for the **a** northern shallow-water community, **b** southern deep-water community, and **c** between communities of southern Australian bottlenose dolphins along Adelaide's metropolitan coast. Standard errors were calculated using jackknife procedures

Table 2 Mean relatedness within and between communities for female (F-F), male (M-M), and opposite-sex (F-M) pairs of southern Australian bottlenose dolphins along Adelaide's metropolitan coast. An asterisk indicates a significantly higher mean pairwise relatedness within than between communities ($p < 0.05$). All data shown as the means ± SD

	Within cluster	Between cluster
All	0.075 (± 0.118)*	0.056 (± 0.094)
F-F	0.097 (± 0.127)*	0.067 (± 0.111)
M-M	0.060 (± 0.093)	0.042 (± 0.066)
F-M	0.070 (± 0.121)	0.055 (± 0.093)

develop social relationships with close kin. However, we found a difference between the sexes, with greater mean pairwise genetic relatedness within communities for females rather than for males. This finding is consistent with other populations of *T. aduncus*, where females associate more closely with kin (Möller et al. 2006; Frère et al. 2010), likely providing a means to enhance inclusive fitness gains. Female southern Australian bottlenose dolphins exhibit higher levels of philopatry than males (Bilgmann et al. 2007b), further increasing opportunities for females to associate with kin. On the other hand, our results suggest that other factors, irrespective of kinship, may be more important in determining male associations. Male bottlenose dolphins may form alliances or coalitions with other males to benefit from increased protection from predators and/or for enhancing access to females for reproduction (Möller et al. 2001; Wiszniewski et al. 2012). During our survey efforts, we observed synchronised swimming and the herding of females by suspected males, behaviour that is indicative of male alliances (Connor et al. 2006; Connor and Krützen 2015). In addition, male dispersal (Bilgmann et al. 2007b) further reduces opportunities for males to associate with kin. Increased survey effort and biopsy sampling along the metropolitan coast may further elucidate the potential influences of kinship and sex-specific dispersal on within-community associations.

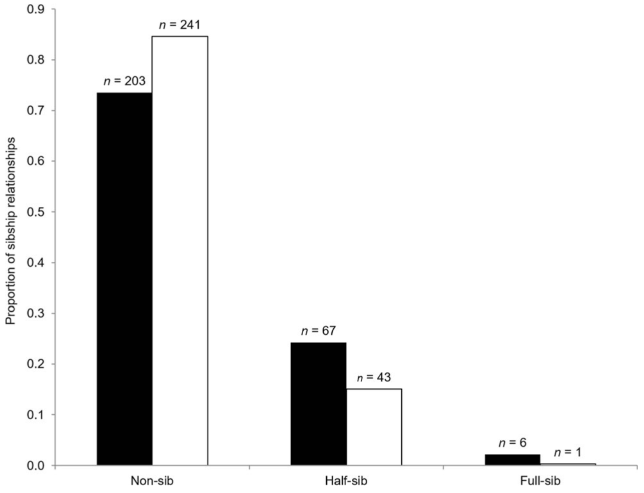

Fig. 3 Proportion of sib-ship relationships between southern Australian bottlenose dolphins within (shaded) and between (unshaded) communities along Adelaide's metropolitan coast. Relationships were categorised as either 'non-sib', 'half-sib', or 'full-sib' (pairwise likelihood method, COLONY (Jones and Wang 2010)). *N* values are presented above bars

Associations between members of the two communities

Despite the observed separation of the social network into two dolphin communities, some individuals were found to have preferred associations between communities. Between community associations have been documented previously for kangaroos (Best et al. 2013) and bottlenose dolphins (Wiszniewski et al. 2009), and can play an important role in maintaining connections at the population level (Lusseau and Newman 2004). The dolphins from this study are part of one genetic population that encompasses GSV (Pratt et al. 2018). Therefore, gene flow occurs between the northern shallow-water and southern deep-water communities (also shown by our genetic relatedness estimates), which may be facilitated by between-community associations. The slight range overlap of communities may provide individuals with the opportunity for associating with individuals of adjacent communities. Groups of socialising and mating dolphins were predominantly sighted within the southern metropolitan waters throughout summer (NZ, personal observations), around the area of community overlap. This area, which is an area of transition between the two habitat types, may therefore be an important breeding ground for dolphins and provide a means to facilitate gene flow between the communities. Alternatively, individuals may change their community membership over time (see Urian et al. 2009), but this was not observed during our study period and requires long-term monitoring efforts.

Overall, our results are indicative of a hierarchical fission-fusion social system. Based on the dolphins' spatial ranging patterns, individuals had more opportunities to associate with individuals within communities, and therefore, fission-fusion patterns may be more prevalent within communities. However, as dolphins appear to temporarily, and non-randomly, associate with others between communities, the dynamics of their fission-fusion may extend to higher levels of social organisation, similar to patterns found in giraffes (*Giraffa camelopardalis*, VanderWaal et al. 2014a, b) and white-tailed deer (*O. virginianus*, Miller et al. 2010). In this case, individual dolphins may be members of a core group, where core groups are embedded in communities, and communities are embedded within the population. Increased survey and sampling efforts, within and beyond the study area, are now needed to define the boundaries of the dolphin communities identified in this study, to determine ecological, social, and anthropogenic drivers of intra-population community variation, and to elucidate the putative hierarchical social organisation within this population.

Management implications

Information on intra-population community structure can be used to improve conservation efforts, as it can, for example, identify specific communities that are at risk of negative impacts from anthropogenic activities. Human activities have significant effects on the behaviour and social structure of some dolphin populations and other group living mammals (Rutledge et al. 2010; Ansmann et al. 2012). Core ranges of the NSWC identified here are located directly adjacent to popular Adelaide metropolitan beaches, which show increasing levels of anthropogenic activities. Frequent interactions with recreational fishing, boating, and water activities may change the grouping, fission-fusion, and association dynamics of the NSWC, leading to potential negative impacts on long-term reproductive success, increased levels of displacement, and/or population decline as observed elsewhere for bottlenose dolphins (Lusseau 2005; Bejder et al. 2006; Caro and Sherman 2011).

Long-term monitoring programmes are needed to quantify potential impacts of human activities, identify short- and long-term changes in intra-population community structure, and assess the resilience of a populations' social structure to disturbance. These studies should also investigate whether dolphin communities in GSV exhibit small-scale differences in demographic parameters (i.e. survival/birth rates). Such information is critical for effective population management and will enhance our understanding of the evolution of complex fission-fusion societies in odontocetes and other mammals, and their capacity to persist in today's changing environments.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval International, national, and institutional guidelines for the use of animals were followed. Field work was conducted under permits from the Department of Environment, Water and Natural Resources (DEWNR), South Australia, permit #K25761-6, and under Ministerial Exemption from Primary Industries Resources South Australia (PIRSA), exemption #9902648. Ethics approval was obtained from the Flinders University Animal Welfare Committee, project #E375.

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