Original Article

Genetic relatedness delineates the social structure of southern Australian bottlenose dolphins

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Social relationships represent an adaptive behavioral strategy that can provide fitness benefits to individuals. Within mammalian societies, delphinids are known to form diverse grouping patterns and show a variety of social systems. However, how ecological and intrinsic factors have shaped the evolution of such diverse societies is still not well understood. In this study, we used photo-identification data and biopsy samples collected between March 2013 and October 2015 in Coffin Bay, a heterogeneous environment in South Australia, to investigate the social structure of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*). Based on the data from 657 groups of dolphins, we used generalized affiliation indices, and applied social network and modularity methods to study affiliation patterns among individuals and investigate the potential presence of social communities within the population. In addition, we investigated genetic relatedness and kinship relationships within and between the communities identified. Modularity analysis revealed that the Coffin Bay population is structured into 2 similar sized, mixed-sex communities which differed in ranging patterns, affiliation levels and network metrics. Lagged association rates also indicated that nonrandom affiliations persisted over the study period. The genetic analyses suggested that there was higher relatedness, and a higher proportion of inferred full-sibs and half-sibs, within than between communities. We propose that differences in environmental conditions between the bays and kinship relationships are important factors contributing to the delineation and maintenance of this social structure.

Key words: **affiliation patterns, bottlenose dolphins, generalized affiliation indices, kinship, *Tursiops cf. australis*.**

INTRODUCTION

The quality and patterning of social relationships among individuals reflects the social structure of a population (Hinde 1976). These social relationships are usually nonrandom (e.g., Gero et al. 2005; Wolf et al. 2007; Croft et al. 2008; Wiszniewski et al. 2009; Beck et al. 2012; Best et al. 2013) and represent an adaptive behavioral strategy that can provide advantages (Emlen and Oring 1977), such as foraging benefits (Krause and Ruxton 2002; Aplin et al. 2012) and enhanced breeding success (Pope 2000; Frère, Krützen, Mann, Connor, et al. 2010); or reduced predation risk (Hill and Lee 1998; Gowans et al. 2007), aggression (Asensio et al. 2008), and risk of infanticide (e.g., Lukas and Huchard 2014). Stable and cooperative relationships are expected to emerge when the benefits of such associations offset the costs (Krause and Ruxton 2002).

Resource distribution and predation risk have been identified as the major ecological drivers of variation in social structure (Rubenstein and Wrangham 1986; Clutton-Brock 2009; Kelley et al. 2011; Kappeler et al. 2013), although factors associated with life-history, demography, intrasexual competition, intersexual conflict, and anthropogenic stressors may also play a role in shaping social behavior (Sterck et al. 1997; Clutton-Brock 2009; Bro-Jørgensen 2011; Ansmann et al. 2012; Möller 2012). In complex societies, such as those of African elephants, *Loxodonta africana* (e.g., Wittemyer et al. 2005), chimpanzees, *Pan troglodytes* (Wakefield 2013), and bottlenose dolphins, *Tursiops* spp. (e.g., Connor et al. 2000), individuals may form long-term cooperative relationships with some individuals, while a high degree of fluidity may be observed at a higher level (e.g., Wittemyer et al. 2005; Wiszniewski et al. 2009).

Kinship is an additional factor that can influence social relationships (e.g., Hirsch et al. 2012). Social groups or communities

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(clusters of individuals that are socially more connected among them than with the rest of the population; Krause and Ruxton 2002) may represent kin clusters characterized by high levels of genetic relatedness. For example, it has been shown that association patterns in giraffes, *Giraffa camelopardalis* (Carter et al. 2013), kangaroos, *Macropus giganteus* (Best et al. 2014), bottlenose dolphins (Möller et al. 2006; Frère, Krützen, Mann, Watson-Capps, et al. 2010; Wiszniewski et al. 2010; Diaz-Aguirre et al. 2018), and common dolphins, *Delphinus delphis* (Zanardo et al. 2016), are correlated with genetic relatedness. Kin selection theory predicts that individuals can obtain indirect fitness benefits by associating with kin (Hamilton 1964). Social preferences towards kin can increase the fitness of an individual through cooperative foraging, reduced aggression, protection from predators, rearing of offspring, and shared social and ecological knowledge (e.g., Silk 2002; Smith 2014).

Social network analysis based on association indices (a measure of the proportion of time that 2 individuals spent together in relation to the rest of the individuals in the population, Cairns and Schwager 1987) is now a common tool used to quantify, compare, and understand the social structure of a population at a range of spatial and temporal scales (e.g., Croft et al. 2008; de Silva et al. 2011; Stanton et al. 2011; Blonder et al. 2012; Pinter-Wollman et al. 2014; Farine and Whitehead 2015). A social network is a representation of a dynamic society that can be influenced by numerous factors. For example, home range overlap has been demonstrated to correlate with association patterns in a number of species, including bottlenose dolphins (Frère, Krützen, Mann, Watson-Capps, et al. 2010; Diaz-Aguirre et al. 2018), kangaroos (Best et al. 2014), chimpanzees (Wakefield 2013), and giraffes (Carter et al. 2013). Social network analyses can also be affected by individual variation in gregariousness (typical number of associates of an individual, Godde et al. 2013) or sample size (number of observations of each individual, Farine and Strandburg-Peshkin 2015). Thus, controlling for the effects of these factors when studying animal social structure is important for revealing the true association patterns among individuals (Whitehead and James 2015).

The bottlenose dolphin (genus *Tursiops*) is a highly social mammal that lives in fission–fusion societies, where individuals join and leave groups frequently on small spatial and temporal scales (Connor et al. 2000; Möller et al. 2001; Möller et al. 2006; Aureli et al. 2008; Gowans et al. 2007). Most of the well-studied inshore populations of these species are composed of relatively small communities which remain resident in small areas over long periods of times (e.g., Wells and Scott 1999; Connor et al. 2000; Gowans et al. 2007; Wiszniewski et al. 2009; Möller 2012). However, these communities are usually not isolated, with nonresident individuals occurring in adjacent habitats and often observed within the core range of other communities (Gowans et al. 2007). Numerous factors potentially affect the social structure of bottlenose dolphins, including predation risk (Heithaus and Dill 2002), habitat characteristics (Rossbach and Herzing 1999; Wiszniewski et al. 2009; Wiszniewski et al. 2010), prey distribution and abundance (Gowans et al. 2007), human activities (Ansmann et al. 2012), cultural transmission (Krützen et al. 2005; Sargeant et al. 2005; Daura-Jorge et al. 2012), reproductive status and demography (Möller and Harcourt 2008; Möller 2012), male competition (Connor et al. 1992a, 1999, 2001; Moller et al. 2001; Möller 2012; Wiszniewski et al. 2012; Diaz-Aguirre et al. 2018), and risk of infanticide (Dunn et al. 2002). In addition, foraging specializations may also play an important role in shaping their societies (e.g., Krützen et al. 2005;

Sargeant et al. 2005; Daura-Jorge et al. 2012; Kopps et al. 2014). For example, in Port Stephens, eastern Australia, Wiszniewski et al. (2009) found that dolphin community divisions coincided with changes in benthic substrate, suggesting that adaptation to local habitat types, possibly driven by resource specializations, may have played a key role in the social structuring of this population.

Using generalized affiliation indices (Whitehead and James 2015), social network techniques, and genetic relatedness analyses, we investigated the social structure of southern Australian bottlenose dolphins in Coffin Bay, South Australia. The southern Australian bottlenose dolphin, or Burrunan dolphin (*Tursiops australis*), was described as a new species (Charlton-Robb et al. 2011) based on genetic, morphological, and stable isotope data (Möller et al. 2008; Charlton-Robb et al. 2011; Owen et al. 2011). Their taxonomic identity however is still contentious (Perrin et al. 2013; Committee on Taxonomy 2018; IWC Report of the Sub-Comitee on Small Cetaceans 2018), and thus, we refer to them here as southern Australian bottlenose dolphins (*Tursiops* cf. *australis*).

Coffin Bay is a small, heterogeneous embayment with high density of dolphins (1.57–1.70 dolphins/km^2; Passadore et al. 2017), and similar male to female ratio of genetically sexed individuals (males = 46–52; females = 52–60; Passadore et al. 2017). Males form small social units in which kinship influences their association patterns (Diaz-Aguirre et al. 2018), and females associate based on their reproductive condition and genetic relatedness (Diaz-Aguirre et al., unpublished data). We predict that differences in ecological conditions between the different areas of Coffin Bay should promote fine scale social structure in this population, similar to the patterns found in other bottlenose dolphin populations (e.g., Rossbach and Herzing 1999; Wiszniewski et al. 2009). In addition, if kinship is an important factor in delineating the social structure of this population, we expect to find greater genetic relatedness, and a higher number of close kinship relationships, within rather than between communities. We aim to determine the social structure of this population while controlling for factors that can be confounding true association patterns. We compare the level and temporal stability of the associations, connectedness across the social network, and genetic relatedness within and between the communities identified. We provide novel information about the social structure of this population that will add to our current understanding of the factors driving social evolution in dolphins and other aquatic mammals.

MATERIALS AND METHODS
Ethics statement

This study was carried out under Flinders University Animal Welfare Committee approval number E310 and under permits to undertake scientific research: E26171-1, E26171-2, E26171-3, and MR00056-1 from the Department of Environment, Water and Natural Resources (DEWNR), South Australia, and under S115 ministerial exemptions (MEs: 9902601, 9902660, 9902714, and 9902779) from Primary Industries Resources South Australia (PIRSA).

Study area and data collection

Coffin Bay is situated in the southern tip of the Eyre Peninsula in South Australia (Figure 1). This study focused on the inner area of Coffin Bay, which encompasses 123 km^2 of shallow heterogeneous habitats (Figure 1b). The bay is mostly between 3 and 12 m deep, but with about 20% of the area shallower than 1 m. The

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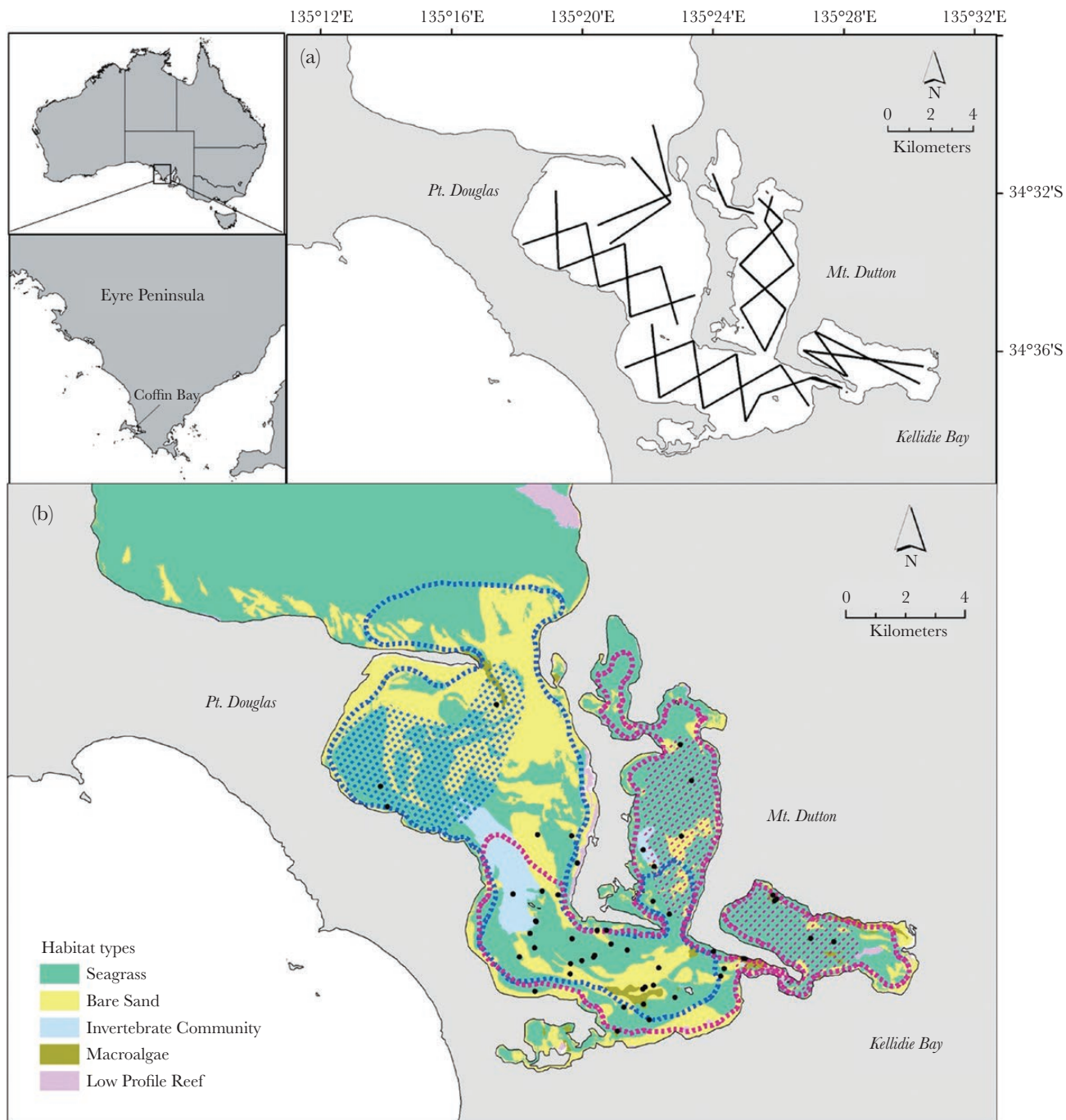
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Figure 1

(a) Coffin Bay inner area showing predetermined transects lines followed during boat-based surveys between March 2013 and October 2015. (b) Habitat types and ranging patterns of the 2 communities of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) identified in Coffin Bay, South Australia. Dotted filled areas and contour lines represent community core areas (50% kernel ranges) and representative ranges (95% kernel ranges), respectively. Blue: Pt. Douglas community; Pink: Mt. Dutton-Kellidie Bay community. Black circles represent the locations of groups containing individuals from both communities.

area contains shallow bays with benthic substrates dominated by seagrass as in Mt. Dutton and Kellidie Bay, and tidal sandflats, rocky coastline, seagrass meadows, temperate reefs, and deeper waters with sandy bottom in Pt. Douglas. Coffin Bay is considered a reverse estuary because of the hypersalinity found in the inner areas, although some freshwater input occurs during winter (Kämpf and Ellis 2015).

Regular boat-based surveys were conducted between March 2013 and October 2015, and were designed to cover all austral seasons (spring, summer, autumn, and winter) and habitat types within the inner area of Coffin Bay. We used a 6.5 m semirigid inflatable boat with 3 to 4 observers on-board while searching for dolphins. Boat surveys were completed in calm sea conditions (Beaufort scale <3), at an average speed of 15 km/h, and followed predetermined

zigzag line transects designed to optimize coverage of all areas and habitat types within the inner area (Figure 1a). Once a group of dolphins was sighted, we approached the animals to record their GPS location, and group size and composition. It was difficult to distinguish among age classes in the field because of the small size of bottlenose dolphins in Coffin Bay (up to approximately 2.5 m) in comparison to other study populations of bottlenose dolphins (Diaz-Aguirre and Passadore, personal observation). Therefore, we categorized individuals as: noncalves > 1.5 m in length, and calves ≤ 1.5 m in length and closely accompanied by a noncalf individual.

During each sighting, we attempted to collect photographs from each dolphin in a group using digital SLR cameras equipped with 80–300 and 100–400 mm zoom lenses. Individuals were identified using long lasting marks, such as nicks and notches on the edges of their dorsal fins (Würsig and Jefferson 1990), and the best images of each individual within a group were selected. High-quality images were then assigned a new identification number or matched with the already known individuals included in the Coffin Bay master catalogue (for photo-identification protocols, see Passadore et al. 2017). All photographs were sorted and matched using Discovery v. 1.2 (Gailey and Karczmarski 2013). In addition, we collected biopsy samples from photographically identified noncalf individuals using the PAXARMS remote biopsy system for small cetaceans (Krützen et al. 2002), or a biopsy pole system for bow-riding dolphins (Bilgmann et al. 2007). Briefly, when using the PAXARMS system, one observer was obtaining photographs of dolphins while another was aiming at collecting a sample of the same individual at an approximate distance between 5 and 8 m. When using the pole system, a photograph was usually obtained of a determined dolphin and subsequently if the same individual approached the boat to bow-ride it was then sampled. Samples were preserved in a 20% dimethyl sulphoxide solution saturated with sodium chloride, and then frozen in a −20° freezer (Amos and Hoelzel 1991).

Defining associations and estimating generalized affiliation indices (GAIs)

A group of dolphins was defined as all individuals within a 100 m radius and participating in similar behavioral activities (Wells et al. 1987). For social analyses, we included only those groups in which at least 75% of the individuals were photo-identified, based on the visually estimated group size. An individual was only included in the first group if it was sighted in a particular day and if different individuals joined a group during a sighting, they were considered part of that group. We excluded all identical groups that were resighted during the same day. These procedures were used to avoid resampling of individuals within short-time frames, which could lead to an overrepresentation of the association patterns of individuals that are just briefly associated (e.g., Whitehead 2009).

All dolphins identified in the same group were considered associated. To minimize the potential for false null associations in the social analyses between pairs of individuals with very low number of sightings, we included noncalf individuals observed on more than the median number of sightings for all individuals identified in the population (median = 11, see Results section for more details). Additionally, we controlled for the number of sightings during the GAI estimation.

The strength of the associations between pairs of individuals was estimated using GAIs (Whitehead and James 2015). The main advantage of this method is that it takes into account the effects of confounding structural factors that could influence the true pattern of associations between individuals, thus revealing true affiliations. We constructed a matrix of associations based on the half-weight index (HWI; Cairns and Schwager 1987) and tested, using multiple regression quadratic assignment procedures (MRQAP), the partial correlations between the association indices and 3 predictor structural factors which could be affecting association patterns: spatial home range overlap, gregariousness, and the cumulative number of sightings for each pair of individuals. The correlations where calculated for each predictor variable while controlling for the others.

Individual home ranges for individuals observed on more than 11 occasions were estimated as 95% utilization distributions using the AdehabitatHR (Calenge 2006) package in R v 3.2.3 (R Development Core Team 2014). First, we estimated the smoothing parameter (h) using the href function and then adjusted that value by visually examining individual ranges. Subsequent trials were performed and a value of h = 550 was chosen as this provided the best representation for the individuals considered in the analysis. The home ranges estimated in this study, which were based on this minimum number of sightings per individual corresponded well with the described ranging patterns and areas of spatial usage reported for this population by Passadore et al. (2018). Areas of home range overlap between individuals were then calculated in AdehabitatHR using 95% utilization distributions following the kernel-based utilization distribution overlap index method described by Fieberg and Kochanny (2005). Gregariousness (typical number of associates of an individual, Godde et al. 2013) values were calculated in SOCPROG 2.7 (Whitehead 2009). Significant predictor variables were retained and included for estimating GAIs. MRQAP tests and GAIs estimation were calculated in SOCPROG 2.7 (Whitehead 2009).

Social structure of the population

We calculated the social differentiation of the population using the coefficient of variation of the true association indices (S), and the correlation between true and estimated association indices (r) (Whitehead 2008). S describes how much variation there is in the association data, where a value of less than 0.3 indicates a homogenous society, and values of approximately 0.5 or greater indicate a very well-differentiated society. The correlation coefficient r indicates the power of the analysis to detect the true social structure, with values close to 1 indicating a good representation, and values close to 0.4 a moderate representation (Whitehead 2008).

To examine for potential structure into social communities, we used Newman's modularity coefficient (Newman 2004; Newman and Girvan 2004; Newman 2006) implemented in SOCPROG 2.7 (Whitehead 2009). The modularity coefficient attempts to divide the population into clusters (also called communities) that have higher association indices between members of the same cluster than expected by chance, using the eigenvector-based method described in Newman (2004; 2006). This method aims to maximize the values of modularity that best divide the network into different clusters. Modularity values above 0.3 are generally considered to represent a meaningful description of the data (Newman 2004). Social networks with nodes representing individuals connected by links representing GAIs were used to display affiliations and community structure using the program NETDRAW 2.1.5.5 (Borgatti 2002). We also mapped core (50%) and representative range (95%) areas for the communities identified based on the locations and identity of the groups observed, using the kernel-based utilization distribution method implemented in AdehabitatHR (Calenge 2006) package for R v 3.2.3 (R Development Core Team 2014).

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Comparisons within and between communities

We used 3 different approaches to examine potential differences in association patterns between communities identified in the previous analyses:

(1) We compared median group size, and mean and maximum affiliation levels between communities, and tested for the presence of preferred/avoided companionships at the population level and within communities. For comparing group sizes and affiliation levels, we used nonparametric Mann–Whitney U-tests with 10,000 permutations. To assess whether individuals associate at random or have preferred/avoided companionships, we used Whitehead's (2009) modification of the permutation test by Bejder et al. (1998) using daily sampling periods to remove demographic effects (Whitehead 1999). The affiliation matrices were permuted randomly until the P values stabilized, using as test statistic the standard deviations (SD) of the mean affiliation indices. For identifying pairs of preferred, casual and avoided companionships, we converted raw residuals of the GAIs into deviance residuals (Whitehead and James 2015). Pairs of individuals with deviance residuals values above 2.5 were considered preferred companionships, between 2.5 and −2.5 casual pairs, and below −2.5 avoided affiliates (Whitehead and James 2015).

(2) We used 3 social network metrics to evaluate differences in the social connectivity between communities: strength, which is the sum of all GAIs of any individual with all other individuals (Barrat et al. 2004); clustering coefficient, which shows how well the associates of an individual are themselves associated (Holme et al. 2007); and affinity, which estimates if individuals were strongly connected to individuals who also had strong connections (Barthélemy et al. 2005). We compared observed and expected values within communities using 1000 permutations in SOCPROG 2.7 (Whitehead 2009), and means between communities using randomization tests in Poptools 3.2 (Hood 2010).

(3) To investigate changes in affiliation rates over time at the population and community levels, we estimated lagged association rates (LAR) and compared these with null association rates (Whitehead 1995). The lagged association rate is the probability that 2 individuals associating at a given time will still be associating after a time lag. The null lagged association rate is the lagged association rate expected if individuals were associating at random.

DNA extraction, microsatellite amplification, and sex determination

Total DNA was extracted from biopsy samples by proteinase K digestion followed by a salting-out protocol (Sunnucks and Hales 1996). A set of 11 polymorphic cetacean microsatellite loci were genotyped: 8 tetranucleotides (Tur4_80, Tur4_87, Tur4_91, Tur4_105, Tur4_111, Tur4_141, Tur4_142, Tur4_E12; Nater et al. 2009) and 3 dinucleotides (MK9 (Krützen et al. 2001), EV37 (Valsecchi and Amos 1996), and TexVet5 (Rooney et al. 1999)). Thermal cycler conditions for the tetranucleotide loci consisted of an initial denaturation at 94 °C for 3 min followed by 5 cycles of 94 °C for 20 s, 63 °C for 45 s, and 72 °C for 1 min. This was preceded by 30 cycles of 94 °C for 20 s, 53 °C for 45 s, and 72 °C for 1 min, and a final extension step of 72 °C for 10 min. Minor modifications were made for Tur4_91, Tur4_142, and Tur4_111.

PCR conditions for EV37 and MK9 are reported in Möller et al. (2001), with TexVet5 run under the same program as EV37. Samples were mixed with an internal size standard and run on an ABI 3130 Genetic Analyser, with allele fragment sizes scored using GENEMAPPER v.4.1 (Applied Biosystems). MICRO-CHECKER v 2.2.3 (Van Oosterhout et al. 2004) was used to check for evidence of null alleles and allelic dropout, and deviations from Hardy-Weinberg equilibrium (HWE) and linkage disequilibrium were assessed in GENEPOP v 4.2 (Raymond and Rousset 1995) based on the Markov chain method with 1000 iterations. Significance levels were adjusted using Bonferroni corrections (Holm 1979).

To genetically determine the sex of each biopsied dolphin, we amplified a fragment of the ZFX and SRY genes using the protocols described by (Gilson et al. 1998). In addition, we also categorized females by visual observation of a closely associated calf on more than 10 separate days.

Genetic relatedness and kinship relationships

We used the simulation method with known allele frequencies implemented in COANCESTRY v 1.0.1.5 (Wang 2011) to determine the best estimator of genetic relatedness for our dataset. The highest correlation with the true values was obtained with the triadic likelihood estimator (TrioML; Wang 2007) (data not shown). TrioML was then used to estimate pairwise relatedness within and between communities. Between groups comparisons were evaluated using 10,000 permutation tests in COANCESTRY (Wang 2011). TrioML relatedness values were also compared with random expectations among preferred, casual and avoided companionships (identified using deviance residuals) using the permutation method implemented in PERM (Duchesne et al. 2006). We also inferred sib-ship relationships using the likelihood method implemented in COLONY v 2.0 (Jones and Wang 2010), and compared the frequencies of estimated full-sibs, half-sibs, and nonsibs within and between communities using a chi-square test with 10,000 Monte Carlo permutations.

RESULTS

Between March 2013 and October 2015, we completed a total of 152 survey days in Coffin Bay. During this period, we sighted 967 groups of dolphins and catalogued 227 noncalf individuals. Of the 227 catalogued dolphins, 143 were observed on more than 11 times, and thus included in the remaining analyses. These 143 individuals represent 82% of the estimated noncalf population inhabiting the inner area of Coffin Bay by Passadore et al. (2017).

Social structure

The correlation between true and estimated association indices ($r = 0.864$; SE = 0.009) and the likelihood estimator of social differentiation ($S = 1.814$; SE = 0.083) indicated, respectively, that the data set had good power to detect the true social pattern, and that the study population has a very well-differentiated society. MRQAP tests showed a significant correlation between the 3 structural predictor variables and the association indices, and therefore, these were included when calculating GAIs (Table 1).

Newman's modularity algorithm revealed that the Coffin Bay dolphin population is structured into 2 communities composed of 73 and 70 individuals, respectively ($Q_{max} = 0.4$; Figure 2a). Estimated core areas (50% kernel ranges) and representative ranges

(95% kernel ranges) indicated that members of the same community had similar ranging patterns with overlap between communities occurring only at their representative ranges (Figure 1b). Based on the estimated ranging patterns, the first community inhabits the Pt. Douglas area which is close to the entrance of Coffin Bay, while the second community occupies the most enclosed Mt. Dutton and Kellidie Bay areas. In subsequent analyses, we refer to these communities as Pt. Douglas (PD) and Mt. Dutton-Kellidie Bay (DK). Although no overlap was detected in the core areas of usage between communities, their home ranges overlapped at the boundaries of the communities. PD's representative range overlapped with 45% of DK's home range, and DK used 31% of the estimated PD's home range (Figure 1b). Median group size was larger in PD than in DK (PD = 4; DK = 3; z = 3.03, P < 0.01), and groups containing individuals from both communities represented only 8% (n = 51) of the groups included in the analyses. Median size for mixed community groups was also larger than single community groups (median mixed = 6; z = 4.03, P < 0.01). Of the 143 dolphins included in the social analyses, we were able to determine the sex of 100 individuals: 24 females and 23 males in PD community and 31 females and 22 males in DK community.

Social structure within and between communities

As expected according to the modularity analysis, affiliation levels were significantly higher within than between communities (P < 0.001). The mean and maximum affiliation indices between communities were −0.01 (SD = 0.00) and 0.04 (SD = 0.06), respectively. Mean affiliation indices obtained were the same within each community (mean = 0.01, SD = 0.02), but DK had higher maximum affiliation indices than PD (PD = 0.25, SD = 0.06; DK = 0.29, SD = 0.11; P < 0.01). Preferred/avoided companionships were detected using the permutation method at the population (Observed SD = 0.063, random SD = 0.055, P < 0.001) and community levels (PD: observed SD = 0.088, random SD = 0.085, P < 0.001; DK: observed SD = 0.086, random SD = 0.078, P < 0.001). Using deviance residuals, we detected 142 preferred, 8676 casual, and 57 avoided pairs of affiliates in the population (Figure 2b,c).
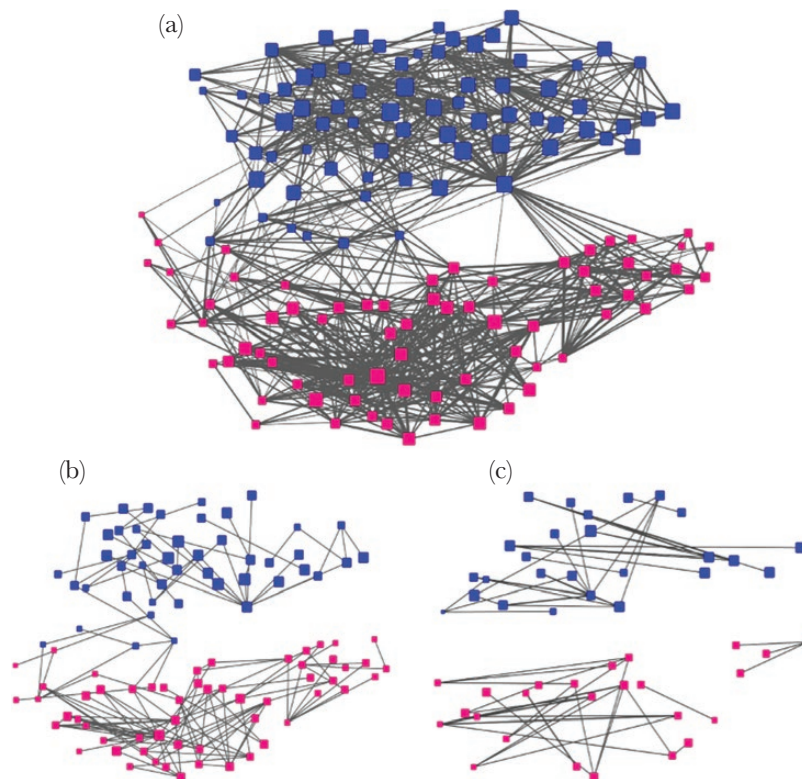
Table 1

Effectiveness of predictor structural variables in explaining association indices among southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia

Predictor variable	Partial correlation	MRQAP *P*-value
Home range overlap	0.784	<0.0001
Gregariousness	0.231	<0.0001
Sightings per dyad	0.105	<0.0001

Partial correlation coefficients and results of MRQAP tests were obtained using 10,000 permutations in SOCPROG 2.7 (Whitehead 2009).

Figure 2

Social networks of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. (A) Network representing 143 individual dolphins used in the social analysis. For clarity, only edges above twice the median affiliation index for the population (edges ≥1.2) are depicted. B and C networks represent preferred (deviance residuals ≥2.5) and avoided (deviance residuals ≤2.5) affiliations, respectively. Blue and pink nodes represent individuals assigned to Pt. Douglas and Mt. Dutton-Kellidie Bay communities, respectively, according to Newman's algorithm. Node sizes represent the gregariousness of the individuals, and edge width is proportional to the strength of the affiliations.

Social network metrics generally differed between communities, with higher strength, clustering coefficient and affinity within DK than PD (Table 2), although these differences were not statistically significant ($P > 0.05$ for all comparisons). Community comparisons with random expectations showed different patterns within each community. The PD community had higher strength than expected by chance, whereas the strength of the DK community was significantly lower, and their affinity higher, than expected (Table 2).

The analysis of lagged association rates indicated that non-random associations persisted over the study period within both communities (Figure 3). Although community associations slightly declined with time, they did not fall below the null association rate or the population rate.

Genetic relatedness and kinship relationships within and between communities

We obtained microsatellite data for 91 dolphins considered in previous analyses: 42 and 49 individuals belonging to PD and DK communities, respectively. We did not detect any deviations from HWE but we identified linkage disequilibrium between loci Tur4_80 and MK9. Linkage disequilibrium at this locus pair is highly unlikely based on the results of an extensive geographic genetic population study on this species in southern Australian waters (Pratt et al. 2018). Therefore, we retained both loci for subsequent analyses. The number of alleles, frequency of missing alleles, and heterozygosity values for each locus are provided in Supplementary Table S1.

Relatedness values for the population ranged from 0 to 0.83 (mean = 0.11, SD = 0.14), and within each community they varied from 0 to 0.74 (mean = 0.12, SD = 0.15) and 0 to 0.83 (mean = 0.12, SD = 0.14) for PD and DK, respectively. We found that mean genetic relatedness within communities was significantly higher than between communities (within $R = 0.12$, between $R = 0.10$, $P < 0.05$). Additionally, the proportion of sib-ship relationships differed, with a higher frequency of estimated full-sibs and half-sibs within communities, and a higher frequency of non-sibs between communities ($P < 0.05$; Figure 4). However, we did not detect a significant difference in the average relatedness among preferred, casual, and avoided affiliates (preferred $R = 0.09$, casual $R = 0.08$, avoided $R = 0.09$, $P > 0.05$).

DISCUSSION

We have demonstrated fine-scale social structure in southern Australian bottlenose dolphin inhabiting Coffin Bay, South Australia. Taking into account the confounding effects of 3 structural variables (home range overlap, gregariousness, and sample size), which are recognized to influence association patterns (e.g., Godde et al. 2013; Pinter-Wollman et al. 2014; Farine and Strandburg-Peshkin 2015), we identified 2 mixed-sex communities that differ in their ranging and association patterns, and demonstrated that genetic relatedness and kinship relationships play a role in the formation of social communities within this population.

The 2 communities identified correspond to differences in core ranging patterns of individuals, although representative ranges overlapped at the boundaries of both communities. Furthermore, these communities are not isolated from each other and larger groups containing individuals from both communities were observed on a small number of occasions. Most of the mixed community groups occurred in the area of range overlap between the 2 communities, which suggests that these likely represent temporary aggregation of animals, which could function to facilitate social relationships, information transfer and gene flow between communities (e.g., Lusseau and Newman 2004). A similar pattern of social communities having discrete core areas and overlapping representative ranges have been reported previously in other bottlenose dolphin populations (Lusseau et al. 2006; Wiszniewski et al. 2009; Louis et al. 2015), and it has been suggested to be a result of individual adaptations to local ecological conditions (e.g., Rossbach and Herzing 1999; Wiszniewski et al. 2009). Within Coffin Bay, a similar pattern of ecological adaptation to specific areas could be affecting the observed community divisions. Port Douglas, which represents the core area for one of the communities, differs in depth, benthic substrate, water properties, and probably productivity (Kämpf et al. 2004; Kämpf and Ellis 2015) to Mt. Dutton and Kellidie Bay, where the other community concentrates. These differences between embayments could influence the assemblage of potential prey species for the dolphins, and subsequently promote different foraging strategies between the communities. Indeed, a recent pilot study using baited underwater videos suggested that fish assemblage composition differs among the different bays (S. Whitmarsh, personal communication, 14 March 2017). Thus, dolphins from different communities may attain more benefits by remaining in their natal habitats and with conspecifics that have similar foraging strategies (Möller et al. 2006; Gowans et al. 2007; Wiszniewski et al. 2009; Ansmann et al. 2015). While observations of distinct foraging techniques were not observed in our study, PD dolphins may have adapted to forage in deeper sandy/seagrass areas, whereas DK individuals could have specialized to shallow seagrass habitats and associated prey. Alternatively, dolphins may have separated into 2 communities to explore the food resources of each embayment motivated by a reduction in competition. More information about prey assemblages and observations of dolphin foraging strategies in the different areas of Coffin Bay would be of valuable help to test this hypothesis.

Table 2

Social network metrics estimated for the 2 communities of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) identified in Coffin Bay, South Australia

	Strength(SD)	Clustering coefficient (SD)	Affinity (SD)
Pt. Douglas (PD)	−0.19(1.67)	−0.86 (4.73)	−0.46 (11.36)
Random	−0.21(1.34)	0.72 (41.11)	5.45 (80.65)
	$P < 0.001$	$P = 0.4$	$P = 0.09$
Dutton-Kellidie (DK)	0.24 (1.58)	0.46 (4.99)	12.25 (101.51)
Random	0.25 (1.26)	−0.61 (17.43)	−1.70 (15.27)
	$P < 0.001$	$P = 0.8$	$P < 0.05$

Significant differences from a random network were evaluated using 1000 permutations in SOCPROG 2.7 (Whitehead 2009).
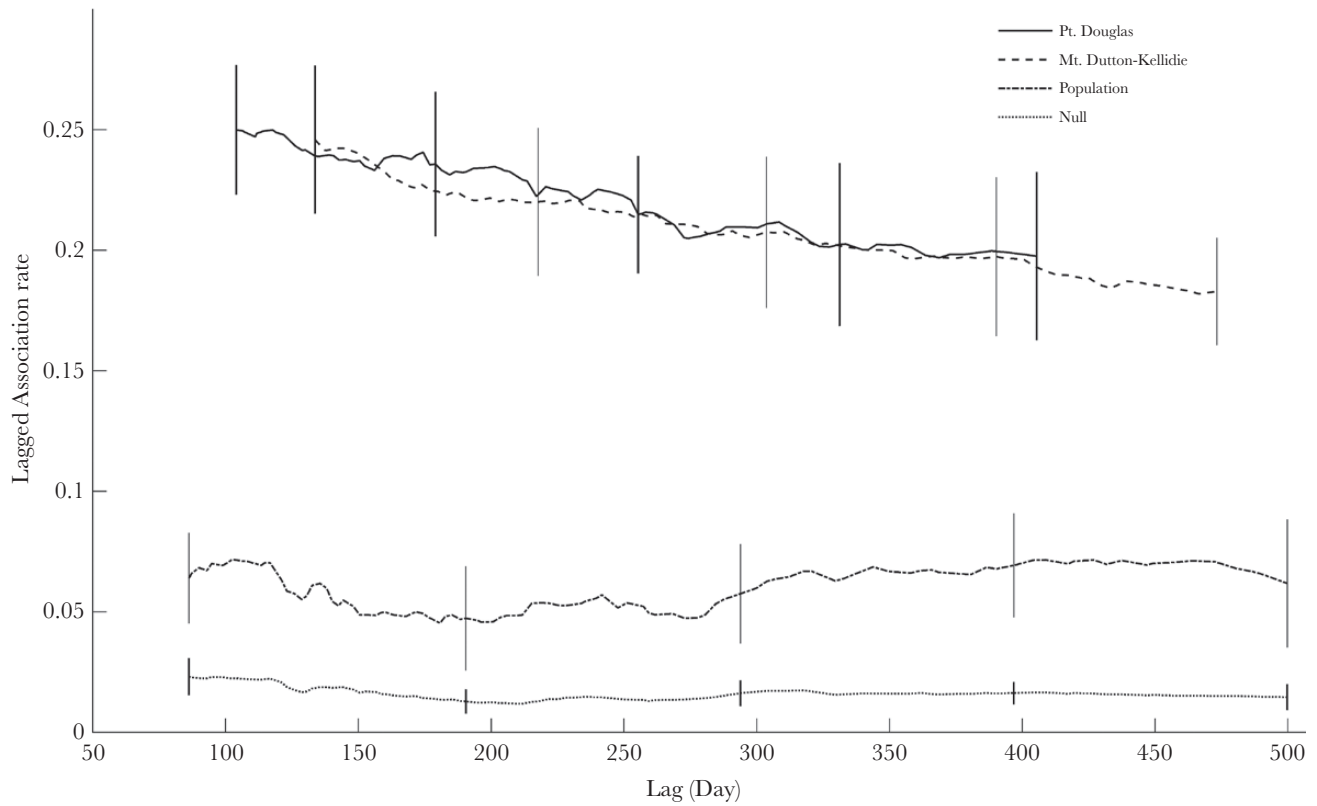
Figure 3

Lagged association rates for the population, and within communities, of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. SE bars (vertical lines) were estimated using jack-knife procedures in SOCPROG 2.7 (Whitehead 2009).
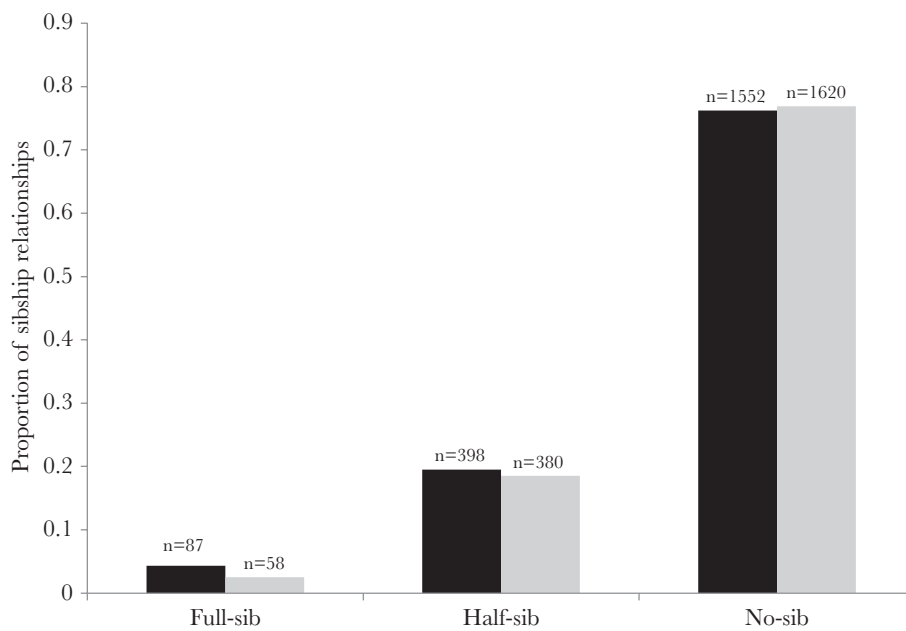

Figure 4

Proportion of sib-ship relationships observed within (black) and between (grey) communities of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. *N*-values above bars indicate the numbers of pairs in each category.

We found nonrandom affiliates at both the population and community levels, as expected based on results of sex-specific association patterns (Diaz-Aguirre et al. 2018; Diaz-Aguirre et al., unpublished data), and similar to other bottlenose dolphin studies (e.g., Connor et al. 2000; Gero et al. 2005; Wiszniewski et al. 2009; Augusto et al. 2012; Blasi and Boitani 2014) and species whose

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societies have fission–fusion dynamics (e.g., Galapagos sea lions [Wolf et al. 2007]; gray kangaroos [Best et al. 2013]). Additionally, we found preferred affiliates within and between communities, but individuals that avoided each other were only found within communities. The presence of avoided affiliates within communities could either indicate social substructuring within each community or can be related to differences in associations between the sexes. In addition, preferred affiliates between communities could indicate that some individuals may act as social links.

Social network analyses and LAR revealed differences in the connectedness and temporal stability of the associations within these communities, which could be partly explained by differences in ecological conditions within the Coffin Bay environment. In mammalian societies, differences in grouping patterns are usually explained as an adaptive strategy to spatially and temporally variable food resources (Clutton-Brock 2009; Kappeler et al. 2013). For example, female Asian elephants (*Elephas maximus*) form a great proportion of strong associations during the dry season as compared with the wet season, probably for accessing and protecting resources when they are scarce (de Silva et al. 2011). At group level, chimpanzees, spider monkeys (*Ateles geoffroyi*) and fish-eating killer whales occur in larger groups when resources are abundant (Chapman et al. 1995; Lusseau et al. 2004). In this context, it is possible that PD dolphins form larger aggregations with loose social connections (when compared with DK) as a response to a higher abundance of resources. In DK, smaller group sizes and strong associations may be more effective at accessing scarcer resources.

Predation risk is another factor influencing social relationships in animal societies (Rubenstein and Wrangham 1986), although apparently low within our study area (Diaz-Aguirre and Passadore, personal observation), this could be influencing to some extent the association patterns of these communities (e.g., Heithaus and Dill 2002). Great white sharks, *Carcharodon carcharias*, have been observed within the core range of PD, and at least one individual from this community showed severe injuries, which were likely inflicted by a shark of this species (Diaz-Aguirre and Passadore, personal observation). PD dolphins showed on average larger group sizes than DK, which is in agreement with theoretical expectations that an increase in group size is generally correlated with an increase in predation risk (e.g., Connor et al. 2000; Gowans et al. 2007). Despite these observations, social network experiments conducted with fishes demonstrated that in habitats with high predation risk animals tend to show higher connectedness than in those with lower risk (Kelley et al. 2011). This contrasts with our results of lower connectedness in PD, where the risk of predation may be higher. Based on these observations, it is plausible that food distribution within our study site could be playing a more important role than predation risk in shaping association patterns.

In addition to the aforementioned factors, genetic relatedness and kinship relationships appear to influence association patterns among individuals within these communities. Higher levels of genetic relatedness and a large proportion of sib-ships relationships were found within than between communities. While acknowledging that the number of microsatellite markers used in this study might be somewhat low for inferring sib-ship relationships, our sampling protocol was robust. Samples were obtained randomly over a 2-year study period and involved many different groups and individuals of both sexes (with similar proportion) belonging to the different communities. A similar pattern of higher genetic relatedness within social groups has been previously reported in bottlenose dolphins (Möller et al. 2006; Wiszniewski et al. 2009;

Frère, Krützen, Mann, Watson-Capps, et al. 2010; Diaz-Aguirre et al. 2018) and other mammals (e.g., giraffes, Carter et al. 2013; kangaroos, Best et al. 2014; common dolphins, Zanardo et al. 2016). Social communities and subgroups within these may form kin clusters, where individuals could increase their fitness through cooperative foraging, protection from predators, rearing of calves, and shared social and ecological knowledge (e.g., Silk 2002; Smith 2014). In this context, cooperative feeding or foraging specializations could involve an important learning and culturally transmitted component (Mann and Sargeant 2003; Krützen et al. 2005; Sargeant et al. 2005; Weiss 2006; Daura-Jorge et al. 2012; Kopps et al. 2014). Thus, if feeding strategies used by dolphins in Coffin Bay differ between communities and are transmitted from mother to calves and other relatives, kinship relationships between members of the same community are expected to occur and provide fitness benefits. However, at dyad level we did not find significant differences in relatedness among preferred, casual and avoided affiliates. Other factors, such as reproductive status (e.g., Möller and Harcourt 2008) or sex-specific differences in association patterns (e.g., Connor et al. 1992b, 1999, 2001; Möller 2012; Wiszniewski et al. 2012; Diaz-Aguirre et al. 2018) could be more important at an individual level.

In conclusion, using a GAIs approach to reveal affiliations among individuals while controlling for the effects of structural variables, we provided information on the social structure of southern Australian bottlenose in Coffin Bay, South Australia. We have demonstrated the occurrence of fine-scale social structure and differences in ranging, affiliation and temporal patterns of the communities identified. We propose that environmental factors and kinship relationships play an important role in the delineation and maintenance of this social structure, similar to that suggested to other inshore populations of bottlenose dolphins. Further studies aiming to study prey assemblages and predator presence would be of great value to understand the drivers of the social differences observed between the 2 dolphin communities identified. The results reported here contribute towards our understanding of the factors shaping sociality in dolphins and other aquatic mammals.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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Data accessibility: Analyses reported in this article can be reproduced using the data provided by Diaz-Aguirre et al. (2019).

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