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Socio-genetic structure of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in a South Australian embayment.

by

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SUMMARY

Bottlenose dolphins live in complex and dynamic fission-fusion societies which are shaped by a combination of ecological, behavioural and genetic factors. However, how these factors interact and promote the emergence of such social complexity is still poorly understood. This thesis explores the social structure and sex-specific patterns of affiliation, genetic relatedness and kinship relationships of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) inhabiting a small, South Australian embayment. Photo-identification data and biopsy samples were collected in Coffin Bay between 2013 and 2015 through systematic boat-based surveys along pre-determined transect lines within a 123km^2 of heterogeneous habitat encompassing different semi-enclosed bays and channels. Based on data from 657 groups of dolphins, I used recently developed generalized affiliation indices (GAI), which takes into account the effects of structural factors that confound social analyses (e.g. home range overlap, differences in gregariousness and number of sightings), in combination with a set of nuclear microsatellite markers and mtDNA sequences, to investigate dolphin affiliations, genetic relatedness and kinship relationships at population, and sex-specific levels within Coffin Bay. Chapter one provides background on animal societies and the interplay of ecological, behavioural and genetic factors, focusing on dolphin societies, and outlines the specific aims of the thesis. In chapter two, I investigated the social structure, genetic relatedness and kinship relationships at the population level using clustering and social network techniques based on GAI. I found that dolphins inhabiting Coffin Bay are structured into two well defined communities that differed in ranging and affiliation patterns, and demonstrated that genetic relatedness and kinship relationships appears to influence the social structure of this population. In chapter three, I explored male social bonds, genetic relatedness and kinship relationships, and found that male dolphins form small groups (2-5 individuals) of preferred affiliates that generally differ in their ranging patterns. The strength of these male preferred affiliations was found to be correlated with matrilineal kinship. In chapter four, I investigated the affiliation patterns, genetic relatedness and kinship relationships of female dolphins inhabiting Coffin Bay. I found that females form clusters of preferred affiliates that, similar to the males, also differ in their ranging patterns. Moreover, I found a correlation between the strength of the affiliations and the reproductive

condition of females, as well as their genetic relatedness. In chapter five, I discuss factors that may explain the patterns of associations observed at the population and sex-specific levels in relation to the demography of this population, its social environment, and genetic structure, and the ecological conditions of Coffin Bay. Furthermore, I discuss and compare the results of the present study with theories for the formation of social bonds in mammals, and in that context I suggest that ecological as well as intrinsic factors such as demography, sex ratio, sexual size dimorphism and the availability of relatives within communities may have promoted the patterns of affiliations, genetic relatedness and kinship observed in this population.

DECLARATION

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

Date.................21/11/2017......................

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And finally here it is! Still can't believe it! Probably the most exciting and hard adventure of my life contained in these pages, that without the help and support of my supervisors and friends at Uni, and of course my family at home would not have been conceivable.

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PUBLICATIONS

Manuscripts produced from this thesis for peer-reviewed journals:

In review:

1. Diaz-Aguirre F., Parra G.J. Passadore C. & Möller, L. (In review) Fine scale social structure in southern Australian bottlenose dolphins (Tursiops cf. australis) inhabiting a small inshore embayment (submitted to journal *Animal Behaviour*). This corresponds to Chapter 2 of this thesis.

In preparation:

2. Diaz-Aguirre F., Parra G.J. Passadore C. & Möller, L. (In preparation) Male social bonds and kinship in southern Australian bottlenose dolphins (*Tursiops* cf. *australis*). This corresponds to Chapter 3 of this thesis.

3. Diaz-Aguirre F., Parra G.J. Passadore C. & Möller, L. (In preparation) Kinship, reproductive condition and affiliation patterns in female southern Australian bottlenose dolphins (*Tursiops* cf. *australis*). This corresponds to Chapter 4 of this thesis.

Statement of authorship

I am (Fernando Diaz-Aguirre; F.D.A.) the principal author/contributor of each chapter. My supervisor, A/Prof Luciana Möller (L.M.) and co-supervisor, Dr Guido J. Parra (G.J.P.), are co-authors of the manuscripts derived from this thesis due to their significant input, advice and guidance during all the stages of this thesis preparation. Cecilia Passadore (C.P.) is co-author because her PhD project was completed in coordination with mine, and data collection for both of our projects was done simultaneously. We both catalogued and verified photographs for photo-identification of dolphins, and she calculated home range estimations that I have incorporated into chapters 3 and 4. Eleanor Pratt (E.P.) sequenced (mtDNA) and scored (microsatellites) for some of the samples used in chapters 2, 3 and 4.

Contributions per chapter

Chapter I:

-Fernando wrote this chapter and received input and comments from both of his supervisors. Contributions: F.D.A. (85%), L.M. (10%), G.J.P (5%).

Chapter II:

-Fernando collected data for this chapter using the same boat-surveys as Cecilia Passadore (including Photo-ID, and dolphin groups' parameters). The processing of the photo-identification catalogue was done between Fernando and Cecilia. Contribution to data collection and photo-ID processing: F.D.A. (50%), C.P. (50%).

-Biopsy samples and laboratory analysis: Fernando collected all of the biopsy samples from dolphins for this chapter. Eleanor Pratt analysed and sequenced 10 of the 91 samples used in this chapter. Contribution to biopsy samples and laboratory analysis: F.D.A. (90%), E.P. (10%).

- Fernando implemented all the statistical analysis for this chapter: F.D.A. (100%).

-This chapter was written by Fernando with comments and input from his supervisors: F.D.A. (85%), L.M. (10%), and G.J.P. (5%).

Chapter III:

-Fernando collected data for this chapter using the same boat-surveys as Cecilia Passadore (including Photo-ID, and dolphin groups' parameters). The processing of the photo-identification catalogue was done between Fernando and Cecilia. Contribution to data collection and photo-ID processing: F.D.A. (50%), C.P. (50%).

-Biopsy samples and laboratory analysis: Fernando collected all of the biopsy samples from dolphins for this chapter. Eleanor Pratt analysed and sequenced 4 of the 38 samples used in this chapter. Contribution to biopsy samples and laboratory analysis: F.D.A. (95%), E.P. (5%).

-Fernando implemented all the statistical analysis for this chapter with exception of the home ranges estimation which received input from Cecilia Passadore. Contribution to analysis: F.D.A. (90%), C.P. (10%).

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-Fernando collected data for this chapter using the same boat-surveys as Cecilia Passadore (including Photo-ID, and dolphin groups' parameters). The processing of the photo-identification catalogue was done between Fernando and Cecilia. Contribution to data collection and photo-ID processing: F.D.A. (50%), C.P. (50%).

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CHAPTER 1. GENERAL INTRODUCTION

Animal social systems

Complex social systems are those in which individuals frequently interact in different contexts with many different individuals, and often repeatedly interact with numerous of the same individuals over time (Freeberg et al. 2012). Complex societies have been found across a range of ecologically and phylogenetically disparate taxa such as primates (Strier 2007), birds (Bond et al. 2003), elephants (Wittemyer et al. 2005), bats (Vonhof et al. 2004), insects (Quevillon et al. 2015) and dolphins (Mann et al. 2000). In these societies, individuals may form long-term cooperative relationships with a few individuals coupled with high degree of fluidity in larger groups and movements between areas, sometimes including multi-level hierarchically-organized social structures (e.g. Wittemeyer & Getz 2007; Wiszniewski et al. 2009; Holekamp et al. 2012). Some individuals encounter and interact with others whom they know very little or not at all, as well as with well-known long term associates. The interplay of interactions among individuals within and across social groups leads to more complex communicative signals, hierarchical recognition and potentially to large scale cooperative societies (Grueter et al. 2012a; Grueter et al. 2012b), which in turn impacts on the genetic structuring of the populations (Dobson et al. 1998). Exploring the interaction between social behaviour and patterns of genetic relatedness is therefore crucial for understanding the evolution of animal social systems (Emlen, 1994).

Social systems can be generally decomposed into three interrelated components. First, the *social organization*, which is defined as the size, composition, cohesion and genetic structure of a social unit (Kappeler & van Schaik 2002). Three main types of social organization can be distinguished: adult individuals who associate and coordinate activities with other conspecifics forming groups; an adult individual that coordinates its activities with a conspecific of the opposite sex by forming a pair; or an adult individual that leads a solitary lifestyle. However, great variably and flexibility has been found in this trait among species, populations or even among social units within populations (Kappeler et al. 2013).

The second component is the *mating system*, which describes who mates with whom, and how frequently (Kappeler & van Schaik 2002). Generally four types of mating systems can be distinguished depending on the average number of mating partners of males and females: monogamous, polygynous, polyandrous and promiscuous (Clutton-Brock 1989). A species or population mating system represents the outcome of the combination of sex-specific reproductive strategies and that of an underlying sexual conflict (Clutton-Brock 2007; Bro-JØrgensen 2011). Because of variation in the operational sex ratio, age- or condition dependent mating preferences and others factors, individual mating decisions tend to be flexible both among individuals and across time, but they may also be constrained by aspects of the social organization or dominance hierarchy (e.g. Kappeler & van Schaik 2002; Clutton-Brock 2007; Bro-JØrgensen 2011; Möller 2012). The extent to which mating can be monopolized by a few dominant individuals (i.e. reproductive skew) is also influenced by several factors, including group size and kinship relationships; thus the outcome of mating strategies varies within and among species (Port & Kappeler 2010; Nonacs & Hager 2011).

The third component is the *social structure*, which is defined as the sum of all social relationships. Each dyadic social relationship is defined by the quality and patterning of interactions between its members (Kappeler & van Schaik 2002). How individuals interact with others depend on a number of factors, including age, sex, kinship, dominance, personality and condition (e.g. Parsons et al 2003; Wittemeyer & Getz 2007; Möller & Harcourt 2008; Chiyo et al. 2011; Holekamp et al. 2012; Fury et al. 2013; Jacoby et al. 2014). Therefore substantial behavioural plasticity is usually observed across an individual's lifetime, as well as between individuals, social units within a population (Whiten & van Schaik 2007), and among populations inhabiting ecologically different habitats and/or demographically dissimilar (Koenig 2000).

In mammals, remarkable similarities in social systems have been found among elephants, primates and dolphins (e.g. Baird 2000; Connor et al. 2000; Pearson 2011), suggesting an independent origin for social behaviour complexity possibly shaped by similar ecological, social and evolutionary conditions. Most evidence suggests that social systems have evolved as a by-product of individual strategies to maximize their inclusive fitness (Clutton-Brock 2009). Food distribution and predation risk have been identified as the major ecological causes of variation in mammalian social strategies (Rubenstein & Wrangham 1986), but other factors related with life-history, demography, anthropogenic impacts, intra-sexual competition and inter-sexual conflict may also play an important role in shaping social behaviour (e.g. Sterck et al. 1997; Clutton-Brock 2007; Gowans et al. 2008; Bro-JØrgensen 2011; Ansmann et al. 2012a; Möller 2012).

In mammals, females generally remain in their natal group or area while males tend to disperse before breeding (Clutton-Brock 2009). Females usually form stable social groups, often consisting of matrilineal relatives that frequently cooperate in rearing young or providing protection against predators (Clutton-Brock 2009). In addition, because of their potential rate of reproduction, females obtain more benefits by being familiar with the distribution of food resources, which is generally best attained by being philopatric (Clutton-Brock & Lucas 2011). In males, because of their potential rate of reproduction and sex differences in parental investment, their reproductive fitness is mostly affected by their access to receptive females, which could lead to strong competition among males for mates (Clutton-Brock & Parker 1992; Clutton-Brock & Parker 1995; Connor et al. 2000). When females associate within a defensible home range, males usually cooperate in order to exclude other males from entering their territories. However, if the home ranges of females are too large or not defendable, single males tend to protect receptive females and compete intensively for them (Clutton-Brock 1989). Interestingly, in a few primate and dolphin species, males cooperate with each other to protect and gain access to receptive females, forming alliances and/or coalitions (Watts 1998; Connor et al. 2000).

The interplay between genetic and social structure in cetaceans

The distribution of genetic diversity in cetacean populations may be affected by a variety of ecological, demographic, social, and anthropogenic factors. Despite their range over vast areas and without obvious barriers to gene flow in the marine environment, many cetacean species studied to date have shown significant population genetic differentiation, including over small spatial scales (e.g. Hoelzel & Dover 1991; Hoelzel et al. 1998; Bilgmann et al. 2007). In dolphins, genetic differentiation is often associated with oceanographic features such as fronts, currents, salinity or temperature, or is generally present between oceanic populations and those inhabiting nearby estuaries or coastal embayments (e.g. Natoli et al. 2005; Sellas et al. 2005; Bilgmann et al. 2007; Möller et al. 2007). Intra-specific specialization for resources, such as habitat or foraging specializations have been proposed as one of the leading mechanisms influencing population genetic differentiation in dolphins at small spatial scales (Hoelzel 1998; Bilgmann et al. 2007; Möller et al. 2007; Ansmann et al. 2012b; Kopps et al. 2014). In addition, the pattern and level of sex-biased dispersal could also play an important role in structuring cetacean populations (Ansmann et al. 2012b). Several studies on inshore and nearshore delphinids have demonstrated female-biased philopatry (e.g. Möller & Beheregaray 2004; Sellas et al. 2005; Möller et al. 2006; Bilgmann et al. 2007; Frère et al. 2010), although in some populations of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) males also show a moderate degree of philopatry (Krützen et al. 2004b; Möller & Beheregaray 2004). By contrast, studies on dolphins inhabiting open and pelagic waters suggest that both males and females disperse, with no sex-bias in dispersal (Natoli et al. 2005; Quérouil et al. 2007). The predictability of resources has been suggested as an important factor influencing dispersal patterns (Gowans et al. 2008). In inshore and nearshore habitats food resources are relatively predictable, which likely promote a high degree of philopatry. On the other hand, in open and pelagic habitats food resources are less likely to be predictable and animals have to range over vast areas for gaining access to food resources, which may promote dispersal by both sexes (Gowans et al. 2008; Möller 2012).

The social system of a population exerts important influences on the genetic structuring of a species (Ross 2001), although how this interaction occurs is still little understood. In fission-fission societies (Aureli et al. 2008), such as those of many dolphin species, individuals show complex patterns of association, which vary in strength and temporal stability. For example, in the fission-fusion society of bottlenose dolphins (*Tursiops* sp.) inhabiting Shark Bay, Western Australia, males generally form pair or trios that aggressively herd females to copulate with them (Connor & Krützen 2015). Individuals from these alliances achieved the majority of the paternities assessed in the population, although some solitary males also sired offspring (Krützen et al. 2004a). Understanding the interplay between social and genetic structure, and the demographic and ecological factors affecting them is important to understand the origins of complex societies.

Genetic structure in the bottlenose dolphin (genus *Tursiops*)

The bottlenose dolphin (genus *Tursiops*) is distributed in tropical and temperate oceans worldwide (Perrin et al. 2009). The taxonomy of the genus has been controversial for a long time, and currently two species within the genus are widely accepted: the common bottlenose dolphin (*Tursiops truncatus*) and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) (Perrin et al. 2009). However, recent morphological and genetic analyses have revealed the potential presence of a third species endemic to coastal waters of southern Australia (Möller et al. 2008; Charlton-Robb et al. 2011). This was described as the Burrunan dolphin (*Tursiops australis*) by Charlton-Robb et al. (2011), but its validity as separate species is still debated (Committee on Taxonomy 2016). Due to the controversy currently surrounding its acceptance as a separate species, in this thesis the common name, southern Australia bottlenose dolphin, and the species name, *Tursiops* cf. *australis*, are used (Fig. 1.1).

Fig. 1.1. Southern Australian bottlenose dolphin (*Tursiops* cf. *australis*) external morphology and colouration in Coffin Bay, South Australia.

Apart from the great dispersal capabilities of *Tursiops*, genetic population structuring has been found over small geographic scales in many coastal locations around the world, such as those found inshore and nearshore in the Gulf of Mexico, Florida, Bahamas, New Zealand, Australia, United Kingdom, Mediterranean and Black seas (Hoelzel et al. 1998; Parsons et al. 2002; Torres et al. 2003; Natoli et al. 2004; Natoli et al. 2005; Sellas et al. 2005; Parsons et al. 2006; Bilgmann et al. 2007; Möller et al. 2007; Remington et al. 2007; Viaud-Martinez et al. 2008; Tezanos-Pinto et al. 2009; Urian et al. 2009; Ansmann et al. 2012b). By contrast, a panmitic population have been found to inhabit oceanic waters of the northern Atlantic Ocean around the Azores archipelago (Quérouil et al. 2007).

Dispersal patterns of inshore and nearshore bottlenose dolphins seem to be similar to that of other mammalian species. Females are generally philopatric, while males tend to be the dispersing sex (e.g. Möller & Beheregaray 2004). In coastal and protected embayments genetic analyses have demonstrated female-biased philopatry, which creates the opportunity for females to live in close proximity with their kin, and for the development of kin-biased associations and behaviours (Möller 2012). In addition, some studies have suggested that male bottlenose dolphins can also show some degree of philopatry to their natal areas, which could lead to the formation of kin-based male alliances (e.g. Krützen et al. 2003; Parsons et al. 2003), as well as associations between male and female kin (e.g. Frère et al. 2010; Wiszniewski et al. 2010).

Coastal Bottlenose dolphin (*Tursiops* spp.) societies

Bottlenose dolphins are highly social mammals characterized by complex and diverse fission-fusion societies in which the patterns of associations among individuals vary in strength and temporal stability (reviewed in Connor et al. 2000). Most of the well-studied inshore populations are composed of relatively small communities which remains resident in small areas over very long periods of times (e.g. Wells & Scott 1999; Connor et al. 2000; Wiszniewski et al. 2009). However, these communities are generally not isolated and non-resident individuals usually occur in adjacent habitats, and are often observed within a community's range (Gowans et al. 2008). Bottlenose dolphin school size vary widely among populations and seems to be influenced by the openness of the habitat, predation risk, food distribution and abundance, and intrinsic factors, such as behavioural state and composition of the school (e.g. Shane et al. 1986; Connor et al. 2000). Sex and age segregation also occurs between or within schools, depending on the school size and activity, and the reproductive status of females (e.g. Connor et al. 2000; Möller & Harcourt 2008; Fury et al. 2013).

Females generally form moderate bonds with other females and males, and these associations are sometimes related to kinship relationships (e.g. Connor et al. 2000; Möller et al. 2006; Wiszniewski et al. 2010). In addition, females may associate with other females and males with whom they interact less frequently compared to their core group members (Connor et al. 2000). The strongest social bond reported in bottlenose dolphins is that between mothers and their calves, and the long-term social bonds observed in alliances of males (e.g. Connor et al. 1992; Connor et al. 2000; Möller et al. 2001; Parsons et al. 2003, Connor & Krützen 2015). Male alliance members have been observed to sequester or coerce maturing or adult females to accompany and copulate with them (e.g. Connor et al. 2000). In some populations, these long-term alliances are formed by related males (Krützen et al. 2003; Parsons et al. 2003), but in others there is no relationship between alliance membership and kinship (Möller et al. 2001). Formation of male alliances may be correlated with population density, as areas of high density of dolphins may lead to increased competition between males for access to females, and thus the only viable strategy for 'weaker' males may be the formation of alliances for increasing their reproductive success (Connor et al. 2000).

Socio-genetic studies on other closely related species inhabiting similar or different habitats could further improve the understanding of dolphin sociality, and the causes and consequences for the genetic structuring of delphinid populations.

The use of social networks in the study of animal societies

During the last decade there has been an increased interest in the use of social network approaches for studying animal societies (e.g. Krause et al. 2007; Wey et al. 2008; Krause et al. 2009; Pinter-Wollman et al. 2014; Farine & Whitehead 2015). This has been mainly triggered by the idea that animal societies are dynamic entities, which can change in time and space or according to different ecological conditions; and also by the comparative approach that social network analysis can offer (Croft et al. 2008). Social network methods allow for examining aspects of the social relationships between different species, populations or age and sex-classes; and also for evaluating changes in social relationships within populations at different temporal or behavioural scales (e.g. Sundaresan et al. 2007; Henzi et al. 2009; Barret et al. 2012; Hobson et al. 2012; Brent et al. 2013). In addition, social network approaches have been used for assessing the roles of particular individuals within their social networks (Lusseau 2007), and to reveal aspects of the personality of individuals based on their social network positions (Krause et al. 2010; Wilson et al. 2012; Wolf & Weissing 2012). In cetaceans, social networks have been mainly used to investigate the social structure of populations (e.g. Wiszniewski et al. 2009; Ansmann et al. 2012a; Cantor et al. 2012; Blasi & Boitani 2014; Louis et al. 2015), or for testing differences in association patterns between species, and how ecological factors can influence social structure (e.g. Parra et al. 2011; Foster et al. 2012). Most of the studies conducted using social network analyses on inshore dolphins have revealed complex segregation into social communities which can differ in their patterns of social temporal stability or cohesiveness (e.g. Wiszniewski et al. 2009; Ansmann et al. 2012a; Cantor et al. 2012; Blasi & Boitani 2014; Louis et al. 2015). Similarly, these analyses have revealed different patterns of association between sex-classes and have helped to understand the formation of social preferences in dolphins (e.g. Krützen et al. 2003; Möller et al. 2006; Möller & Harcourt 2008; Frère et al. 2010; Fury et al. 2013; Connor & Krützen 2015). These studies demonstrate the wide range of applications that social network approaches have in the study of social behaviour.

Despite the great advantages of this method (referring to social networks from previous section), there has been an increased interest in recent years into understanding and controlling, or eliminating, structural confounding factors that inherently affect social networks (e.g. Cantor et al. 2012; Best et al. 2013; Pinter-Wollman et al. 2014; Farine & Strandburg-Peshkin 2015; Farine & Whitehead 2015; Whitehead & James 2015). For example, one typical confounding factor is shared space use or home range overlap between pairs of individuals (e.g. Frère et al. 2010; Carter et al 2013; Shizuka et al. 2014). Generally, two individuals are considered associated if they are proximate in space, but this does not necessarily implies that they are actively maintaining a social relationship, and could mainly represent individual preferences for the same or similar space. Similarly, other factors such as individual variation in gregariousness (typical number of associates of an individual; Godde et al. 2013), differences in sample size (number of observations for each individual; Farine & Strandburg-Peshkin 2015), and temporal overlap (e.g. Cantor et al.

2012) have been recognized to affect social network analyses, and different approaches to control independently for them have been proposed by the aforementioned authors. However, for revealing the true association patterns among individuals, it is important to control or eliminate the influence of these factors concurrently (Whitehead & James 2015). Recently, in an attempt to control for confounding factors, Whitehead & James (2015) developed a generalized affiliation indices approach, which allows to test and control for the influence of numerous structural factors before the calculation of social network metrics. This method used the residuals of a multiple regression among the association indices of the individuals and the confounding variables of interest, which can then be used as weights of links in a social network and the subsequent analyses of social relationships (Whitehead & James 2015). This advancement is capable of revealing true affiliation patterns among individuals and overcoming previous issues imposed by the combined noise of structural factors that was commonly included in social networks.

The study species, the southern Australian bottlenose dolphin (*Tursiops* cf. *australis*).

The Southern Australian bottlenose dolphin is a robust and large sized delphinid (about 3 m in length) with a short rostrum and a tall and falcate dorsal fin. It has a two-banded colouration dorsally slate grey-black, ventrally off white, lacking a pale shoulder blaze and with no ventral spotting (Charlton-Robb et al. 2011). The species is distributed in nearshore and inshore waters of southern and south-eastern Australia (Charlton-Robb et al. 2011). Off the coast of Victoria, two inshore populations have been studied, one in Port Phillip Bay (80–120 individuals) and another in Gippsland Lakes (50–150 individuals) (Charlton-Robb et al. 2011; Charlton-Robb et al. 2015). In South Australia, there have been studies of the species in Spencer Gulf, Gulf St. Vincent, St. Francis Island and Coffin Bay (e.g. Bilgmann et al. 2007; Kemper et al. 2008; Möller et al. 2008b; Zanardo et al. 2016). In Gulf St. Vincent, approximately 30 resident dolphins inhabit the inshore waters of the Port River estuary and

Barker Inlet (Steiner & Bossley 2008; Cribb et al. 2013). In the adjacent Adelaide metropolitan waters, dolphins show varying patterns of site fidelity and residency, with a population size varying from 95 to 239 individuals seasonally (Zanardo et al. 2016). In Coffin Bay, where this study was conducted, there is a high density of dolphins (1.4 dolphins/ km^2; Passadore et al. 2017) with similar male to female ratio of genetically sexed individuals (males= 46–52; females= 52–60; Passadore et al. 2017). The population size is estimated at approximately 193-209 individuals all year round (Passadore et al. 2017). More information is clearly needed for this species considering its potential endemism and limited geographic distribution as a potential separate bottlenose dolphin species.

The study site: Coffin Bay, South Australia.

Coffin Bay is situated at the southern tip of the Eyre Peninsula (Fig 2.1), which encompass the eastern limit of the Great Australian Bight (GAB). Oceanographic conditions in the outer, open area are seasonally variable and mostly affected by the oceanographic regime of the eastern GAB. A well-mixed and isothermal water mass is present during the austral winter and spring, and upwelling and stratified waters occurs during the summer and autumn. On the outer area the Leeuwin current flows forming a well-mixed water mass from May to November (Godfrey & Ridgway, 1985). During summer, the presence of localized upwelling events off Kangaroo Island and Eyre Peninsula, in conjunction to the influence of the Flinders Current, creates plumes of cool waters extending to the outer area of Coffin Bay. This phenomenon is combined during late summer and autumn with intrusions of warm water coming from the GAB Plume (Herzfeld, 1997).

The inner area of Coffin Bay encompasses approximately 123km^2 of shallow heterogeneous habitats. Nearly 20% of this area is less than 1 metre deep and the remaining is between 3 and 12 metres. The area contains sheltered bays, inlets, seagrass meadows, tidal sandflats, rocky coastline, reefs and large areas of sandy seafloor. Coffin Bay is considered an inverse estuary because of the hypersalinty found in the inner areas beyond Point Longnose, although some freshwater input occurs during the winter (Kämpf & Ellis 2014).

Aims of the thesis

Delphinids are long-lived mammals that inhabit numerous habitats and show great variability in social structures and life-history traits (reviewed in Gowans et al. 2008; Möller 2012). Therefore, they represent an important taxa to study the interaction between ecological, social and genetic factors underlying the evolution of mammalian social systems. In this context, the population of southern Australian bottlenose dolphins inhabiting the sheltered and heterogeneous environment encountered in Coffin Bay, represents a good candidate for studying factors that could be shaping the complex societies of these aquatic mammals.

The overall aim of the thesis is to investigate the social structure and sex-specific patterns of affiliations, genetic relatedness and kinship relationships of southern Australian bottlenose dolphin in Coffin Bay, South Australia.

The specific aims are to:

- Investigate if the Coffin Bay dolphin population is segregated into social communities or modules that differ from each other in their intrinsic characteristics, and are associated with the Bay’s ecological conditions and the dolphins’ kinship relationships (Chapter 2).
- Assess if male southern Australian bottlenose dolphins in Coffin Bay form social clusters and if these are associated with their kinship relationships (Chapter 3).
- Examine if female dolphins in Coffin Bay show social preferences and if these are associated with their kinship relationships and reproductive condition (Chapter 4).

Structure of the thesis

The thesis consists of five chapters structured in three parts. Part one (Chapter 1) corresponds to a general introduction to animal societies, with particular focus on dolphin societies and socio-genetic structure. Part two (data chapters 2, 3 and 4) assess the social structure and sex-specific affiliation patterns, genetic relatedness and kinship relationships of southern Australian bottlenose dolphins in Coffin Bay. Part three (Chapter 5) provides a synthesis and discussion of the major findings of this study from a socio-ecological, genetic and conservation perspective.

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CHAPTER 2. Fine scale social structure in southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) inhabiting a small inshore embayment.

Abstract

Social relationships represent an adaptive behavioural 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 embayment in South Australia, to investigate the social structure of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*). Based on 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 two similar sized communities which differed in ranging patterns, affiliation levels and network metrics. Lagged association rates also indicated that non-random affiliations persisted over the study period and that differences in social stability occurred between these communities. The genetic analyses suggested that there was higher relatedness, and a higher proportion of 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.

Introduction

The quality and patterning of social relationships among individuals reflects the social structure of a population (Hinde, 1976). These social relationships are usually non-random (e.g. Gero et al. 2005; Wolf et al. 2007; Croft et al. 2008; Wiszniewski et al. 2009; Beck et al. 2011; Best et al. 2013) and represent an adaptive behavioural strategy that can provide advantages (Emlen & Orin 1977), such as foraging benefits (Krause & Ruxton 2002; Aplin et al. 2012) and enhanced breeding success (Pope 2000; Frère et al. 2010a), or reduced predation risk (Hill & Lee 1998; Gowans et al. 2008), aggression (Asensio et al. 2008) and risk of infanticide (e.g. Lukas & Huchard 2014). Stable and cooperative relationships are expected to emerge when the benefits of such associations offset the costs (Krause & Ruxton 2002).

Resource distribution and predation risk have been identified as the major ecological drivers of variation in social structure (Rubenstein & Wrangham 1986; Clutton-Brock. 2009; Kelley et al. 2011; Kappeler et al. 2013), although factors associated with life-history, demography, intra-sexual competition, inter-sexual conflict and anthropogenic stressors may also play a role in shaping social behaviour (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. Wittemeyer et al. 2005), chimpanzees, *Pan troglodytes* (Wakefield, 2013) and bottlenose dolphins, *Tursiops* spp. (e.g. Mann 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. Wittemeyer 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 (clusters of individuals that are socially more connected among them than with the rest of the population; Krause & 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), Indo-Pacific bottlenose dolphins, *T. aduncus* (Möller et al. 2006; Wiszniewski et al. 2010; Frère et al. 2010b), and short-beaked 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 calves, 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 two individuals spent together in relation to the rest of the individuals in the population, Cairns & 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 & 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 et al. 2010b), 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 & 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 & 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. 2008). 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 & Scott 1999; Connor et al. 2000; Gowans et al. 2008; Wiszniewski et al. 2009; Möller 2012). However, these communities are usually not isolated, with non-resident individuals occurring in adjacent habitats and often observed within the core range of other communities (Gowans et al. 2008). Numerous factors potentially affect the social structure of bottlenose dolphins, including predation risk (Heithaus & Dill 2002), habitat characteristics (Wiszniewski et al. 2009; 2010b; Rossbach & Herzing 1999), prey distribution and abundance (Gowans et al. 2008), 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 & Harcourt 2008; Möller 2012), male competition (Connor et al. 1992; 1999; 2001; Möller et al. 2001; Möller 2012; Wiszniewski et al 2012) 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, Wizniweski 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 recently developed generalized affiliation indices (Whitehead & James 2015), social network techniques and genetic relatedness analyses, we investigated the social structure of southern Australian bottlenose dolphins in Coffin Bay, a heterogeneous embayment in 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 2016), and thus we refer to them here as southern Australian bottlenose dolphins (*Tursiops* cf. *australis*). 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 pattern found in other bottlenose dolphin communities (e.g. Rossbach & 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 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 putative species that will add to our current understanding of the factors driving social evolution in dolphins and other aquatic mammals.

Materials and methods

Study area and data collection

Coffin Bay is situated in the southern tip of the Eyre Peninsula in South Australia (Fig. 2.1a). This study focused on the inner area of Coffin Bay, which encompasses 123 km^2 of shallow heterogeneous habitats (Fig. 2.1a). The bay is mostly between 3 and 12 metres deep, but with about 20% of the area shallower than 1 metre. The 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 & Ellis 2014).

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. Boat surveys were completed in calm sea conditions (Beaufort scale <3) and followed pre-determined zigzag line transects designed to optimise coverage of all areas and habitat types within the inner area (Fig. 2.1).

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 (pers. obs.). Therefore we categorized individuals as: non-calves > 1.5m in length, and calves ≤ 1.5m in length and closely accompanied by a non-calf individual.

During each sighting, we attempted to collect photographs from each dolphin in a group using digital SLR cameras equipped with 80-300mm and 100-400mm zoom lenses. Individuals were identified using long lasting marks, such as nicks and notches on the edges of their dorsal fins (Würsig & 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 & Karczmarski 2012). In addition, we collected biopsy samples from photographically identified non-calf 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). Samples were preserved in a 20% dimethyl sulphoxide solution saturated with sodium chloride, and then frozen in a -20° freezer (Amos & Hoelzel 1991).

Defining associations and estimating Generalized Affiliation Indices (GAIs)

A group of dolphins was defined as all individuals within a 100m radius and participating in similar behavioural 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. We excluded all identical groups that were resighted during the same day, and considered just the first sighting of each individual in a group per day.

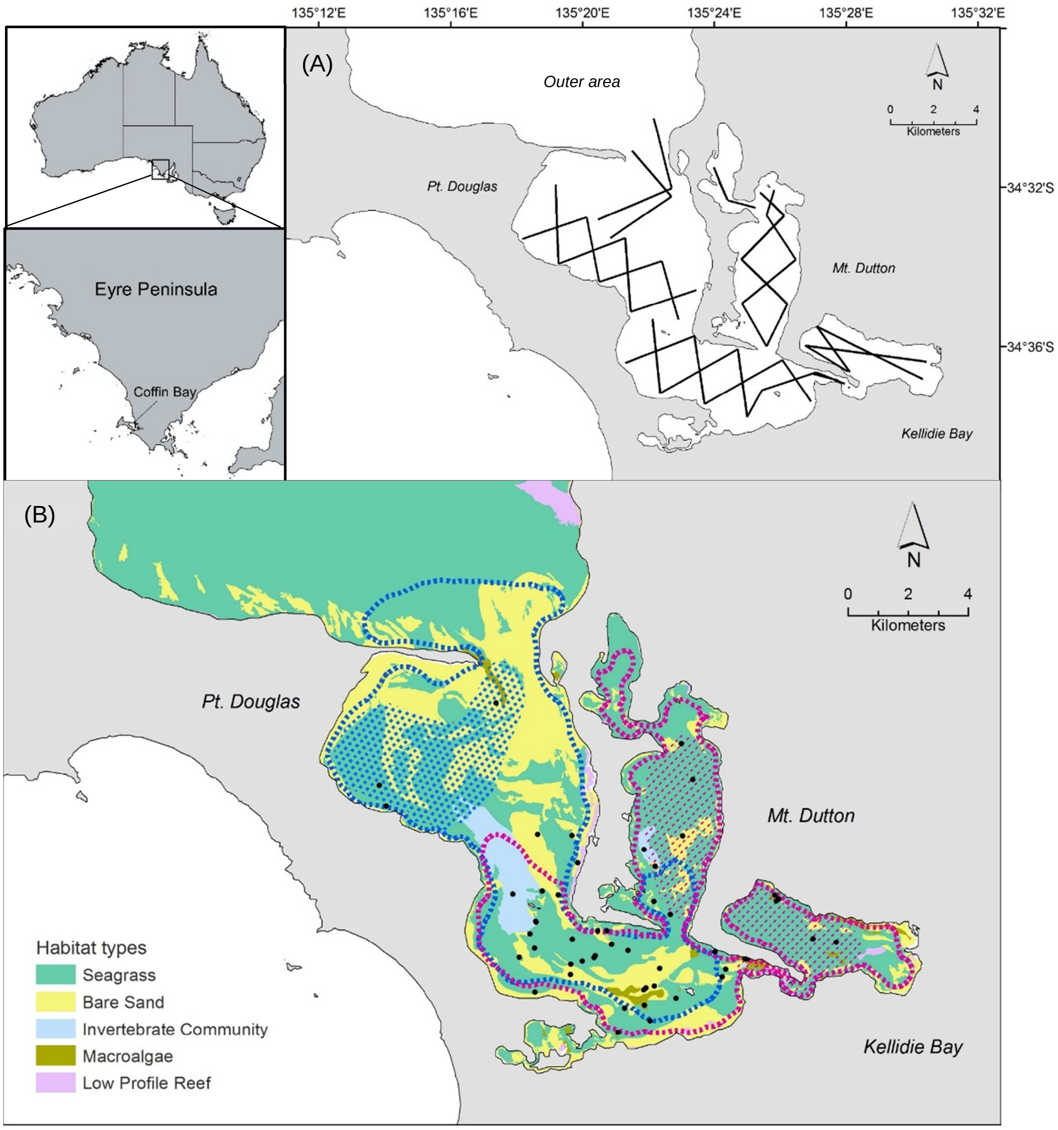

Fig. 2.1. A) Coffin Bay inner area showing pre-determined transects lines followed during boat-based surveys between March 2013 and October 2015. B) Habitat types and ranging patterns of the two communities of southern Australian bottlenose dolphins identified in Coffin Bay, South Australia. Dotted filled areas and contour lines represent community core areas (50% kernel range) and representative ranges (95% kernel range), respectively. Blue: Pt. Douglas community; Pink: Mt. Dutton-Kellidie Bay community. Black circles represent the locations of groups containing individuals from both communities.

If new individuals joined a group during an encounter, these were considered associated with the original group members. 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 only individuals observed on more than the median number of sightings for all individuals identified in the population. Additionally, we controlled for the number of sightings during the Generalized Affiliation Indices estimation (GAIs, see below).

The strength of the associations between pairs of individuals was estimated using GAIs (Whitehead & 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 & Schwager 1987) and tested, using multiple regression quadratic assignment procedures (MRQAP), the partial correlations between the association indices and three 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 were estimated as 95% utilization distributions using the AdehabitatHR (Calenge, 2006) package in R v 3.2.3 (R 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. 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 et al. (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

To test whether our data set accurately describes the social structure of the population, we calculated the social differentiation (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; 2006; Newman & Girvan 2004) 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 estimated core (50%) and representative range (95%) areas of usage for the communities identified using the kernel-based utilization distribution method implemented in AdehabitatHR (Calenge, 2006) package for R v 3.2.3 (R Core Team 2014).

Comparisons within and between communities

We used three 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 non-parametric Mann-Whitney U tests with 10000 permutations. To assess whether individuals associate at random or have preferred/avoided companionships we used Whitehead (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 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 & 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 & James 2015).

(2) We used three 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 strongly connected to individuals who also had strong connections (Barthelemy 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 two 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. LAR were tested against different models of temporal stability described in Whitehead (2009) to characterize the population and to compare different communities. The model best describing the temporal dynamics of association patterns was selected by the smallest quasi-Akaike information criterion (QAIC; Whitehead 2007).

DNA extraction and microsatellite amplification

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

& Rousset 1995) based on the Markov chain method with 1000 iterations. Significance levels were adjusted using Bonferroni corrections (Holm 1979).

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 group comparisons were evaluated using 10000 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 & Wang 2010), and compared the frequencies of estimated full-sibs, half-sibs and non-sibs within and between communities using a chi-square test with 10000 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 non-calf individuals. After excluding identical groups resighted in the same day and groups with less than 75% of dolphins photo-identified, 657 groups of dolphins remained for social analyses. Of the 227 catalogued dolphins, 143 were observed on more than 11 times (population median), and thus included in the remaining analyses. This number represents 82% of the non-calf population inhabiting the inner area of Coffin Bay estimated 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 three structural predictor variables and the association indices, and therefore these were included when calculating GAIs (Table 2.1).

Table 2.1. Effectiveness of predictor structural variables in explaining association indices among southern Australian bottlenose dolphins in Coffin Bay, South Australia. Partial correlation coefficients and results of MRQAP tests were obtained using 10000 permutations in SOCPROG 2.7 (Whitehead 2009).

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

Newman's modularity algorithm revealed that the Coffin Bay dolphin population is structured into two communities composed of 73 and 70 individuals, respectively (Qmax = 0.4; Fig. 2.2a). 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 (Fig. 2.1b). 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 (Fig. 2.1b). 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).

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 (± 0.00) and 0.04 (± 0.06), respectively. Mean affiliation indices obtained were the same within each community (0.01± 0.02), but DK had higher maximum affiliation indices than PD (PD= 0.25±0.06; DK= 0.29±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 (Fig 2b & 2c).

Social network metrics differed between communities, with higher strength, clustering coefficient and affinity within DK than PD (Table 2.2), 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 2.2).

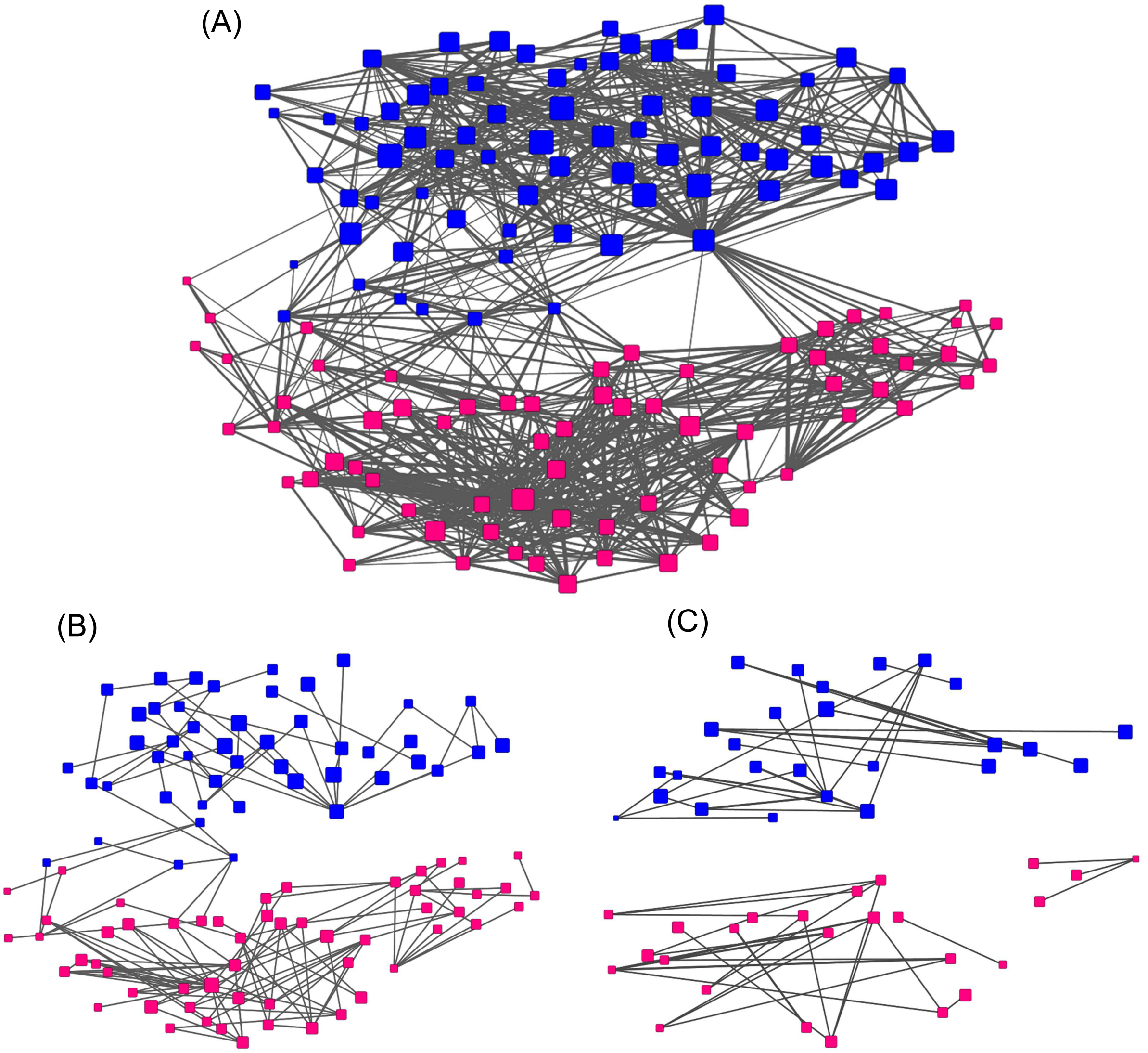

Fig. 2.2. Social networks of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. A) Network representing 143 individual dolphins used in the social analysis. For clarity, only edges above twice the median affiliation index for the population (edges ≥1.2) 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.

The analysis of lagged association rates indicated that non-random associations persisted over the study period within both communities (Fig. 2.3). Although community associations slightly declined with time, they did not fall below the null association rate or the population rate. The best fitting model of associations for the overall population and for PD was rapid disassociations and casual acquaintances, whereas for DK it was two levels of casual acquaintances (Table 2.3).

Table 2.2. Social network metrics estimated for the two communities of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) identified in Coffin Bay, South Australia. Significant differences from a random network were evaluated using 1000 permutations in SOCPROG 2.7 (Whitehead 2009).

	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

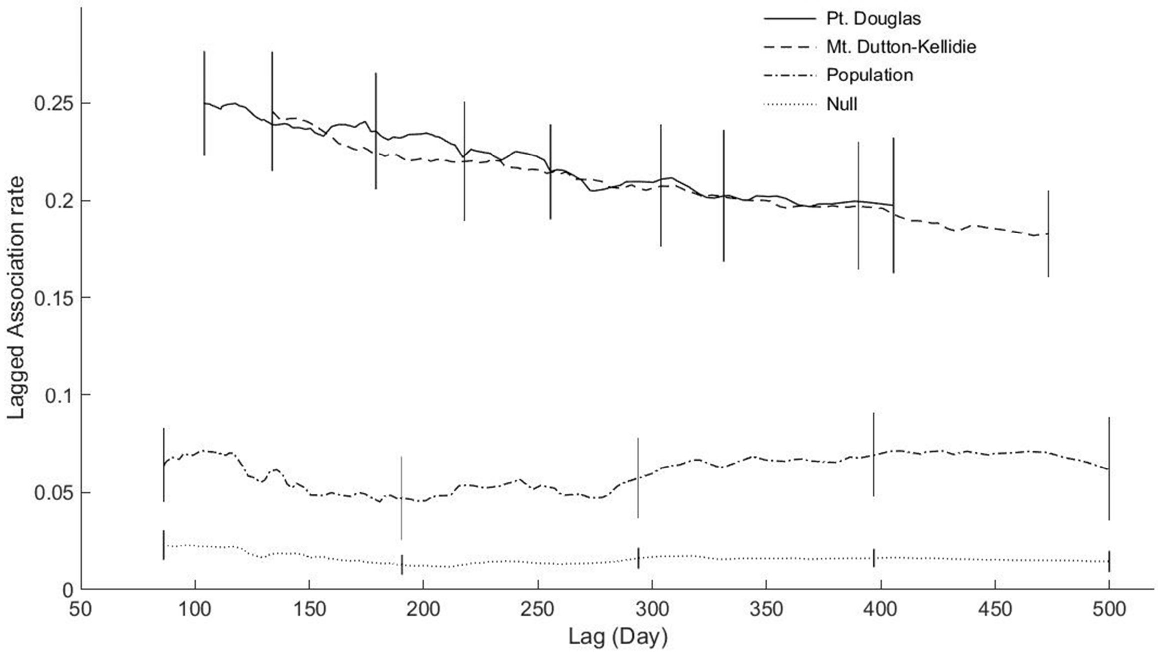

Fig. 2.3. Lagged association rates for the population, and within communities, of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. SE bars (vertical lines) were estimated using jack-knife procedures in SOCPROG 2.7 (Whitehead 2009).

Genetic relatedness and kinship relationships within and between communities

We obtained 91 biopsy samples from the animals considered in previous analyses: 42 and 49 individuals belonging to PD (59%) and DK (70%) 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. in review). Therefore we retained both loci for subsequent analyses. The number of alleles, frequency of missing alleles and heterozygosity values for each locus of the biopsied animals are provided in supplementary table 2. S1. Moreover

Table 2.3. Models of temporal stability fitted to the lagged association rates for the overall population and communities of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. (g'): describes the temporal association patterns as a function of time lag (td). The best fitting model was chosen based on the lowest quasi-Akaike information criterion (QAIC). No support was found for any other competing models (ΔQAIC>10). For a description of other models fitted, see Whitehead (1995).

	Model	Model formula	No. of parameters	Estimate of parameters	QAIC
PD	Rapid disassociations+ casual acquaintances	$g' = a2 \times \exp(-a1 \times td)$	2	a1 = 0.00064 a2 = 0.26161	5415
DK	Two levels of casual acquaintances	$g' = a3 \times \exp(-a1 \times td) + (1-a3) \times \exp(-a2 \times td)$	3	a1 = 0.57646 a2 = 0.00086 a3 = 0.72715	8676
Population	Rapid disassociations+ casual acquaintances	$g' = a2 \times \exp(-a1 \times td)$	2	a1 = 0.000421 a2 = 0.066702	443

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 ($p < 0.05$; Fig. 2.4). 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 $R = 0.09$, $p > 0.05$).

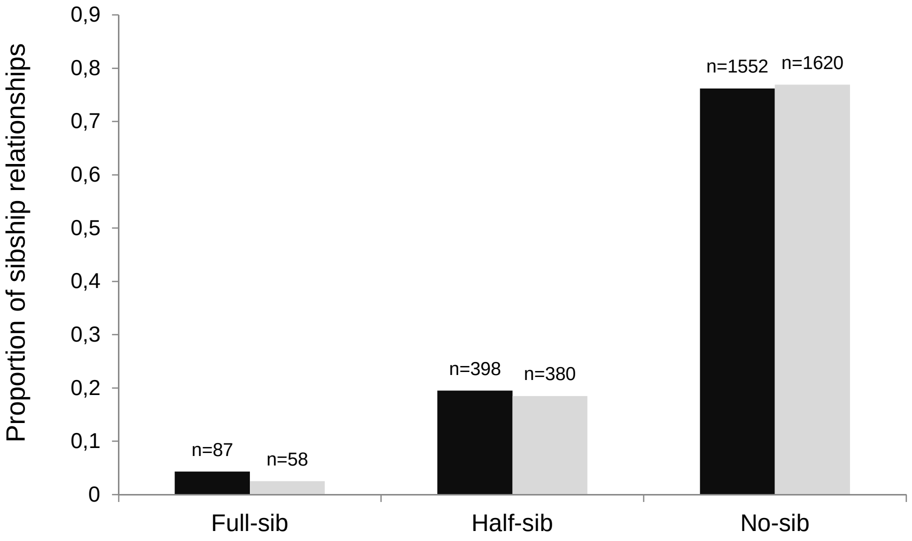

Fig. 2.4. Proportion of sib-ship relationships observed within (black) and between (grey) communities of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. N-values above bars indicate the numbers of pairs in each category.

Discussion

We have demonstrated fine scale social structure in southern Australian bottlenose dolphin (*Tursiops* cf. *australis*) inhabiting Coffin Bay, South Australia. Taking into account the confounding effects of three 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 & Strandburg-Peshkin 2016), we identified two 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 two 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 occasions. Most of the mixed community groups occurred in the area of range overlap between the two communities, which suggests that these likely represent temporary aggrupations of animals, which could function to facilitate social relationships, information transfer and gene flow between communities (e.g. Lusseau & 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 & 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 & Ellis 2014) 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 suggested that fish assemblage composition differs among the different bays (S. Whitmarsh, pers. comm. 14 March 2017). Thus, dolphins from different communities may attain more benefits by remaining in their natal habitats and with their conspecifics that have similar foraging strategies (Möller et al. 2006; Gowans et al. 2008; Wiszniewski et al. 2009; Ansmann, 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 two 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.

We found non-random affiliates at both the population and community levels, as expected for bottlenose dolphins (e.g. Connor et al. 2000; Wiszniewski et al. 2009; Gero et al. 2005; Augusto et al. 2011; Blasi & Boitani 2014) and other species whose societies have fission-fusion dynamics (e.g. Galapagos sea lions, *Zalophus wollebaeki*, Wolf et al. 2007; Grey 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 sub-structuring 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. A more detailed analysis on male and female association patterns within each community may help elucidate what factors are driving these preferred and avoided affiliations.

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 to 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 el. 2004). In this context, it is possible that PD dolphins form larger aggregations with loose social connections when compared to 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 & Wrangham 1986), although apparently low within our study area (pers. obs.), this could be influencing to some extent the association patterns of these communities (e.g. Heithaus & 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 (pers. obs.). 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. 2008). 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. More information about the abundance and distribution of prey and predatory sharks in Coffin Bay is necessary to further explore these hypotheses.

In addition to ecological factors, we found that 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. A similar pattern of higher genetic relatedness within social groups has been previously reported in bottlenose dolphins (Möller et al. 2006; Wiszniewski et al. 2010; Frère et al. 2010b) and other mammals (e.g. giraffes, Carter et al. 2013; kangaroos, Best et al. 2014; short-beaked 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 & Sargeant 2003; Weiss 2006; Krützen et al. 2005; Sargeant et al. 2005; 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 & Harcourt 2008) or sex-specific differences in association patterns (e.g. Connor et al. 1992; 1999; 2001; Möller 2012; Wiszniewski et al 2012) could be more important at an individual level and entails further examination.

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 a putative new dolphin species (*T. australis*) 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 (*T. truncatus* and *T. aduncus*). 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 two dolphin communities identified. The results reported here contribute towards our understanding of the causes and consequences of sociality in dolphins and other aquatic mammals, and provide information for the conservation management of this population.

Table 2. S1. Number of alleles, frequency of missing values, and expected (He) and Observed Heterozygosity (Ho) values for the 11 microsatellites loci of *Tursiops cf. australis* biopsied in Coffin Bay, South Australia and considered in this study.

Locus	N° of alleles	% missing data	H_e	H_o
Tur4_91	6	0	0.64109	0.61111
Tur4_142	4	0.08	0.64191	0.68675
Tur4_141	7	0.01	0.74138	0.65169
Tur4_E12	5	0	0.64382	0.62222
Tur4_105	6	0.02	0.71253	0.67045
Tur4_87	5	0.01	0.30045	0.30090
Tur4_80	6	0.02	0.68149	0.63636
TexVet5	7	0.03	0.37685	0.28736
MK9	6	0	0.76915	0.74444
Tur4_111	4	0	0.68175	0.61111
EV37	9	0.01	0.70006	0.68539

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CHAPTER 3. Male social bonds and kinship in southern Australian bottlenose dolphins (T*ursiops* cf. *australis*)

Abstract

Male mammals employ a wide variety of mating strategies in order to increase their reproductive success, which in turn influence their social behaviour. In some populations of bottlenose dolphins (*Tursiops* spp.) males cooperate in small groups or alliances to gain access to females for mating. However, the occurrence of these male cooperative groups has been predicted to occur only under certain social and ecological conditions, driven by factors such as differences in population density, operational sex ratio and sexual size dimorphism. Here we used generalized affiliation indices, social network techniques, and maternally and bi-parentally inherited genetic markers to investigate the affiliation patterns, genetic relatedness and kinship relationships among male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in a small embayment in South Australia. Photo-identification data and biopsy samples were collected in Coffin Bay from 2013 to 2015 through systematic boat-based surveys. We found that male dolphins formed twelve social clusters composed of two to five individuals. Genetic analyses revealed that general male affiliation patterns were significantly correlated with mtDNA haplotype sharing. In addition, preferred affiliates showed significantly higher levels of genetic relatedness compared to casual and avoided male pairs. Our results corroborates theoretical expectations for the formation of social bonds in small delphinids, and suggests that a high density of southern Australian bottlenose dolphins, with an expected skewed operational sex ratio, and no apparent sexual size dimorphism likely favoured the formation of strong male affiliations. In addition, the availability of genetic relatives within the population may have favoured male affiliations based on kinship relationships.

Introduction

Social relationships among male mammals are usually determined by the strategies they use to increase their reproductive success (Emlen & Oring 1977; Clutton-Brock 1989). Males employ a variety of mating strategies to maximize the number of receptive females with whom they mate, such as physical contests (e.g., red deer *Cervus elaphus;* Clutton-Brock et al. 1979), or female defence, where solitary males accompanies a group of females and prevents access to other conspecifics (e.g., Blainville's beaked whales, *Mesoplodon densirostris*; McSweeney et al. 2007). Alternatively, males can employ a roving strategy, ranging widely to search and copulate with females while competing against other males (e.g., African elephants, *Loxodonta Africana*; Barnes 1982; sperm whales, *Physeter macrocephalus*; Whitehead 1990; 1993), or they can coerce females individually or in groups (e.g., Orangutans, *Pongo pygmaeus*; Mitani 1985; bottlenose dolphins, *Tursiops* spp.; Smuts & Smuts 1993; Connor et al., 2000a). Moreover, these mating strategies may vary among populations of the same species living in different social and ecological conditions (Clutton-Brock 1989; Krützen et al. 2004; Gehrt et al. 2008). Male mammals usually provide no parental care to their offspring, and therefore their ability to mate with multiple females is largely determined by the spatial and temporal distribution of females, which in turn depends on ecological factors such as food availability and protection from predators (Emlen & Oring, 1977; Clutton-Brock 1989; Whitehead & Connor 2005; Silk 2002).

Male alliances and coalitions, characterized by long-term cooperative relationships (Harcourt 1992), are amongst the most complex social strategies of mammals (Connor & Krause 2015). Alliances and coalitions have been described in various species of mammals such as chimpanzees (*Pan troglodytes*; Watts 1998, 2004), lions (*Panthera leo*; Grinnell et al. 1995; Packer et al. 1991), raccoons (*Procyon lotor*, Gehrt et al. 2008), otters (*Lontra canadensis*; Blundell et al. 2002), cheetahs (*Acinonyx jubatus*; Caro & Collins 1987; Caro 1994) and bottlenose dolphins (Connor et al. 1992b; Möller et al. 2001; Parsons et al. 2003), and they generally function to defend or gain access to females for mating (Packer et al. 1991; Connor et al. 1996; Moller et al. 2001; Wiszniewski et al. 2012a), increase rank (Goodall 1986), compete for territory (Caro 1994), improve foraging efficiency (Blundell et al. 2004), or reduce predation risk (Waterman 1997). The formation of alliances, however, is only expected to occur under certain social and ecological conditions (Packer et al. 1991; Caro 1994; Grinnell et al. 1995; Connor & Whitehead 2005; Whitehead & Connor 2005; Möller 2012). For example, using individual-based models, Whitehead and Connor (2005), suggested that alliances in mammals should be formed when male competition for receptive females is high and the benefits of group living (e.g. increased mating opportunities) offset the costs (e.g. feeding competition), or if by forming an alliance they are able to outcompete single males.

Kinship relationships have often been proposed as an important factor in the formation and maintenance of social bonds across several taxa (e.g. Packer et al. 1991; Parker et al. 1995; Krützen et al. 2003; Parsons et al. 2003; Holekamp et al. 2012; Chiyo et al. 2011; Carter et al. 2013). Hamilton's (1964) kin selection theory suggests that individuals can obtain indirect fitness benefits by associating with kin, such as those related to cooperative foraging, reduced aggression, protection from predators, increased growth rates, enhanced reproductive success, and shared social and ecological knowledge (e.g. Olsen & JäUrvi 1997; Silk 2002; Krützen et al. 2004; Gerlach et al. 2007; Smith 2014). However, the influence of kinship in establishing and maintaining male cooperative associations vary in different species and populations, and it does not seem to be a prerequisite for the formation of alliances or coalitions (Packer et al. 1991; Mitani et al. 2000; Möller et al. 2001; Parsons et al. 2003; Krützen et al. 2003; Whitehead & Connor 2005; Möller 2012). For example, in some but not all bottlenose dolphin populations, kinship is an important factor for the establishment of male alliances (Möller et al. 2001; Krützen et al. 2003; Parsons et al. 2003). In male chimpanzees closest associates are also not chosen on the basis of kinship (Mitani et al. 2000). Nonetheless, both strategies appear to provide fitness advantages to the members of an alliance (e.g. Möller et al. 2001; Krützen et al. 2004; Wiszniewski et al. 2012a). In kinship-based alliances, the less successful individual may achieve inclusive fitness gains through kin selection if the other members of the alliance are successful (e.g. Packer et al. 1991; Krützen et al. 2004). In non-related alliances, cooperation and assistance in the form of reciprocal altruism or mutualism at defending females or territories could also increase mating success of all alliance members (e.g. Feh 1999; Kays et al. 2000; Möller et al. 2001; Wiszniewski et al. 2012a).

In cetaceans, defence of receptive females by roving males is a common mating strategy, however much variation is present in whether females are defended or coerced by individual males or alliances (Connor et al. 2000a). In bottlenose dolphins, male association patterns appear to vary widely between, as well as within, populations (e.g. Connor et al. 2000b; Möller 2012; Connor & Krützen 2015). In some populations males may search for potential mates alone (Wilson 1995) or form stable mixed-sex groups (Lusseau et al. 2003; Lusseau 2007), while in others they can form alliances for gaining access to females (e.g. Möller et al. 2001; Parsons et al. 2003; Wiszniewski et al. 2012b; Connor & Krützen 2015). The variability in male association patterns in dolphins has been mainly attributed to differences in population density, operational sex ratio and sexual size dimorphism (Whitehead & Connor 2005; Möller 2012). In populations with small male-biased sexual size dimorphism, high population densities and male-biased operational sex ratio (OSR), male dolphins may favour to form alliances to successfully monopolize receptive females (Whitehead & Connor 2005; Möller 2012). In contrast, when population densities are low, males are larger than females, and/or with an even OSR, search for potential mates alone may be more advantageous (Whitehead & Connor 2005; Möller 2012; Wiszniewski et al. 2012a). Male alliance formation has been reported for Indo-Pacific bottlenose dolphins (*T. aduncus*) in Shark Bay and Port Stephens, Australia (Connor & Krützen 2015; Möller et al. 2001), and for common bottlenose dolphins (*T. truncatus*) in Sarasota Bay (Wells et al. 1987), and the Bahamas, USA (Parsons et al. 2003). In Shark Bay, male dolphins form alliances at different levels of association in an open social network: stable first-order alliances of two-three males cooperate to form consortships with individual females, while second-order alliances, which are aggregations of two first-order alliances, attack or defend females from other alliances (Connor et al. 1992a; b; Connor & Krützen 2015). Second-order alliances can also show preferred associations and compete against other alliances forming third-order alliances (Connor et al. 2011; Connor & Krützen 2015). In addition, a super-alliance composed of four to 14 dolphins, which function as labile coalitions to attack and defend females from other alliances has also been reported in Shark Bay (Connor et al. 1999).

The importance of kinship in alliance formation and stability in bottlenose dolphins also appear to differ among populations. In the Bahamas and Shark Bay populations, stable alliances are formed among related males (Parsons et al. 2003; Krützen et al. 2003), while in Port Stephens and Sarasota, alliance membership was not associated with genetic relatedness (Möller et al. 2001; Owen 2003), suggesting that kinship is not a prerequisite for cooperation and alliance formation among male bottlenose dolphins. Möller (2012) proposed that alliances in delphinids could be formed irrespective of kinship relationships, but if related individuals are available within the population, kin associations could be favoured through kin selection.

Here, we used generalized affiliation indices (Whitehead & James 2015), social networks, and maternally and bi-parentally inherited genetic markers to investigate the affiliation patterns and kinship relationships among male southern Australian bottlenose dolphins (*Tursiops* cf. *australis;* Charlton-Robb et al. 2011) in Coffin Bay, South Australia. Coffin Bay is a small protected embayment with high density of dolphins (1.4 dolphins/ km^2; Passadore et al. 2017), similar male to female ratio of genetically sexed individuals (males= 46–52; females= 52–60; Passadore et al. 2017), but likely male-biased OSR considering an inter-birth interval for females similar to that reported to other bottlenose dolphins population (3-6 years: reviewed in Connor et al. 2000b; Möller 2012), and no apparent sexual size dimorphism (pers. obs.). The population, estimated at approximately 150 individuals (Passadore et al. 2017), is socially structured into two communities with discrete home ranges, in which individuals of the same community are on average more bi-parentally related than individuals from opposite communities (Chapter 2). We predict that male southern Australian bottlenose dolphins in Coffin Bay may form social clusters similar to the alliances reported for other high density populations, with male-biased OSR and no apparent sexual size dimorphism, such as Shark Bay and Port Stephens. In addition, we expect that the formation of male social affiliations may be influenced by kinship relationships as observed for Shark Bay's first-order alliances, given the availability of genetic relatives within the communities identified in Coffin Bay.

Materials and methods

Study site and data collection

From March 2013 to October 2015, we carried out regular boat surveys in the inner area of Coffin Bay, South Australia (Fig. 3.1). Boat surveys were designed to cover all seasons and were completed in calm sea conditions (Beaufort scale <3). The inner area of Coffin Bay (123km^2) encompasses shallow heterogeneous habitats (<12 metres) mainly dominated by seagrass meadows, and it is characterized as a reverse estuary because of the hypersalinity found in the inner most areas (Kämpf & Ellis 2014). Further details about boat surveys and the study area were provided in Chapter 2.

We approached all groups sighted and recorded their GPS location, group size and composition, and collected photographs of their dorsal fins as explained in Chapter 2. High quality images were then matched to the already known individuals included in the Coffin Bay master catalogue, or assigned a new identification number if no matches were found, using Discovery v. 1.2 (Gailey & Karczmarski 2012).

Biopsy samples from identified non-calf individuals were also collected and stored in the field and lab as described in Chapter 2.

Genetic analyses

DNA extraction and quantification used the methods reported in Chapter 2. The sex of each dolphin was genetically determined by using the polymerase chain reaction (PCR) to amplify a fragment of the ZFX and SRY genes, following the protocol developed by Gilson et al. (1998). A mitochondrial DNA (mtDNA) control region fragment of approximately 450 base pairs (bp) in length was amplified by PCR with primers Dlp-5 (5'-CCA TCG WGA TGT CTT ATT TAA GRG GAA-3') and Dlp-1.5 (5'-TCA CCC AAA GCT GRA RTT CTA-3') (Baker et al. 1993), as per conditions detailed in Möller & Beheregaray (2001). PCR products were sequenced on an Applied Biosystems 3130xl genetic analyser. MtDNA sequences were aligned and cleaned using SEQUENCHER v5.2.4 (Gene Codes Corporation, Ann Arbor, MI, USA), and resulted in a 437bp fragment.

A set of 11 polymorphic cetacean microsatellite loci were genotyped (see Chapter 2 for name of markers and associated references). PCR conditions are reported in Pratt et al. (in review). The 11 loci used in this study showed no evidence of null alleles, linkage disequilibrium or departures from Hardy-Weinberg equilibrium (Chapter 2). Furthermore, there was no evidence of population genetic subdivision within the inner area of Coffin Bay (Pratt et al. in review).

Defining associations and estimating male affiliation indices

Dolphin groups were defined as all individuals within a 100m radius and participating in similar behavioural activities following Wells et al. (1987). Groups with at least 75% of the individuals photo-identified (based on the visually estimated group size) were used for analysis, with the exception of identical groups resighted within the same day. An individual was only included in the first group it was sighted in a particular day, and if different individuals joined a group during a sighting they were considered part of that group. In addition, only dolphins observed on more than the median number of sightings (median = 11, Chapter 2) for all individuals identified in the population were included in social analyses to minimize the potential for false null associations due to low number of sightings. We also controlled for the number of cumulative sightings of a given pair of dolphins during the Generalized Affiliation Indices (GAIs) estimation (see below). In the subsequent analyses, we only considered individuals genetically identified as males through the sexing analysis (above).

The strength of the associations between pairs of individuals was estimated using GAIs (Whitehead & James 2015) as described in Chapter 2. In summary, we constructed a matrix of associations based on the half-weight index (HWI; Cairns & Schwager 1987), and tested using multiple regression quadratic assignment procedures (MRQAP) the correlation between the association indices and three predictor structural factors ((spatial home range overlap, gregariousness (typical number of associates of an individual, Godde et al. 2013), and cumulative number of sightings for each dolphin pair)).

Areas of home range overlap between male dolphins were calculated using the kernel-based utilization distribution overlap index method (Fieberg et al. 2005), as explained in Chapter 2. Gregariousness was calculated in SOCPROG 2.7 (Whitehead 2009), with significant predictor variables included for estimating GAIs in SOCPROG 2.7 (Whitehead 2009).

Analysis of male affiliation patterns

Preferred and avoided associations between males were assessed using Whitehead's (2009) modification of the permutation test by Bejder et al. (1998) as explained in Chapter 2.

In addition, GAIs raw residuals were converted to deviance residuals for identifying pairs of individuals with preferred, casual or avoided affiliations using deviance values as suggested in Whitehead & James (2015), and detailed in Chapter 2.

We used Newman's modularity matrix clustering technique (Newman 2004; 2006; Newman & Girvan 2004) implemented in SOCPROG 2.7 (Whitehead, 2009) to examine male social divisions, and social network diagrams to display male clusters and affiliations (using NETDRAW 2.1.5.5Borgatti (2002)). Details about the modularity coefficient are presented in Chapter 2. Furthermore, to examine the spatial distribution of males, we estimated core (50%) and representative ranges (95%) for the social clusters identified using the kernel density method explained above.

Genetic relatedness and kinship relationships

To assess the role that kinship plays on male affiliations, we examined maternal kinship and genetic relatedness between pairs of males included in the social analysis using maternally inherited mtDNA control region sequences and bi-parentally inherited microsatellites, respectively. With the mtDNA sequences a matrix of pairwise haplotypes was constructed, with values of 1 or 0 for pairs with identical or different haplotypes, respectively. We assumed that males with the same mtDNA control region fragment, or haplotype, were from the same maternal lineage. With the microsatellite genotype data we used the simulation method (with known allele frequencies) in COANCESTRY v 1.0.1.5 (Wang 2011) to determine that the triadic likelihood estimator (TrioML; Wang 2007) was the best estimator for our population data set. This estimator was subsequently used for estimating relatedness between male pairs using the same software. For evaluating the correlation between the strength of affiliations and either mtDNA haplotype sharing or microsatellite bi-parental relatedness, we used Mantel tests with 10000 permutations implemented in SOCPROG 2.7 (Whitehead 2009).

We also compared the frequencies of shared mtDNA haplotypes between pairs of preferred, casual and avoided affiliates, and tested for differences among classes using a randomization chi-square test with 10000 Monte Carlo permutations. Average pairwise relatedness was also compared with random expectations among the three affiliation classes using the permutation method implemented in PERM (Duchesne et al. 2006). Further, we inferred sib-ship relationships using the likelihood method in COLONY v 2.0 (Jones & Wang 2010). We then compared the frequencies of estimated full-sibs, half-sibs and non-sibs among preferred, casual and avoided affiliates using a randomization chi-square test as explained in Chapter 2.

In addition, we examined whether individuals belonging to the same social cluster (identified by the modularity clustering technique) had higher average pairwise relatedness than those belonging to different clusters. We also estimated the frequencies of shared haplotypes within and between clusters, and tested for differences using a randomization chi-square test (with 10000 Monte Carlo permutations). For the microsatellite data we compared within and between clusters average pairwise relatedness in COANCESTRY v 1.0.1.5 (Wang 2011) using 10000 permutations. Finally we compared frequencies of sib-ship relationships (full-sibs, half-sibs and non-sibs) within and between male clusters using a randomization chi-square test (with 10000 Monte Carlo permutations).

Results

We conducted 152 boat surveys in Coffin Bay and encountered 967 dolphin groups during the study period. Of these, 657 groups were retained after excluding identical groups resighted on the same day and groups with less than 75% of dolphins photo-identified. Using genetic sexing we identified 42 males with more than 11 sightings (376 groups), which were then included in the social analyses.

Male affiliation patterns

MRQAP tests showed a significant correlation between the three structural predictor variables and the association indices, and therefore they were retained for calculating male GAIs (Table 3.1). Affiliation indices using deviance residuals ranged from -3.11 to 8.93 (mean= -0.47; SD= 1.83; n= 779). Preferred/avoided affiliates were detected among male dolphins using the permutation method (Observed SD= 0.13, random SD= 0.10, p<0.01), and after transforming GAIs to deviance residuals we identified 55 preferred, 707 casual, and 17 avoided pairs of affiliates (Table 3.2).

Social network analysis based on Newman's modularity technique identified 12 social clusters (Q max= 6.07; Fig. 3.2; Table 3.3) that ranged in size from two to five individuals (median= 4; SE= 0.29). No single males were identified according to the modularity analysis. Social clusters showed a mixture of discrete and overlapping areas of space usage within Coffin Bay, with two to four clusters sharing any particular area (Fig. 3.1). As expected, closer affiliates in the social network also showed similar areas of spatial usage.

Table 3.1. Effectiveness of predictor structural variables in explaining association indices among male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. Partial correlation coefficients and results of MRQAP tests were obtained using 10000 permutations in SOCPROG 2.7 (Whitehead 2009).

Predictor variable	Partial correlation	MRQAP
Home range overlap	0.50	p<0.01
Gregariousness	0.13	p<0.01
Cumulative sightings per pair	0.16	p<0.01

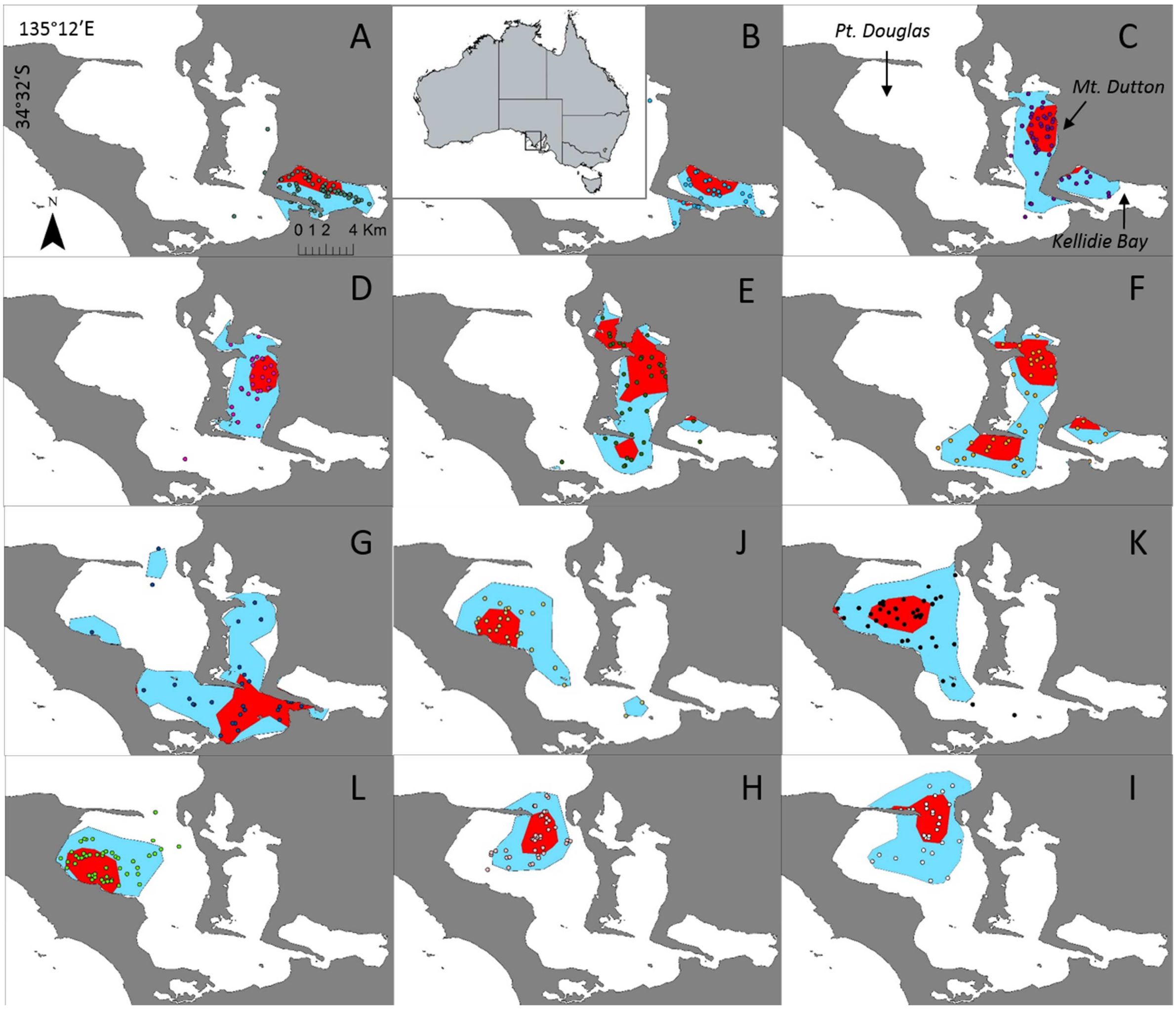

Fig. 3.1. Map of Coffin Bay, South Australia, showing kernel density estimates (KDE) for each of the twelve males social clusters of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) identified. The red shades represents core areas (50% KDE) and blue shades are the representative ranges (95% KDE) for each cluster, with capital letters following those identified using Newman's modularity algorithm (Fig.3.2). Coloured dots represent the locations of distinct groups of males for each social cluster following the colours used in the social network (Fig. 3.2).

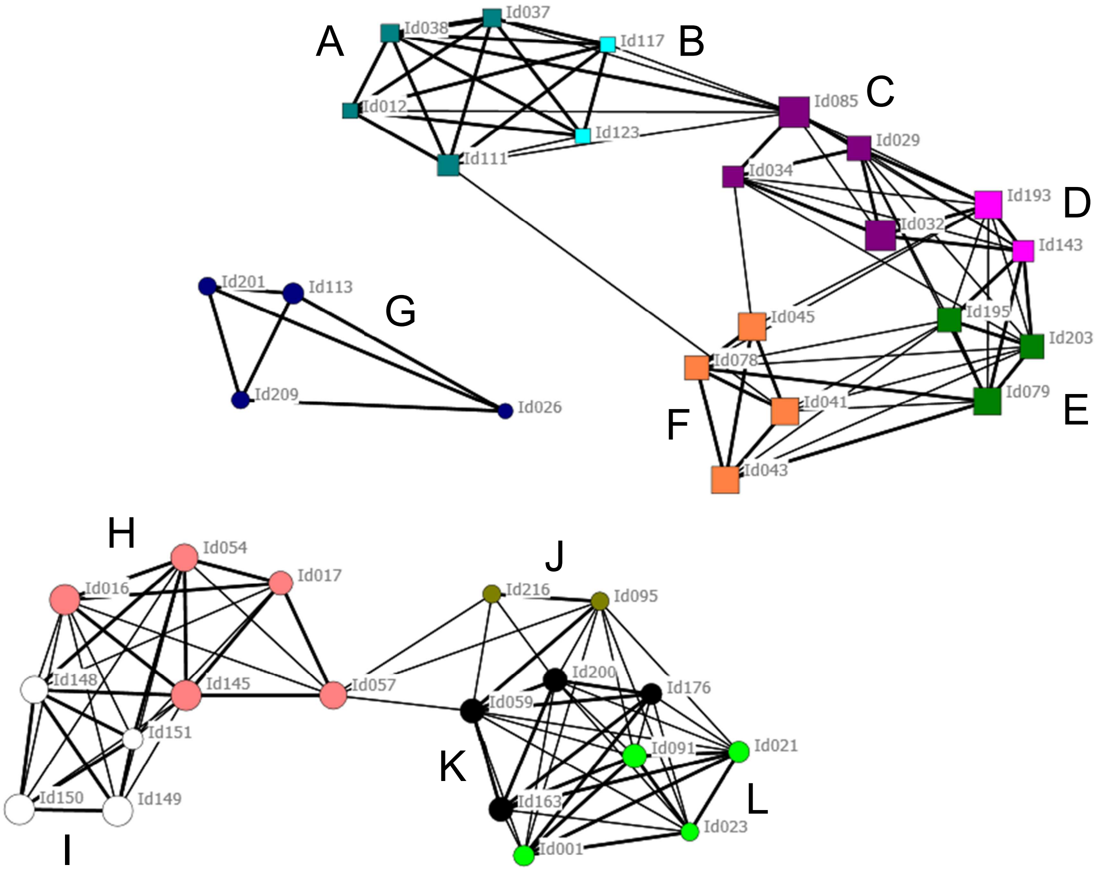

Fig. 3.2. Social network of male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. The colour of the nodes represents the clusters identified using Newman's modularity algorithm (denoted by a capital letter). Node sizes represent the gregariousness of the individuals and the nodes shape the community: square and circles represents Mt. Dutton-Kellidie Bay and Pt. Douglas communities, respectively (Chapter 2). Edge width is proportional to the strength of the affiliations and for clarity are only displayed for affiliation indices greater than 0.94 (twice the mean affiliation index over all male individuals).

Affiliation patterns and kinship

We obtained mtDNA haplotype and microsatellite data for 38 of the 42 male dolphins considered in the social analysis (Table 3.S1). There was a significant correlation between pairwise haplotype sharing and affiliations between males (*r*= 0.1; p<0.05), however there was no significant correlation between pairwise genetic relatedness and affiliations (*r*= 0.02; p=0.48).

We found significant differences for both mtDNA haplotype frequencies and mean pairwise genetic relatedness in respect to the type of affiliations that individuals formed. There was a higher frequency of shared mtDNA haplotypes (Fig. 3.3; p<0.05) among preferred than casual or avoided affiliates (Table 3.2). Similarly, mean pairwise genetic relatedness was higher than expected among preferred affiliates, and lower than expected among avoided affiliates (p<0.05; Table 3.2). However, the sib-ship analysis did not detect significant differences in the proportion of relationships among the three affiliation categories (p=0.48).

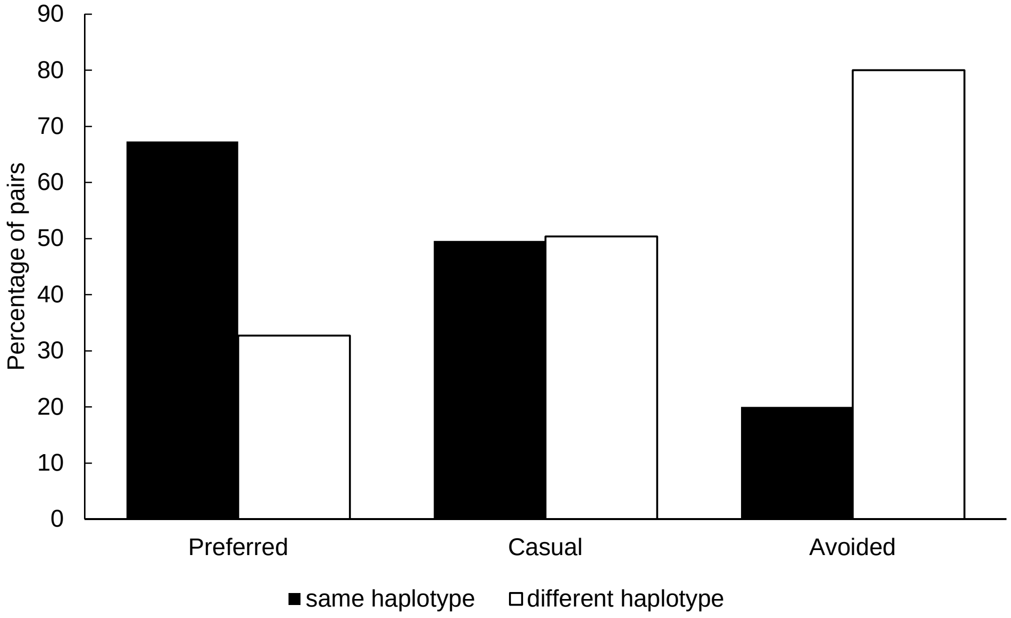

Fig. 3.3. Proportion of male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) with same and different mtDNA haplotypes with respect to affiliation categories identified in Coffin Bay, South Australia.

Table 3.2. Mean GAIs and genetic relatedness, and count of haplotype sharing pairs for each affiliation category of male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) identified in Coffin Bay, South Australia. Asterisks denotes mean genetic relatedness values that differed from random expectations.

Affiliation category	N of pairs (N with genetic data)	Mean GAIs deviance (SD)	Pairs sharing haplotype (%)	Mean genetic relatedness
Preferred	55 (49)	4.62 (1.36)	33 (67.3)	0.09*
Casual	707(639)	-0.83 (1.12)	317 (49.6)	0.07
Avoided	17(15)	-2.75 (0.19)	3 (20)	0.03*

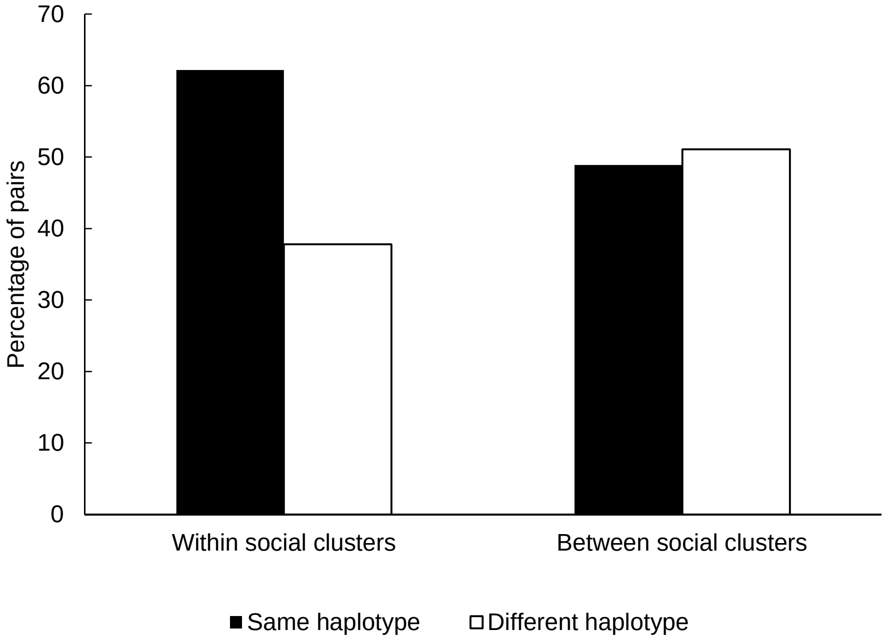

Fig. 3.4. Proportion of male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) with same and different mtDNA haplotypes within and between social clusters identified in Coffin Bay, South Australia.

At social cluster level, we observed a higher frequency of mtDNA sharing within than between the identified social clusters (Fig. 3.4; Table 3.3; Table 3.S1), however this difference was non-significant (p= 0.08). Similarly, there was a tendency for higher average pairwise genetic relatedness between individuals of the same cluster than between individuals of opposite clusters, but this difference was not statistically significant (Table 3.3; p=0.12). Similarly, the sib-ship analysis did not reveal significant differences in the proportion of relationships within and between clusters (p= 0.66).

Table 3.3. Mean GAIs and genetic relatedness, and count of haplotype sharing pairs for each of the twelve male social clusters of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) identified in Coffin Bay, South Australia. Social cluster IDs are represented as in Fig. 3.2. Asterisks denote clusters where genetic data are missing for some of the members.

Cluster ID	N of individuals	Mean GAIs deviance (SD)	Pairs sharing haplotype (%)	Mean genetic relatedness	Range of genetic relatedness
A	4	5.6 (1.23)	6 (100)	0.33	0-0.52
B	2	7.66 (0)	0	0	0
C	4	3.92 (0.60)	1 (100)*	0.4*	0.4-0.41
D	2	4.24 (0)	1 (100)	0.12	0.12
E	3	5.5 (0.39)	3 (100)	0.02	0-0.04
F	4	3.92 (0.67)	1 (33.3)*	0.01*	0-0.03
G	4	5.93 (0.67)	2 (33.3)	0.16	0-0.35
H	5	3.47 (0.41)	2 (20)	0.18	0-0.29
I	4	5.53 (0.71)	6 (100)	0.09	0-0.14
J	2	5.19 (0)	0	0	0
K	4	4.23 (0.14)	3 (100)*	0.05*	0-0.11
L	4	4.55 (0.29)	3 (50)	0.05	0-0.19
Within clusters		4.49 (1.71)	(62.2)	0.11	0-0.52
Between clusters		-0.79 (0.21)	(48.9)	0.09	0-0.64
All males		-0.47 (0.12)	(49.8)	0.08	0-0.64

Discussion

In this study we reveal that male bottlenose dolphins in Coffin Bay form non-random associations and social clusters. In addition, the strength of the associations, and the formation of preferred affiliations was associated with bi-parental genetic relatedness and maternal kinship. The pattern of male associations in clusters resembles that encountered in other bottlenose dolphin populations where males form alliances and groups of those (e.g. Connor et al. 1992a; Möller et al. 2001; Parsons et al. 2003; Wiszniewski et al. 2012b; Connor & Krützen 2015), and conforms to theoretical predictions for the formation of social bonds in male dolphins regarding density, OSR and sexual size dimorphism (Whitehead & Connor 2005; Möller 2012).

Our analytical approach, which considered the effects of three structural variables when estimating affiliation indices, makes comparison with previous studies using association indices somewhat difficult. However, this method provides a better estimation of the true social interactions experienced by animals (Whitehead & James 2015), in particular considering the strong correlation that has been reported between home range overlap and association indices in different taxa (e.g. Frère et al. 2010; Carter et al. 2013; Best et al. 2014). For example, Whitehead & James (2015) found that in northern bottlenose whales (*Hyperoodon ampullatus*) the use of GAIs decreases the structuring of the population while revealing preferred affiliates that were not detected using only association indices . In our study, the use of this method seems to have produced a similar effect, generally decreasing the higher level structuring. Thus, the results reported in other studies that considered only association indices may have overrepresented higher level, and underrepresented lower level, structuring due to the inclusion of structural noise in their social analyses. The use of GAIs into the study of animal societies represents a substantial contribution to overcome these issues.

Male affiliation patterns in Coffin Bay

We identified preferred affiliates at pair level as well as 12 social clusters composed of two to five males in the Coffin Bay population. These preferred affiliations and social clusters are in general similar to the male alliances reported in other bottlenose dolphin populations, where pairs, trios or larger aggregations of those (e.g. second-order, super alliance) associate preferentially for gaining access to females for mating (Wells et al. 1987; Connor et al. 1992a; Möller et al. 2001; Parsons et al. 2003; Krützen et al. 2004; Wiszniewski et al. 2012a). We observed a mixture of preferential areas of usage for males within Coffin Bay, with social clusters showing overlapping or discrete home ranges, similar to the mosaic of home ranges reported for male alliances in Shark Bay (Randic et al. 2012). The spatial usage and social clustering of males in Coffin Bay corresponded well with the social divisions and spatial ranges of the communities reported at the population level (Chapter 2). Six male social clusters are found within each dolphin community, suggesting a possible hierarchically organized social structure in Coffin Bay, which is characteristic of some bottlenose dolphin societies (e.g. Wiszniewski et al. 2009). We did not observe aggressive interactions among male dolphins or between members of different male social clusters, which suggest that similar to other dolphin populations (e.g. Connor et al. 2000b; Randic et al. 2012), defence of territory may be an unlikely explanation for the mosaic of spatial usage displayed by male social clusters. Alternatively, the social hierarchy among males of the population may be well established, and contests among male groups may therefore be rare. Considering that the distribution of male mammals is usually determined by that of females, which in turn largely depends on ecological factors (Emlen & Oring, 1977; Clutton-Brock 1989; Whitehead & Connor 2005; Silk 2002), the pattern of spatial usage observed for male dolphins in Coffin Bay could be reflecting areas of high density of females within each community. Indeed, core areas of usage for female dolphins in Coffin Bay (Chapter 4) are similar to the core areas used by males. Furthermore, differences in spatial ranges observed for males within the same communities could be perhaps explained by preferences for different ecological conditions (e.g., depth, benthic substrate, and productivity) between the bays encountered in the study area, as suggested at the population level (Chapter 2).

The presence of preferred associates and alliances in male dolphins has been proposed to occur in populations with small male-biased sexual size dimorphism and OSR, and in areas of high density of dolphins, where competition for receptive females is likely to be high (Whitehead & Connor 2005; Möller 2012). In Coffin Bay, there is a large density of dolphins, no apparent sexual size dimorphism, and similar male to female ratio of sexed individuals (Passadore et al. 2017) but likely male-biased OSR (below). Moreover, the pattern of spatial usage of the social clusters suggests that males do not rove over extensive areas in search of receptive females. Assuming an inter-birth interval similar to that reported to other bottlenose dolphin populations (3-6 years: reviewed in Connor et al. 2000b; Möller 2012), the availability of receptive females at any given time may be low, and therefore the OSR likely to be male-biased, which in turn should promote competition among males for mating with females. Based on our results, we suggest that preferred male affiliates, and the social clusters formed among male dolphins in Coffin Bay may function to facilitate access to, or for coercion of, receptive females, as has been previously observed in other populations where bottlenose dolphin alliances occur (e.g. Möller et al. 2001; Wiszniewski et al. 2012a; Connor & Krützen 2015). However, it is important to mention that our results point towards greater variation in the size of male social groups compared to other study populations where pairs and triplets have been reported as the norm for male bottlenose dolphin alliances (e.g. Connor et al. 1992a; Möller et al. 2001; Parsons et al. 2003). These differences may be attributed to the more definitions that other studies have used for categorizing individuals within alliances. For example, individuals in one study were considered allied if they were preferred associates, reciprocal closest associates or if not, the second closest associate, and also observed jointly herding females (Connor et al.

1992a). In this study, we based our social groupings on Newman's modularity algorithm (Newman 2004; 2006; Newman & Girvan 2004), which was developed to find the best partitioning of the data set into social clusters, thus allowing more flexibility in the aggrupation of male clusters compared to other studies. Further studies in Coffin Bay examining and comparing male access to females and home range sizes, combined with paternity analyses could provide important insights into the mechanisms promoting and maintaining the association patterns observed among male dolphins in our study population.

The influence of kinship on male bonding

Maternal kinship was significantly correlated with the strength of affiliations between male pairs. Likewise, we found significant differences for both mtDNA haplotype frequencies and mean bi-parental genetic relatedness in respect to the type of affiliations that individuals formed. There was a higher frequency of shared mtDNA haplotypes among preferred than casual or avoided affiliates. Similarly, mean pairwise genetic relatedness was higher than expected among preferred affiliates, and lower than expected among avoided affiliates. At social cluster level, maternal kinship and bi-parental relatedness while higher within than between groups was not statistically significant. The sib-ship analyses also suggested that preferred affiliates and members of the same clusters were not necessarily close relatives (i.e., full or half-sibs).

Overall, pairs of males that spent more time together or that preferentially affiliate to each other were genetically more related. These results point towards kin selection (Hamilton 1964; Smith 2014) potentially playing a role in the formation of male social bonds in Coffin Bay, at least to some degree. This is similar to the patterns encountered in other male mammals such as elephants (*Loxodonta africana*; Chiyo et al. 2011) and lions (Packer et al. 1991), as well as in bottlenose dolphins inhabiting the Bahamas and Shark Bay. In these two populations, mean genetic relatedness was higher within than between male alliances (Parsons et al. 2003; Krützen et al. 2003). However, in Coffin Bay, some social clusters showed on average low genetic relatedness among their members, suggesting that kinship is not the only driving force underlying male social group formation. As has been reported in other mammals (e.g., chimpanzees; Mitani et al. 2000) and bottlenose dolphins (Möller et al. 2001; Owen 2003; Wiszniewski et al. 2012a), other mechanisms such as reciprocal altruism or mutualism, could be operating in male groups within our study area. Alternatively, a dilution effect of relatedness values at cluster level may have affected the results due to some pairs exhibiting low genetic relatedness within social groups. In Shark Bay, bottlenose dolphins showed different patterns of relatedness in respect to the types of alliances they formed (Krützen et al. 2003). In first and second order alliances (2-6 individuals), males were more related than expected by chance, in contrast to males composing the larger super-alliance (14 individuals) which were not (Krützen et al. 2003). This suggests that different mechanisms for male affiliations can be operating on male social groups of the same population. Our results also suggested that male social groups or preferred affiliates were not necessarily formed among close kin or siblings. One explanation for this could be low power of the sib-ship analyses due to the number of genetic markers used to separate different sib-ship categories, or the number of observations in each category estimated. Alternatively, the formation of preferred affiliates or social groups among siblings may not be viable option because of differences in age, sexual and social maturity (e.g., elephants; Chiyo et al., 2011).

The results of this study corroborates theoretical expectations proposed by Möller (2012), who suggested that if related individuals are available for associating, then kin selection may be an important factor promoting social bonds in dolphins. In Coffin Bay, female association patterns and cluster membership were found to be correlated with maternal kinship and bi-parental relatedness (Chapter 4). In addition, females with dependent calves were more likely to associate with others in similar reproductive condition (Chapter 4). These results combined suggest that males during their young years may have numerous opportunities to develop and establish relationships with other males that belong to the same female social clusters, where relatives may occur, thus enhancing the chances for kin-based associations to form. However, as previously suggested in other studies (Möller et al. 2001; Krützen et al. 2003; Owen 2003; Möller 2012; Wiszniewski et al. 2012a), kinship is not a prerequisite for the formation of male social bonds, and other mechanisms may co-exist within the same population.

Based on our results, we propose that kin selection may be an important factor influencing at least some of the strong male associations observed in Coffin Bay bottlenose dolphins. Further behavioural and genetic studies evaluating the reproductive success of males composing different social clusters may provide important information about the function and potential reproductive skew among these groups. This in turn could be valuable for testing the importance of kin selection as well as other evolutionary mechanisms, which may be operating in the formation and maintenance of male social bonds in this population. Our findings add to the growing evidence of complex male social behaviour in bottlenose dolphins and highlight that social, genetic, intrinsic, demographic and ecological factors are likely to contribute to the formation and maintenance of male bonding in dolphins.

Table 3.S2. Pairwise TrioML (Wang 2007; 2011) relatedness values (below diagonal) and mtDNA sharing (above diagonal; 1= same, 0= different haplotype.) between male southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) sampled in Coffin Bay, South Australia. SC= social clusters according to Fig. 3.2. Note that 2 haplotypes H3 and H2, following Bilgmann et al. (2007) were found on the male population with a ratio of 3:2. Asterisks represent values of relatedness or haplotype sharing within social clusters.

SC	L	A	H	H	L	L	G	C	A	A	F	F	H	H	F	E	C	L	J	A	G	B	B	D	H	I	I	I	I	K	K	D	E	K	G	E	G	J
IDs	1	12	16	17	21	23	26	29	37	38	41	45	54	57	78	79	85	91	95	111	113	117	123	143	145	148	149	150	151	163	176	193	195	200	201	203	209	216
1	—	1	0	1	1*	0*	0	1	1	1	0	0	0	0	1	1	1	1*	0	1	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1
12	0	—	0	1	1	0	0	1	1*	1*	0	0	0	0	1	1	1	1	0	1*	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1
16	0	0	—	0*	0	1	1	0	0	0	1	1	1*	0*	0	0	0	0	1	0	1	0	1	0	0*	1	1	1	1	0	0	0	0	0	0	0	0	0
17	0.3	0.26	0.11*	—	1	0	0	1	1	1	0	0	0*	0*	1	1	1	1	0	1	0	1	0	1	1*	0	0	0	0	1	1	1	1	1	1	1	1	1
21	0.19*	0	0	0.04	—	0*	0	1	1	1	0	0	0	0	1	1	1	1*	0	1	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1
23	0.07*	0.05	0	0	0.03*	—	1	0	0	0	1	1	1	0	0	0	0	0*	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
26	0.08	0.11	0.05	0.09	0.26	0	—	0	0	0	1	1	1	0	0	0	0	0	1	0	1*	0	1	0	0	1	1	1	1	0	0	0	0	0	0*	0	0*	0
29	0	0.23	0	0	0.05	0.06	0.1	—	1	1	0	0	0	0	1	1	1*	1	0	1	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1
37	0.08	0*	0	0	0	0.5	0	0.2	—	1*	0	0	0	0	1	1	1	1	0	1*	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1
38	0.05	0.38*	0	0.06	0.38	0.35	0.24	0.13	0.18*	—	0	0	0	0	1	1	1	1	0	1*	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1
41	0	0	0.01	0	0	0.06	0	0.16	0.51	0.23	—	1*	1	0	0*	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
45	0.13	0	0	0	0.13	0	0	0	0	0	0*	—	1	0	0*	0	0	0	1	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
54	0	0.12	0.22*	0.3*	0	0	0	0.05	0.1	0.01	0.22	0.15	—	0*	0	0	0	0	1	0	1	0	1	0	0*	1	1	1	1	0	0	0	0	0	0	0	0	0
57	0.22	0	0.05*	0.23*	0.09	0.04	0	0.06	0	0	0	0.5	0*	—	0	0	0	0	0	0	0	0	0	0	0*	0	0	0	0	0	0	0	0	0	0	0	0	0
78	0	0.15	0.2	0	0	0.14	0	0.11	0	0.27	0.03*	0*	0	0.08	—	1	1	1	0	1	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1
79	0.1	0.15	0.15	0.07	0.03	0	0.29	0	0.14	0	0.16	0.12	0	0	0.05	—	1	1	0	1	0	1	0	1	1	0	0	0	0	1	1	1	1*	1	1	1*	1	1
85	0.05	0.5	0	0	0	0	0.19	0.4*	0	0	0	0.19	0	0	0	0.2	—	1	0	1	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1
91	0*	0.5	0	0	0*	0*	0.04	0	0	0	0	0.12	0	0	0	0.05	0.5	—	0	1	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1
95	0.06	0.04	0	0	0	0	0.24	0	0	0.15	0	0.14	0.06	0	0.05	0.06	0.14	0.11	—	0	1	0	1	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0*
111	0	0.52*	0	0	0	0	0.1	0.2	0.41*	0.46*	0	0.03	0	0	0.01	0.26	0.37	0.19	0.06	—	0	1	0	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1
113	0.09	0.5	0.03	0	0	0.09	0.35*	0	0	0.04	0	0.1	0.1	0	0.04	0.09	0.18	0.26	0.2	0.31	—	0	1	0	0	1	1	1	1	0	0	0	0	0	0*	0	0*	0
117	0.28	0.34	0.04	0.13	0.04	0.03	0.03	0	0	0.06	0	0	0	0	0	0	0.15	0.09	0.04	0.07	0.2	—	0*	1	1	0	0	0	0	1	1	1	1	1	1	1	1	1
123	0.11	0	0.09	0.09	0	0	0.07	0.27	0.01	0	0.19	0	0.01	0.11	0	0.2	0	0	0	0.04	0	0*	—	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
143	0.02	0	0.21	0	0.02	0.1	0	0.06	0	0.08	0	0.22	0.21	0.09	0.3	0	0	0.05	0	0.01	0	0	0	—	1	0	0	0	0	1	1	1*	1	1	1	1	1	1
145	0	0.19	0.29*	0.26*	0.08	0	0	0.04	0	0.26	0.11	0	0.29*	0	0.12	0	0	0	0.04	0	0	0	0.08	0.12	—	0	0	0	0	1	1	1	1	1	1	1	1	1
148	0	0.06	0	0	0	0.5	0	0.14	0.27	0.25	0.09	0.09	0.33	0	0.15	0	0.01	0	0	0	0	0	0	0.16	0	—	1*	1*	1*	0	0	0	0	0	0	0	0	0
149	0.39	0	0.21	0.47	0.29	0	0	0	0	0.4	0.08	0.19	0.08	0.1	0.31	0	0	0	0	0	0	0.16	0.04	0.5	0.16	0.13*	—	1*	1*	0	0	0	0	0	0	0	0	0
150	0	0	0.12	0	0.03	0.09	0.02	0	0.03	0.09	0	0.01	0	0.25	0	0	0	0	0	0	0	0	0.14	0.29	0.13	0.05*	0.02*	—	1*	0	0	0	0	0	0	0	0	0
151	0	0	0	0.06	0.08	0	0	0.05	0	0	0	0.33	0.31	0.14	0	0	0	0.04	0.3	0	0	0.02	0	0.22	0.21	0*	0.14*	0.2*	—	0	0	0	0	0	0	0	0	0
163	0	0.55	0	0.08	0	0	0.03	0	0	0	0	0	0.11	0	0.04	0.05	0.5	0.28	0	0.13	0.29	0.19	0	0	0	0	0	0	0	—	1*	1	1	1*	1	1	1	1
176	0.02	0	0.06	0	0.14	0	0	0	0	0.07	0	0.4	0.37	0	0.16	0.1	0.01	0	0.06	0	0.1	0	0	0.53	0.05	0.39	0.24	0	0.28	0.11*	—	1	1	1	1	1	1	1
193	0	0.04	0	0	0	0.16	0	0.38	0.07	0	0	0	0	0	0.19	0.02	0.06	0.11	0	0.32	0	0	0.13	0.12*	0	0.08	0	0.29	0.1	0	0	—	1	1	1	1	1	1
195	0	0.25	0	0	0	0.12	0	0	0.31	0.28	0.21	0.12	0.07	0.14	0.14	0*	0	0	0.29	0	0	0	0	0.23	0.03	0	0	0.27	0.1	0.06	0.19	0	—	1	1	1*	1	1
200	0	0	0.5	0	0	0.02	0.07	0	0	0	0.05	0.01	0.09	0.04	0.02	0	0	0.05	0.11	0	0.05	0.15	0.02	0	0.17	0.02	0.05	0.2	0.08	0*	0.02	0	0.16	—	1	1	1	1
201	0	0	0.01	0	0	0	0.21*	0	0	0	0	0	0	0	0.01	0.02	0.14	0.6	0.01	0	0.26*	0.06	0.01	0	0	0	0	0.04	0.06	0.25	0.01	0.05	0	0.05	—	1	1*	1
203	0.01	0.1	0.31	0.19	0	0	0.19	0	0	0.5	0	0	0	0	0.32	0.04*	0.09	0.25	0.09	0.17	0.26	0.3	0	0	0	0	0.14	0	0	0.15	0	0.12	0*	0.11	0.06	—	1	1
209	0	0.08	0	0	0	0	0.1*	0.34	0.22	0.5	0.3	0.09	0.12	0	0.11	0	0.1	0	0.07	0	0*	0	0.42	0.17	0.39	0.01	0.37	0.4	0.04	0	0.14	0.17	0.66	0.03	0.01*	0	—	1
216	0.04	0	0	0.02	0.01	0.06	0	0	0	0.14	0.13	0.06	0	0	0	0.06	0.01	0	0*	0	0	0.01	0.26	0	0.07	0	0	0	0	0	0	0.06	0	0	0.05	0	0	—

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CHAPTER 4. Kinship, reproductive condition and affiliation patterns in female southern Australian bottlenose dolphins (*Tursiops* cf. *australis*)

Abstract

Social relationships among female mammals are usually determined by an interplay among genetic, intrinsic, social and ecological factors that ultimately affect their lifetime reproductive success. However, few studies have attempted to control for and integrate these factors, which have hampered our understanding of the drivers underlying female sociality. Here, we used generalized affiliation indices controlling for factors that affect social analyses, and then combined social network, information on reproductive condition, and maternally and bi-parentally inherited genetic data to investigate drivers of associations and cluster formation in female southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. Our analysis is based on photo-identification data and biopsy samples collected through systematic boat-based surveys over a two year period. Female dolphins formed preferred associations and social clusters that ranged over a mixture of overlapping and discrete home ranges. Furthermore, matrilineal kinship and biparental relatedness, as well as reproductive condition, correlated with the strength of female affiliations, and relatedness for both genetic markers was also higher within than between social clusters. The predictability of resources in Coffin Bay and the availability of close relatives in the population may have favoured the formation of female social bonds among kin and in similar reproductive condition. This study highlights the importance of genetic, intrinsic, social and ecological factors in determining female sociality in dolphins.

Introduction

Female reproductive success in mammals is limited by the costs of lactation, gestation and caring for their young (Clutton-Brock et al. 1989), which in turn generally places constraints on their distribution and behaviour (Whitehead 1996; 2003). Female social relationships and spatial distribution are therefore largely determined by ecological factors which affect the quantity and quality of food they can obtain, and the chances of offspring survival, such as distribution of resources and predation risk (Wrangham 1980; Clutton-Brock 1989; Wittemyer et al. 2005). In most mammals, females tend to remain in their natal areas and associate in groups, but there are some species where females leave their natal ranges or social groups to avoid local competition for resources and mating opportunities (Clutton-Brock & Lukas 2012; Wrangham & Rubenstein 1986). Females living in groups may benefit from reduced risk of predation, assistance in infant rearing, increased access to food resources, increased reproductive output, survival and psychological wellbeing, as well as protection from sexual coercion by males (Wrangham 1980; Wrangham & Rubenstein 1986, Smuts & Smuts 1993; Kelley et al. 2011; Frère et al. 2010a; Massen et al. 2010; Wallen et al. 2016). For example, enhanced offspring survival has been demonstrated in female baboons (*Papio cynocephalus*) that show close social bonds (Silk et al. 2003; 2009). Similarly, social factors have been attributed to partially drive calving success in bottlenose dolphins (*Tursiops* cf. *aduncus*; Frère et al. 2010a), and assistance in protection from male coercion (Wallen et al. 2016).

If social relationships have a positive effect on fitness (e.g. Silk et al., 2003; 2009; Frère et al. 2010a), kin selection theory predicts that social bonds should preferentially form among relatives (Hamilton, 1964). In accordance, kinship has been demonstrated to be an important factor on the development and maintenance of social bonds in many female mammals (but see: Langergraber et al. 2009), such as African elephants (*Loxodonta Africana*; Archie et al. 2006), sperm whales (*Physeter macrocephalus*; Gero et al. 2008), giraffes (*Giraffa camelopardalis*; Carter et al. 2013), spotted hyenas (*Crocuta crocuta*; Holekamp et al. 2007) and rhesus macaques (Widdig et al. 2001; 2002). Associating with kin can provide fitness benefits, such as those related to cooperative foraging, increased growth rates, enhanced reproductive success, reduced aggression, protection from predators, and shared social and ecological knowledge (e.g. Olsen & JäUrvi 1997; Silk 2002; Silk et al. 2003; Krützen et al. 2004; Gerlach et al. 2007; Frère et al. 2010a; Smith 2014). Moreover, the kin structure of a group has implications for the evolution of social behaviour (Clutton-Brock & Lukas 2012). When female groups are composed of close relatives, groups are usually stable and cooperation among females is common. In contrast, when groups are formed by non-related individuals, females usually move between social groups and cooperative behaviours are not frequently observed (e.g. Sterck 1997; Clutton-Brock 2009). For example, the stability, quality and strength of social bonds in female baboons (*Papio cynocephalus*) correlate with maternal, and to a lesser extent, paternal relatedness of the individuals (Silk et al. 2006a; b). Similarly, it has been shown that social cohesion in yellow-bellied marmots (*Marmota flaviventris*) is maintained through affiliative interactions among related individuals (Wey & Blumstein 2010).

Bottlenose dolphins (*Tursiops* spp.) live in societies with fission-fusion dynamics, in which the patterns of associations among individuals vary in strength and temporal stability (Connor et al. 2000). Adult female bottlenose dolphins, apart from having a strong social bond with their calves for the first years of the calf's life, usually form loose to moderate associations with an extensive network of females of various ages and degrees of kinship (Wells et al. 1987; Smolker et al. 1992; Möller et al. 2006; Frère et al 2010b; Wiszniewski et al. 2010). In most well studied populations, females associate more closely within smaller clusters, called 'bands' or 'cliques'. For example, in Sarasota Bay, USA, and Port Stephens and Shark Bay, Australia, female common bottlenose dolphins (*T. truncatus*) and Indo-Pacific bottlenose dolphins (*T. aduncus*), respectively, form clusters or stable subsets of frequent associates that share similar core areas within their home ranges (Wells et al. 1987; Smolker et al. 1992; Möller 2001; Möller et al. 2006; Frère et al. 2010b). The potential advantages of forming close associations in female dolphins include protection from predators, defence against male coercion, increased fitness and infant survival (Connor et al. 2000; Möller et al. 2006; Frère et al 2010a; Wallen et al. 2016).

As reported in other mammals, kinship plays an important role in shaping female associations in bottlenose dolphins. In Shark Bay (Western Australia) and Port Stephens (eastern Australia), female association patterns were positively correlated with genetic relatedness (Frère et al. 2010b; Möller et al. 2006), although at social cluster level, kinship was not a determinant for membership within social clusters (Möller et al. 2006). Shared reproductive state also plays a role in delineating female associations in bottlenose dolphins (Wells et al. 1987; Smolker et al. 1992; Möller & Harcourt 2008; Frère et al. 2010). Möller & Harcourt (2008) found that females in similar reproductive state (with newborns and young calves) had higher association levels than females in different reproductive condition (with older or no calves). In inshore habitats, where resources are likely to be more predictable (Gowans et al. 2008), Möller (2012) suggested that delphinid female philopatry may be favoured because of the benefits of familiarity with food resources. Furthermore, moderate social bonds may emerge between both kin and non-kin, although long-term social bonds may be more common among female kin (Möller 2012).

Here, we investigated the association patterns and kinship relationships of female southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) inhabiting the inner area of Coffin Bay, South Australia, a heterogeneous inshore environment composed of small bays and channels. Coffin Bay is considered a stronghold for southern Australian bottlenose dolphins, with high densities of dolphins reported (1.4 dolphins/km^2: Passadore et al. 2017), similar male-to-female ratio of no-calf individuals (males=46-52; females= 52-60: Passadore et al. 2017), and high site fidelity, and restricted ranging patterns by both sexes (Passadore et al. in review). The Coffin Bay dolphin population is socially structured into two communities with discrete core ranges, where individuals from the same communities are on average more bi-parentally related than individuals from different communities (Chapter 2). Furthermore, males tend to form kin-based associations, which may function for gaining access to females for mating (Chapter 3). Here, we used generalized affiliation indices (Whitehead & James 2015), controlling for factors that could affect social analyses, and then combined social network techniques, information on reproductive condition, and maternally and bi-parentally inherited genetic markers to investigate the factors driving associations in female southern Australian bottlenose dolphins. Based on predictions for female bonding in delphinids (Möller 2012), we expect that females in Coffin Bay will show preferred associates and form social groups, and these may be based on kinship relationships due to the availability of close relatives within the two dolphin communities identified in this population. In addition, given the presence of females in different reproductive conditions in the population (without and with calves of different ages), their reproductive condition may also influence the patterns of female associations.

Materials and methods

Study area and data collection

Boat transects were conducted in the inner area of Coffin Bay, South Australia, between 2013 and 2015. Information on survey design and the study area are given in Chapters 2 and 3. In summary, an even coverage of seasons and habitat types was attempted, with the bay characterised as an inverse estuary and encompassing various shallow heterogeneous habitats. Dolphin groups sighted were approached to record their location, group size and composition, and to obtain photographs of their dorsal fins for photo-identification as detailed in Chapters 2 and 3. Dolphins were classified as calves or non-calves as explained in Chapter 2. Biopsy samples were collected from photo-identified non-calf individuals using one of two sampling methods, and later stored in a freezer in the lab as described in Chapter 2.

Genetic analyses

Methods for genetic analyses are those presented in Chapters 2 and 3. In summary, DNA was extracted and then quantified; sex of biopsied dolphins was determined via PCR of fragments of the ZFX and SRY genes (Gilson et al. 1998); a mitochondrial DNA (mtDNA) control region fragment was sequenced to determine haplotypes (Baker et al. 1993); and genotypes of 11 microsatellites were amplified as reported in Pratt et al. (in review). Microsatellites showed no evidence of null alleles, linkage disequilibrium or departures from Hardy-Weinberg equilibrium (Chapter 2), and there was no evidence for population genetic subdivision within the inner area of Coffin Bay (Pratt et al. in review).

Defining associations and estimating Generalized Affiliation Indices (GAIs)

Definition of dolphin group, and criteria for selection of groups and individuals for social analyses are the same as presented in Chapters 2 and 3. However, in this chapter, only non-calf individuals positively identified as females were included for analyses. Females were identified either through the molecular sexing analysis (explained above) or by visual observation of a closely associated calf on more than 10 sightings.

The strength of the associations between pairs of individuals was estimated using GAIs (Whitehead & James 2015), and the correlation between the associations and three predictor structural factors were tested using multiple regression quadratic assignment procedures (MRQAP) as in the previous two chapters. Areas of home range overlap between females were calculated using the methods described in Chapter 2. SOCPROG 2.7 (Whitehead 2009) was used to calculate gregariousness and to estimate GAIs.

Analysis of female affiliation patterns

Presence of preferred and/or avoided companionships were tested as explained in Chapter 2. GAIs raw residuals were converted to deviance residuals for identifying female pairs that were preferred, casual or avoided affiliates as done for the male dolphins in the previous chapter.

Furthermore, we tested if females with dependent calves associated more often with other females in similar reproductive condition. We constructed a similarity matrix for females according to two categories: 1) observed with a dependent calf for > 18 months and 2) observed without a calf or observed with a calf for < 6 months. The time frame selected allowed us to differentiate females that were observed with calves during most of the study period from those that didn't have calves or had them but for only for a short period of time, either because the calf died or was weaned soon after the start of the study. In category 1 we included 24 females that were observed accompanied by a calf for at least 18 months. In category 2 we included two females that had calves for 4 and 5 months, and 29 females that were never observed with a calf. We tested for a correlation between the similarity matrix and the affiliation indices using a Mantel test with 10000 permutations in SOCPROG 2.7 (Whitehead 2009).

To examine social divisions among the females in Coffin Bay, we used Newman's modularity matrix clustering technique as previously used for the whole population and the male component (Chapters 2 and 3). Furthermore, to examine the spatial distribution of females in Coffin Bay, we estimated areas of usage for the social clusters identified as previously done in Chapters 2 and 3.

Genetic relatedness and kinship relationships

The role of kinship on female affiliations was assessed similarly to male affiliations, which considered both maternal kinship and pairwise genetic relatedness. In summary, a matrix of pairwise haplotype sharing was constructed for the mtDNA dataset, and a matrix of pairwise genetic relatedness was constructed for the microsatellite dataset (see Chapters 2 and 3 for more details). Microsatellite genetic relatedness was estimated using the triadic likelihood estimator (TrioML; Wang 2007) in COANCESTRY v 1.0.1.5 (Wang 2011). This was found to be the best estimator of genetic relatedness for our dataset (Chapters 2). For evaluating the correlation between the strength of affiliations and both matrices, we used Mantel tests (with 10000 permutations) in SOCPROG 2.7 (Whitehead 2009).

In addition, we compared frequencies of shared haplotypes between pairs of preferred, casual and avoided affiliates, and tested for differences among classes, and with random expectations, as previously done in the male chapter (Chapter 3). We also inferred sib-ship relationships and tested for frequency differences among affiliate classes as detailed in Chapters 2 and 3.

Finally, we investigated whether females of the same social cluster had higher average pairwise relatedness than those of opposite clusters; tested for differences in the frequencies of shared haplotypes within and between clusters; and compared frequencies of sib-ship categories within and between female clusters using the methods reported in Chapter 3.

Results

A total of 152 boat surveys were conducted in Coffin Bay during the study period, with 967 dolphin groups sighted. A total of 657 groups were then selected based on the criteria which excluded identical groups resighted on the same day and groups with less than 75% of dolphins identified. We included for the social analyses 55 females with more than 11 sightings (represented in 550 groups): 50 females identified by genetic sexing, and 5 females based only on the presence of a dependent calf.

Female affiliation patterns

We found a significant correlation between home range overlap, gregariousness and the association indices, therefore these variables were included as predictor structural variables for calculating female GAIs. The number of sightings per female dyad did not show a significant correlation with the association indices and thus this variable was not included in the estimation (Table 4.1). GAIs using deviance residuals ranged from -4.52 to 7.06 (mean= -0.41; SD= 1.53; n= 1485). We detected the presence of non-random companionships among female dolphins using the permutation test (Observed SD= 0.1; Random SD= 0.08; p<0.01), and using GAIs deviance residuals 117 preferred, 1331 casual and 37 avoided pairs were identified (Table 4.2).

Table 4.1. Effectiveness of predictor structural variables in explaining association indices among female southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. Partial correlation coefficients and results of MRQAP tests were obtained using 10000 permutations in SOCPROG 2.7 (Whitehead 2009).

Predictor variable	Partial correlation	MRQAP
Home range overlap	0.43	p<0.01
Gregariousness	0.16	p<0.01
Sightings per dyad	0.03	p=0.06

We found a positive correlation between female reproductive condition and affiliation indices (*r*= 0.08; p<0.05). Pairs of females with dependent calves associated more often with other females in similar condition than with females with no calves or females that had calves for only a short period of time. The Newman's modularity clustering technique revealed that the Coffin Bay female population was subdivided into seven social clusters (Qmax= 4.5; Fig 4.2; Table 4.3) that ranged in size from two to 12 individuals (mean= 7.9; SD= 3.63). Social clusters showed a mixture of ranging patterns (Fig. 4.1), with some clusters showing overlapping areas of usage and others using discrete areas. As anticipated, social clusters that were closer in the social network also showed similar areas of spatial use within the bay.

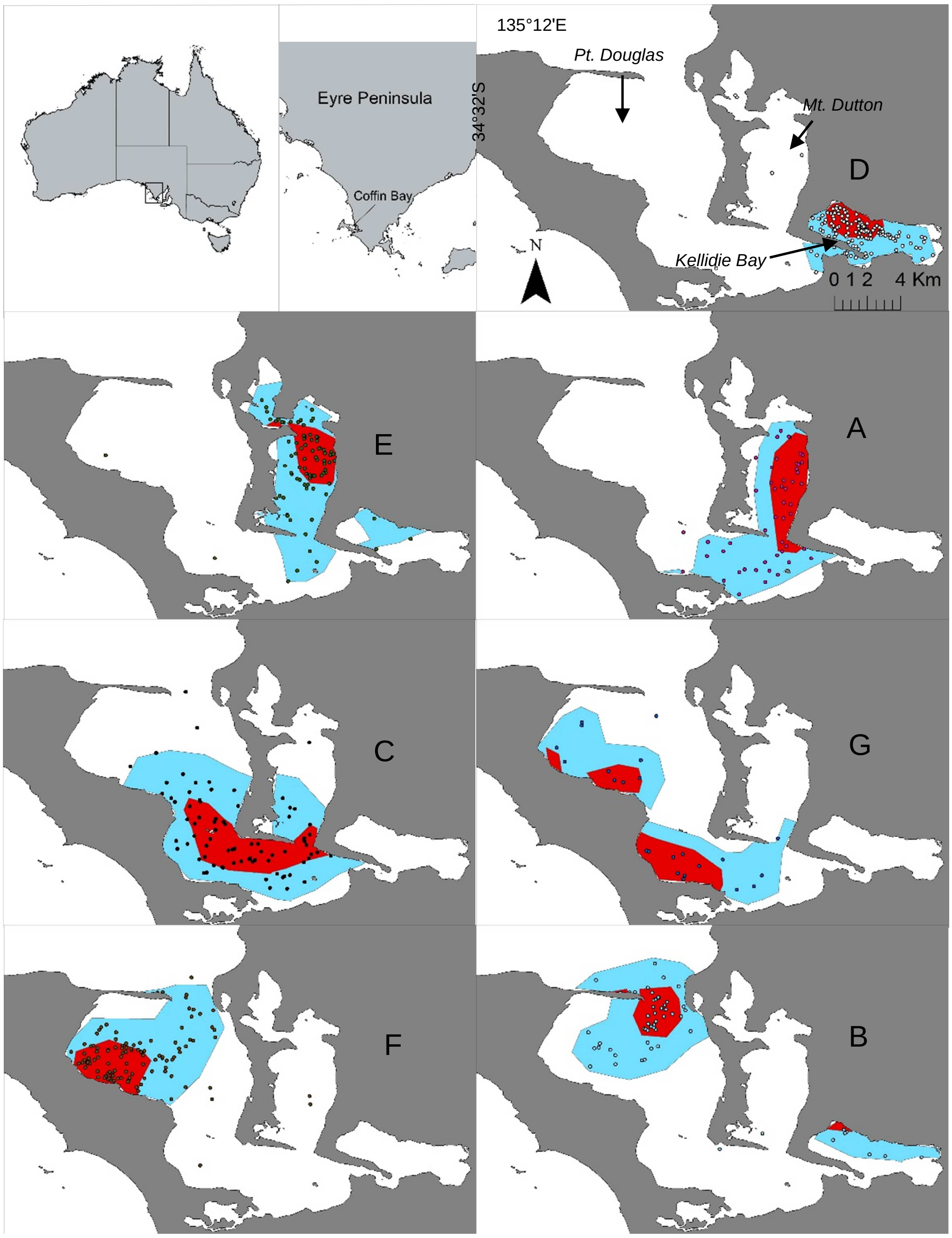

Fig. 4.1. Map of Coffin Bay, South Australia, showing kernel density estimates (KDE) for each of the seven female social clusters of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*)

identified. The red shades represent core areas (50% KDE) and blue shades are the representative ranges (95% KDE). Dots represent distinct groups of animals with colours and capital letters following those in the social network (Fig. 4.2).

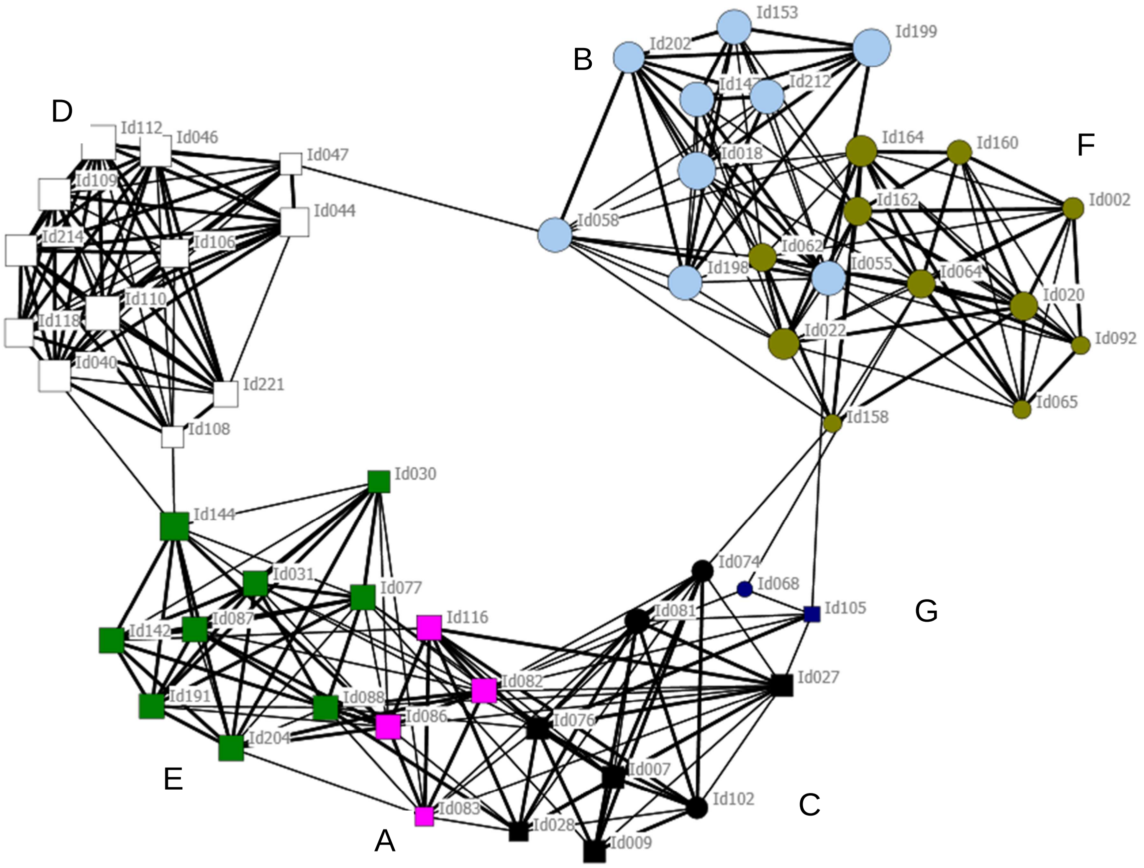

Fig. 4.2. Social network of female southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, South Australia. The colour of the nodes represents the clusters identified using Newman's modularity algorithm (denoted by a capital letter). Node sizes represent the gregariousness of the individuals and shape the communities identified at the population level: square and circles represents Mt. Dutton-Kellidie Bay and Pt. Douglas communities, respectively (Chapter 2). Edge width is proportional to the affiliation index and for clarity are only displayed for affiliation indices greater than 0.82 (twice the mean affiliation index over all female individuals).

Affiliation patterns and kinship

MtDNA haplotype and microsatellite data were gathered for 44 and 49 of the female dolphins considered in the social analysis, respectively. There was a significant correlation between the affiliation indices and both pairwise mtDNA haplotype sharing (*r*=0.1; p<0.05) and genetic relatedness (*r*=0.1; p<0.05; Fig. 4.3).

Comparing different affiliation classes (preferred, casual and avoided), we found that preferred affiliates had higher mean pairwise genetic relatedness than casual and avoided pairs (p<0.05; Table 4.2). However, we did not detect significant differences in the frequencies of shared haplotypes for the different affiliation classes (p=0.16; Table 4.2), or differences in the proportion of sib-ship categories among the different affiliation classes (p=0.21).

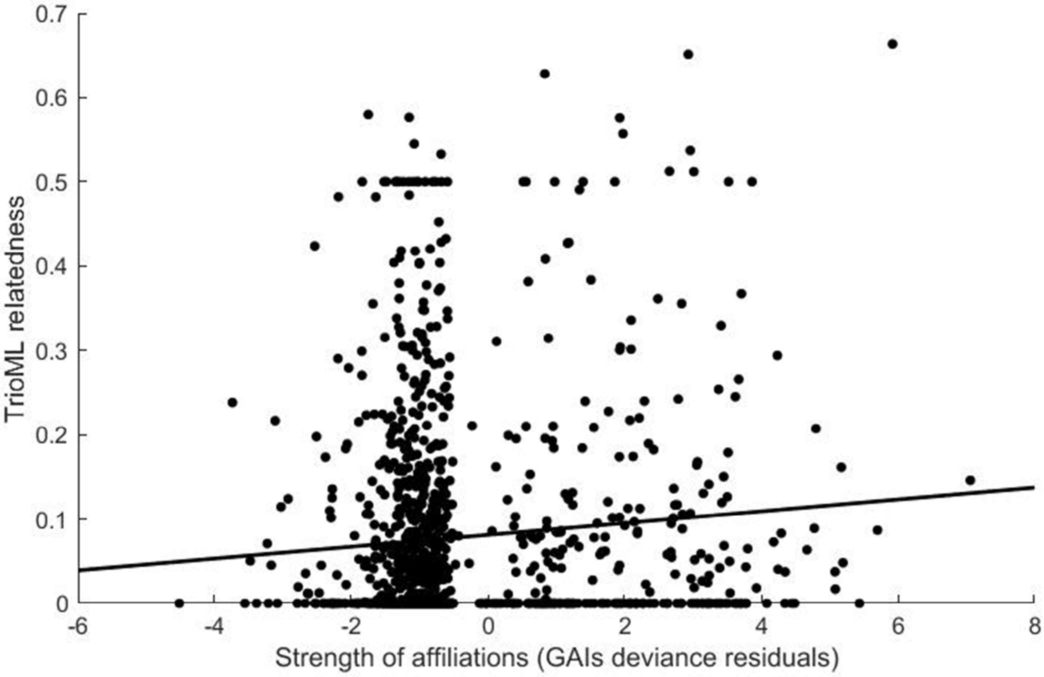

Fig. 4.3. Relationship between affiliation indices and TrioML genetic relatedness in pairs of female southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) inhabiting Coffin Bay, South Australia.

Table 4.2. Mean GAIs and genetic relatedness, and count of haplotype sharing pairs for each affiliation category of female southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) identified in Coffin Bay, South Australia. Asterisks denotes mean genetic relatedness values that differed from random expectations.

Affiliation category	N of pairs	N of pairs with haplotype data	N of pairs with microsatellite data	Mean GAIs deviance (SD)	pairs sharing haplotype (%)	Mean genetic relatedness
Preferred	117	79	99	3.5 (0.79)	44 (55.7)	0.14*
Casual	1331	845	1054	-0.68 (0.99)	405 (48)	0.11
Avoided	37	22	23	-2.94 (0.45)	14 (63.7)	0.11

At social cluster level, we found a higher frequency of mtDNA sharing (Fig. 4.4; Table 4.3; $p<0.05$) and higher mean genetic relatedness (Table 4.3; $p<0.05$) within than between social clusters. However, the sib-ship analysis did not reveal a significantly difference in the frequency of sib-ship categories within than between social clusters ($p=0.1$).

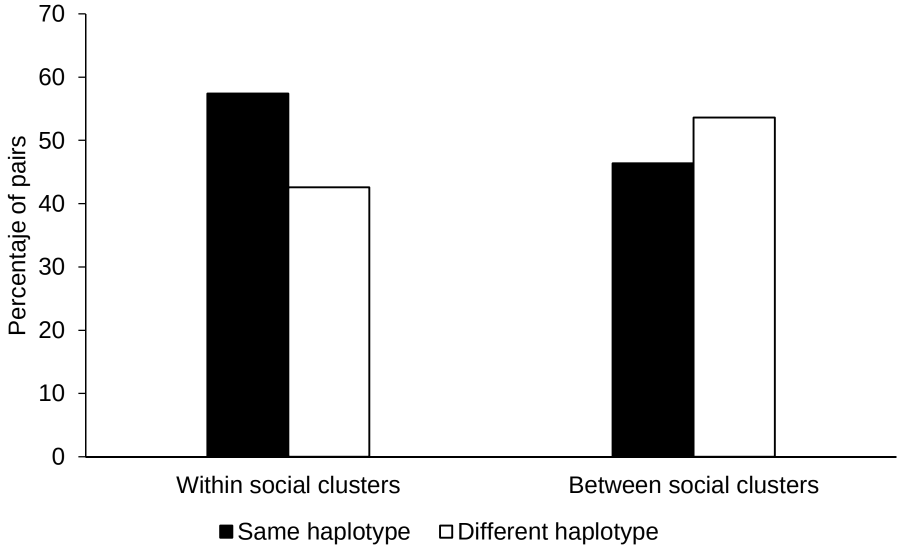

Fig. 4.4. Proportion of mtDNA sharing among female southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) within and between social clusters identified in Coffin Bay, South Australia.

Table 4.3. Mean GAIs, count of haplotype sharing pairs and mean genetic relatedness for each of the seven female social clusters of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) identified in Coffin Bay, South Australia. Social cluster IDs are represented as in Fig. 4.2. Asterisks denotes mean genetic relatedness that differed from random expectations ($p<0.05$).

Cluster ID	N of individuals (pairs)	Mean GAIs deviance (SD)	N pairs with haplotype data	N pairs with microsatellite data	Pairs sharing haplotype (%)	Mean genetic relatedness
A	4 (6)	3.68 (0.83)	3	3	1 (33.3)	0.02
B	9 (36)	2.18 (0.96)	10	10	9 (90)	0.23
C	8 (28)	2.58 (1.69)	28	28	13 (46)	0.09
D	12 (66)	2.6 (1.23)	55	66	25 (45.5)	0.14
E	9 (36)	2.8 (1.25)	15	36	10 (66.7)	0.13
F	11 (55)	1.92 (1.4)	36	45	27 (75)	0.14
G	2 (1)	1.55	1	1	0 (0)	0.13
Within clusters		2.5 (0.69)	148	189	85 (57.4)	0.14*
Between clusters		-0.8 (0.25)	798	987	369 (46.2)	0.11
All females		-0.41 (0.17)	946	1176	454 (48)	0.11

Discussion

We showed that female southern Australian bottlenose dolphins in Coffin Bay, South Australia, form moderate to strong affiliations and social clusters in which kinship generally correlated positively with their social interactions. Furthermore, we found that the reproductive condition of females also correlated with the strength of affiliations. Overall, the socio-genetic structure and ranging patterns of females in Coffin Bay resembles that reported in some other coastal populations of Indo-Pacific and common bottlenose dolphins (e.g. Wells et al. 1987; Smolker et al. 1992; Möller 2001; Möller et al. 2006; Möller & Harcourt 2008; Frère et al. 2010b). The patterns observed also conforms to theoretical expectations for the formation of social bonds in female dolphins inhabiting embayment environments (Möller 2012), suggesting that similar evolutionary forces may be shaping the social behaviour of dolphin populations from disparate geographic areas and different species.

Affiliation patterns in female mammals

The formation of non-random associations in female mammals is common in many species, such as Asian elephants, *Elephas maximus* (de Silva et al. 2011), giraffes (Carter et al. 2013), spotted hyenas (Smith et al. 2007), grey kangaroos, *Macropus giganteus* (Best et al. 2014), zebras, *Equus grevyi,* and onagers, *Equus hemionus* (Sundaresan et al. 2007). In Coffin Bay, female dolphins form preferred associations and social clusters that are similar to those described in some other coastal populations of bottlenose dolphins (e.g. Wells et al. 1987; Connor et al. 2000; Möller et al. 2006). For example, in Port Stephens, eastern Australia, females associated at low to moderate levels with other females, while associating more closely with certain females forming clusters of associates (Möller et al. 2006). Moreover, particular clusters of females used different spatial areas within the Port Stephens embayment with different habitat characteristics (Möller et al. 2006, Wiszniewski et al. 2009). Female dolphins in our study area showed a similar pattern, establishing non-random associations with certain individuals and forming social clusters that showed spatial preferences for particular sub-embayments of Coffin Bay. The social and spatial divisions observed corresponded well with those reported at the population level in Coffin Bay, however in clusters C and G some females were assigned as belonging to different communities (Chapter 2). This could be explained by the fact that these two clusters inhabit the home range area of overlap between the two main communities detected at population level, probably acting as connectors between individuals from both communities (e.g. Lusseau & Newman 2004). The formation of social clusters among females also reinforce the idea of a hierarchically organized society in Coffin Bay dolphins (Chapters 2 and 3), similar to the one reported in Port Stephens (Wiszniewski et al. 2009).

The formation of social groups in female bottlenose dolphins has been attributed to benefits leading to increased fitness and infant survival, and enhanced defence against predators and male coercion (Connor et al. 2000; Möller et al. 2006; Möller & Harcourt 2008; Frère et al 2010a; Wallen et al. 2016). In Coffin Bay, although apparently low (pers. obs.), the risk of predation could be to some extent influencing female behaviour (e.g. Heithaus & Dill 2002). Great white sharks (*Carcharodon carcharias*) are relatively common in South Australian waters, and have been observed within our study area, with at least one dolphin observed with severe shark injuries likely inflicted by this species (pers. obs.). In addition, male dolphins in Coffin Bay form small groups, likely alliances, which could function to increase their access to females (Chapter 3); thus females may also benefit by forming social groups to defend against sequestering or coercion attempts by males (e.g. Wallen et al. 2016).

In societies with fission-fusion dynamics, such as those of bottlenose dolphins (e.g. Connor et al. 2000), females associations may vary according to their developmental stage and reproductive condition, which in turn is affected by ecological and social pressures (e.g. Mann & Smuts 1999; Gibson & Mann 2008). In our study area, we observed that females with calves associated more often with other females in similar reproductive condition. This pattern has been previously reported for bottlenose dolphins inhabiting Port Stephens (Möller & Harcourt 2008), and Sarasota Bay (Wells et al. 1987). It has been suggested by the former authors that females in similar reproductive condition may benefit by associating with each other because of similar energetic and protection requirements. In Coffin Bay, females with calves may have different food requirements (e.g. Bernard & Hohn 1989), and be under higher pressure of predation by sharks and injuries inflicted by coercing males (e.g. Corkeron et al. 1987; Mann & Watson-Capps 2005); thus favouring associations among individuals in similar reproductive condition. Long-term data comparing survival rates among female offspring inhabiting different areas of Coffin Bay (potential for differential risk of predation) or using different social strategies, as well as observations of female-male interactions, could provide important information to further test hypotheses about the functional mechanisms of female group formation.

The influence of kinship on affiliations of female mammals

The importance of kinship in the establishment and maintenance of social relationships has been documented in a wide variety of mammals (e.g. lions, *Panthera leo*, Packer et al. 1991; elephants, Archie et al. 2006; hyenas, Holekamp et al. 2007). Moreover, the establishment of social bonds among philopatric female kin has been suggested as one of the initial steps in the evolution of sociality in mammals (Perrin & Lehmann 2001). In this study, we have demonstrated that association patterns in female southern Australian bottlenose dolphins in Coffin Bay are correlated positively with both matrilineal and bi-parental relatedness. Additionally, we found higher levels of relatedness and haplotype sharing within than between female social clusters in this population. However, when looking at different affiliation classes, we only found support for higher bi-parental relatedness among preferred female pairs, but no significant differences in the proportion of haplotype sharing. Likewise, the sib-ship analyses suggested that preferred affiliations or membership within social clusters were not necessarily restricted to close relatives (siblings). A positive correlation between association patterns and kinship has been previously reported in cetaceans (e.g. sperm whales: Gero et al. 2008) and in other bottlenose dolphins populations inhabiting inshore environments (e.g. Frère et al. 2010b; Möller et al. 2006). However, our study adds to this knowledge by demonstrating that kinship relationships can also be important for membership within social clusters. Overall, our results provide evidence that kinship as well as reproductive condition, play important roles in delineating female dolphin association patterns in Coffin Bay, but we cannot discard that other mechanisms of social bonding are also operating.

The emerging picture from this study corroborates previous predictions that in inshore habitats where resources are relatively predictable (Gowans et al. 2008), female dolphins may benefit by being philopatric and forming strong social bonds with kin and other females in similar reproductive condition, while maintaining moderate and loose social relationships with some other kin and non-kin individuals of the same sex (Möller & Harcourt 2008; Wiszniewski et al. 2010; Möller 2012). The inner area of Coffin Bay is a complex inshore environment, where females exhibit a high degree of site fidelity, and range over relatively small areas, likely due to predictable food resources within the small sub-embayments (Passadore et al. in review). The results of this study also provides insights into the mechanism promoting the formation of male associations based on kinship relationships in Coffin Bay. Considering that the population in Coffin Bay is relatively large (Passadore et al. 2017) and organised into two social communities (Chapter 2), and that females prefer to associate with kin and with others in similar reproductive condition, young male calves may encounter numerous opportunities to associate and develop social bonds with other males that are genetically related. As males grow older these associations may become stronger and form the basis for the formation of social preferences and clusters observed in the adult male population (Chapter 3).

In summary, results from this study demonstrate that kinship and reproductive condition are important factors influencing association patterns of female southern Australian bottlenose dolphins in Coffin Bay, South Australia. Long-term behavioural observations for estimating calving success and how this relates with age, maternal experience, social network metrics, kinship relations and areas of usage would provide important information into the functional mechanisms promoting long-lasting female associations and the formation of social clusters in Coffin Bay. Our results add to the growing knowledge which demonstrates the interplay among social, genetic, intrinsic and ecological factors shaping dolphins and other complex mammalian societies.

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CHAPTER 5. General discussion

Overview

This study provided the first comprehensive evaluation of the socio–genetic structure of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) for a population inhabiting the small embayment of Coffin Bay, South Australia, and revealed the potential mechanisms driving its social structuring and the factors likely to be influencing sex-specific social bonds.

The inner area of Coffin Bay is characterized as a shallow inshore embayment, with a diversity of habitats (Miller et al. 2009; Kämpf & Ellis 2014). Differences in levels of productivity occur from the entrance of Coffin Bay (Pt. Douglas, north area) to the more protected bays found far from the open ocean (e.g. Kellidie and Mt. Dutton Bays) due to the seasonal occurrence of upwellings in the adjacent continental shelf (Kämpf 2004; Kämpf & Ellis, 2014). In addition, the shallow waters (mean depth ~2.5 m) and narrow connection to the open ocean may, to some extent, limit access to large predatory sharks, such as great white sharks (*Carcharodon carcharias*), which are known to commonly occur off this coast (Passadore et al. 2017). Altogether, this protected environment appears to provide a stronghold for southern Australian bottlenose dolphins, with high year-round densities, high survival rates, low emigration rates, and high degree of site fidelity for both males and females (Passadore et al. 2017; Passadore et al. in review). This combination of ecological and intrinsic factors apparently plays an important role in underpinning the dolphin affiliation patterns and social structure observed in this study.

In my thesis, I reported that the Coffin Bay bottlenose dolphin population is socially structured into two similar-sized communities which differed in ranging patterns, affiliation levels and network metrics. In bottlenose dolphins (*Tursiops* spp.), numerous factors likely affect their social structure, including the risk of predation (Heithaus & Dill 2002), habitat characteristics (Rossbach & Herzing 1999; Wiszniewski et al. 2009; 2010; Titcomb et al. 2015), foraging preferences and/or specializations (Krützen et al. 2005; Sargeant et al. 2005;

Daura-Jorge et al. 2012; Kopps et al. 2014), among others (reviewed in chapter 2). My research demonstrated that social divisions observed between the two Coffin Bay dolphin communities corresponded well with differences in ranging patterns of the individuals, which suggest that differences in habitat characteristics encountered among the distinct bays are likely play an important role in the social structuring of the population. I hypothesise that different prey assemblages, which may promote feeding preferences and distinct foraging strategies in the different habitat types, could be an important ecological driver maintaining the structuring of this population. Although no comprehensive studies comparing dolphin prey assemblages has been done in the inner area of Coffin Bay, a pilot study conducted in 2015 using Baited Remote Underwater Video Stations (BRUVS; Cappo et al. 2004) revealed that the diversity of fish assemblages significantly differs among the different bays (S. Whitmarsh, pers. comm., 14 March 2017). This lends support the hypothesis of differential prey resource availability among the different bays. In bottlenose dolphins, feeding strategies have a strong learning and culturally transmitted component from mothers to calves (e.g. Mann & Sargeant 2003; Weiss 2006; Krützen et al. 2005; Kopps et al. 2014). In this context, I found higher genetic relatedness and higher occurrence of estimated siblings within communities when compared to between communities, which suggest that kinship also plays a role in the delineation of the two dolphin communities. I suggest that feeding strategies may potentially be transmitted not only from mother to calves but also among close relatives, and to some extent may influence the areas of individual usage into adulthood, thus explaining kinship relationships observed at community level in Coffin Bay. However, it is important to mention that these communities are not spatially, socially or genetically isolated from each other (Pratt et al. in review), and individuals from different communities were observed to engage in social interactions and share space use with individuals from the other community (chapter 2). These mixed-community groups could function to facilitate knowledge transfer and gene flow between communities (e.g. Lusseau & Newman 2004). In fact, population genetic results suggest no structuring within the inner area of Coffin Bay (Pratt el al. in review), supporting the idea that these communities maintain gene flow between them. In conclusion, I suggest that the interaction between ecological and genetic factors are shaping and maintaining the structuring and the social differences found between the two dolphin communities of inner Coffin Bay. At sex-specific level, I found that both male and female southern Australian bottlenose dolphins in Coffin Bay form preferred affiliates and social clusters, suggesting a organized social structure, in which kinship correlated (at different levels) with the strength of the affiliations (Chapters 3 and 4). Male social behaviour is usually determined by the strategies that they use to maximize their reproductive success (Emlen & Oring 1977; Clutton-Brock 1989). In this context, it has been suggested that the variability in male association patterns could be explained according to differences in population density, operational sex ratio and sexual size dimorphism (Whitehead & Connor 2005; Möller 2012; reviewed in chapter 3). In Coffin Bay, there is a high density of dolphins, similar sex ratios of non-calf individuals (not taken into account their reproductive status) (Passadore et al. 2017), and no apparent sexual size dimorphism (pers. obs.). Thus, I propose that the formation of male social clusters and preferred associations could have evolved in response to high competition for access to females. Moreover, the presence of relatives within communities and the kinship-based association patterns observed among female dolphins (chapter 4), may have favoured the formation of social bonds based on kinship relationships among male dolphins, which could have started at their young years. In addition, males in Coffin Bay ranged over preferred areas that corresponded well with community divisions (chapters 2 and 3), and showed home ranges similar in size to those of females (Passadore et al. in review). This suggests that males did not adopt a strategy of roaming over large areas in search of reproductive females, and that ecological conditions (most likely predictable food availability and feeding preferences) may also be influencing their ranging patterns.

For females, social relationships are usually determined by an interacting set of ecological, genetic and intrinsic factors that ultimately affect offspring survival and lifetime reproductive success (reviewed in chapter 4). In this study, I reported that reproductive condition, and matrilineal and biparental relatedness were all correlated with the strength of female affiliations. Moreover, kinship was an important determinant for membership within social clusters. Ecological factors, such as prey and predator distribution and abundance, could have influenced the patterns observed in this study (e.g. Wrangham 1980; Clutton-Brock 1989; Wittemyer et al. 2005). In the inner area of Coffin Bay, predation risk, although potentially low, could be a factor leading to the formation of social groups and bonds among females in similar reproductive condition. On the other hand, due to the inshore characteristics and complexity of Coffin Bay's habitats, prey resources could be relatively predictable (e.g. Gowans et al. 2008), thus philopatric females may benefit from familiarity with food resources (Möller 2012). Furthermore, the availability of same-sex relatives within communities could have promoted the formation of kinship-based affiliations (Möller 2012). Sexual conflict is another factor that may be involved in the formation of social groups among females in Coffin Bay (e.g. Möller 2012; Wallen et al. 2016). The social groups of males in Coffin Bay may function as alliances, similar to what has been observed in other bottlenose dolphin populations, where they sequester and compete for access to oestrus females (e.g. Connor et al. 2000). Thus the formation of social bonds among females may also have evolved in response to protection from male harassment (Connor et al. 2000; Möller 2012).

The results reported here support the general view of social complexity and similarities among different mammalian taxa such as primates, elephants and dolphins (e.g. Mann et al. 2000; Pearson 2011), suggesting that similar ecological, social and evolutionary conditions may have shaped their societies. For example, in chimpanzees (*Pan bonobo*) males form strong bonds (e.g. Watts 1998), while females tend to form loose to moderate associations with the exception of the strong social bonds formed between mother and calves (reviewed in Pearson 2011). Similarly, in bottlenose dolphins, males form alliances and females tend to establish a wide range of associations from loose to strong relationships (Connor et al. 2000). The formation of social bonds in female mammals has been mainly attributed to enhanced protection from predators (Clutton-Brock 2009) and increased offspring survival (e.g. Silk et al. 2009). In males, the advantages of forming social bonds are mainly attributed to an increase in access to reproductive females (Clutton-Brock & Parker 1992; Clutton-Brock & Parker 1995; Connor et al. 2000). Despite these similarities, living in different environments (land *versus* ocean) have also apparently promoted some differences between female bottlenose dolphin and chimpanzee societies that may be attributable to dissimilarities in their dispersal patterns, presence/absence of territoriality, levels of predation, degree of scramble competition, and costs of locomotion (Pearson 2011). In general, and in accordance with my results, male and female bottlenose dolphins inhabiting inshore habitats tend to be philopatric (although some flexibility occurs; reviewed in Möller 2012). In contrast, female chimpanzees disperse from their natal communities during adolescence to avoid inbreeding with close male relatives (Goodall 1986; Boesch et al. 2000). Due to the low cost of locomotion for dolphins compared to chimpanzees (Pearson 2011), inbreeding avoidance could be attained by mating with individuals from neighbouring communities during occasional movements out of their core areas. The results from this study support the view of interactions among individuals from different communities and thus opportunities for mating with non-community members. Differences in the risk of predation and degree of scramble competition may also be responsible for differences in female associations between bottlenose dolphins and chimpanzees (e.g. Pearson 2011). In the ocean, the risk of predation may be higher and thus strongly impact on the formation of social groups for protection against predators (Connor et al. 2000). On the other hand, the low cost of locomotion for bottlenose dolphins may facilitate the fission and fusion of females groups to avoid scramble competition, therefore facilitating sociality as compared to chimpanzees (Connor et al. 2000; Pearson 2011). Finally, territoriality in chimpanzees (Goodall 1986; Boesch et al. 2000) may be limiting the number of possible associates, which may account for differences in sociality when compared with bottlenose dolphins where territoriality has not been reported (Connor et al. 2000).

In respect to other populations of inshore bottlenose dolphins, Coffin Bay dolphins seem to show many similarities in social structure and sex-specific association patterns (e.g. Port Stephens and Shark bay, Australia; reviewed in chapters 2-4). For example, in Port Stephens, two *T. aduncus* communities inhabit preferentially different geographic areas that differ in habitat characteristics (Wiszniewski et al. 2009). Males showed a similar pattern of associations in small social groups or alliances, however, these associations were not correlated with kinship (Möller et al. 2001). Females also formed preferred associations in which kinship and reproductive state was correlated with the strength of the associations (Möller et al. 2006; Möller & Harcourt 2008). However, in contrast to findings from Coffin Bay, membership within social clusters was not correlated with genetic relatedness (Möller et al. 2006). Despite Coffin Bay and Port Stephens populations sharing many similarities, it is evident that kinship plays a more important role in delineating association patterns in Coffin Bay. This difference could be attributable to different demographic characteristics between the two populations at the time of the study, with the presence of close relatives within communities in Coffin Bay (chapter 2) perhaps promoting kin selection to operate (Hamilton 1964). However, further analyses would be necessary to test this hypothesis. In the next section, I discuss how the patterns of associations observed in Coffin Bay dolphins could be explained according to predictive socio-ecological models proposed for the formation of social bonds in delphinids.

Delphinid socio-ecological models and Coffin Bay dolphins

There have been few attempts to describe the delphinid social structure through predictive models, which could explain the great variability of social patterns observed among species as well as between populations living under different environmental conditions (e.g. Gowans et al. 2008; Möller 2012). In this context, resource availability (e.g. prey, predators and mates) has been proposed as one of the main factors shaping the differences observed (Gowans et al. 2008). The socio-ecological model proposed by Gowans et al. (2008), envisaged that when resources are predictable in space and time (e.g. complex inshore environments), dolphins may show strong site fidelity and form small communities with small home ranges. Furthermore, associations among females are predicted to be loose and they may also form associations with individuals in similar reproductive condition. Males in these environments are predicted to form social bonds for competing with other males for access to females. Some inshore bottlenose populations (*Tursiops* sp.) reflect this pattern (reviewed in Gowans et al. 2008). In contrast, when resources are not predictable (e.g. open ocean), the model predicts that dolphins should have large home ranges and form large mixed-sex groups for protection from predators and cooperative foraging. Under this scenario females are predicted to form long-term social bonds for caring for their young but males are not expected to form close associations because of the difficulties in sequestering females. Not much information is available on the social structure of pelagic dolphins, but some studies have suggested that Eastern tropical Pacific dolphins such as those from the genus *Delphinus* and *Stenella* form large groups that range over wide areas (Johnson & Norris 1994; Pryor & Kang-Shallenberger 1991). Similarly, offshore bottlenose dolphins off the California and Florida coasts appear to range widely and demonstrate few long-term associations (Defran & Weller 1999; Defran et al. 1999; Caldwell 2001). Finally, an intermediate state with medium-sized home ranges and groups is expected to occur in coastal areas (Gowans et al. 2008). The scarce information available for humpback dolphins (genus *Sousa*) fits well with these predictions. These species form small groups that range intermediate distances in search for prey forming medium sized communities. Moreover, they seem to form a few strong social bonds among themselves (Karczmarzcki 1999; Karczmarzcki et al. 1999a; b; Atkins et al. 2004). Thus, although some populations and species fit well with the model proposed by Gowans et al (2008), it is evident that the great variability of social structures observed in delphinids cannot be explained only by the influence of the factors mentioned above.

Möller (2012), subsequently included kinship, life history and phylogenetic data to make predictions for the formation of kin associations and bonding in delphinids. In contrast to the model proposed by Gowans et al. (2008), Möller (2012) predicted that in inshore environments, females may form moderate bonds with kin and non-kin, including females in similar reproductive condition, although long-term social bonds are more likely to occur among kin. Support for this component of the model comes primarily from studies of bottlenose dolphins inhabiting inshore environments (e.g. Port Stephens and Shark Bay, Australia; Möller et al. 2006; Frère et al. 2010). In contrast, in open unpredictable environments, female associations and weak bonds may occur irrespective of kinship relationships. However, moderate to strong bonds may arise in these environments if there is between-group competition or sexual conflict (e.g. resting areas for spinner dolphins, *Stenella longirostris*; reviewed in Möller 2012). For males, Möller (2012) proposed that irrespective of the ranging patterns of the individuals (inhabiting inshore or offshore environments) or kinship relationships, factors such as small sexual size dimorphism and male-biased operational sex ratio were most likely to explain the formation of social bonds and alliances. In addition, if related males of similar level of maturity (sexual and social) are available, social bonds based on kin selection may evolve (Möller 2012). This also contrasts with predictions from the socio-ecological model, which suggested that male social bonds should only be formed in inshore environments and for sequestering individual females (Gowans et al. 2008).

Within this context, Coffin Bay is characterized by a shallow complex inshore environment, where food resources and areas where there is a risk of predation are likely predictable. Abundance estimates indicate that Coffin Bay holds a high density of dolphins with similar non-calf sex ratio (Passadore et al. 2017). Moreover, males and females showed high site fidelity and similar-sized ranging patterns (Passadore et al. in review). In conjunction, the results of this thesis suggest that dolphins in Coffin Bay form small communities (approximately 70 individuals) with preferential areas of usage, and both males and females showed preferred associations in which kinship and reproductive condition (in females) played a role in partner choice. Under the two predictive scenarios discussed above, the Coffin Bay's dolphin population corresponded well with the socio-genetic predictions proposed by Möller (2012) for inshore environments, where females form moderate to strong social bonds in which kinship and reproductive condition may be important factors delineating affiliation patterns. Similarly, a high density of dolphins, possibly male-biased operational sex ratio, and no apparent sexual size dimorphism also corresponded well with the predictions suggested by Möller (2012) as important mechanisms underlying the formation of social bonds in male dolphins. However, the socio-ecological model for male associations in inshore environments (Gowans et al. 2008) also agree with the results of this thesis, suggesting that the interplay of ecological, genetic, and intrinsic factors are likely responsible for the complex and variable affiliation patterns reported for dolphin species and populations.

Limitations of the study and analytical means to overcome issues

Bottlenose dolphins are long-lived mammals that spent most of their life underwater. Thus, the main limitations of this research (as with the majority of cetacean socio-ecological research) are related to the coverage and duration of fieldwork activities, and the sample size obtained (mainly the number of sightings per individual) in our 2-year study period. Our survey design based on two non-overlapping transect routes attempted to cover all habitat types encountered in Coffin Bay during different seasons (chapter 2; for more details see Passadore et al. 2017). In addition, I used a series of analytical approaches for taking into account issues that could arise due to small sample sizes. This, in conjunction with a high degree of site fidelity demonstrated by dolphins in the study area (Passadore et al. in review), facilitated the number of recaptures obtained for each individual (population median = 11). First, I calculated whether the data set accurately described the social structure of the population using only individuals sighted on more than the median number of sightings for the population (chapter 2). This test indicated that at the sighting threshold selected, the data set had good power to detect the true social structure (chapter 2). Second, I implemented recently developed generalized affiliation indices (GAIs; Whitehead & James 2015) to control for multiple factors that are known to affect social analyses (reviewed in chapter 2). Among these factors, I included the cumulative number of sightings for each pair of individuals as a predictor of the strength of associations. Thus, I explored how the number of sightings affected the association indices between pairs of individuals. I found a positive correlation between this variable at the population level and in males, but not in females; therefore, as a precautionary approach, I controlled for this variable during the GAIs estimation at the population level and in the male only chapters. Using this approach I attempted to control for differences in the number of sightings among individuals (e.g. Farine & Strandburg-Peshkin 2015), and for avoiding biases due to small number of sightings during the estimation of affiliations. In a similar way, I controlled for other factors (e.g. range overlap, gregariousness; reviewed in chapter 2) that could also affect social analyses and distort true affiliations (e.g. Whitehead & James 2015). Thus, the application of the GAI approach likely improved my ability to detect true affiliation patterns, excluding structural noise imposed by several confounding factors.

Another limitation of socio-genetic studies on wild animals is usually related to the number of individuals included in the social and genetic analyses, especially when they do not include a considerable component of the population under study, which could lead to biased results. In this respect, at the population level, individuals considered in the social analyses (chapter 2) represented approximately 82% of the estimated marked non-calf dolphin population that inhabited Coffin Bay during the study period (Passadore et al. 2017). Similarly, the number of males and females considered in the social (males= 42; females= 55) and genetic analyses (males= 38; females= 49) (chapters 3 and 4) were close to the estimated male and female abundances for the inner area (Males 46-52; females= 52-60;

Passadore et al. 2017), suggesting that most of the non-calf population inhabiting Coffin Bay at that time was included in the analyses reported here.

Future research directions

This study suggests that social relationships at population level and affiliation patterns among same-sex individuals are likely shaped by synergistic effects of ecological, genetic and intrinsic factors. However, the range of questions that could be answered about dolphin socio-ecological systems could be significantly enhanced by conducting a long-term photo-identification program of this population, and combining with ecological research on prey-predator interactions. To better understand the factors delineating and maintaining the social structuring of this population, studies on prey assemblages, dolphin feeding strategies and diet are needed to test the hypothesis about feeding preferences and/or specialisations among individuals inhabiting different areas and belonging to the different communities, as well as for estimating predation risk. For example, focal-follows of groups of dolphins and underwater video-recording of feeding bouts could provide insights into the different foraging strategies that individuals may be using in different bays (e.g. Kiszka et al. 2014). In addition, the long-term use of BRUVS (Cappo et al. 2004) located in different bays within Coffin Bay may help to characterize differences in potential prey assemblages among the different areas. This, in conjunction with stable isotope analyses of dolphin biopsies (e.g. Owen et al. 2011; Kiszka et al. 2014) could provide vital information to test hypotheses about feeding preferences promoting social structuring in dolphins.

Additionally, to understand the influence of social factors, detailed observations of male and female interactions through focal-follows and genetic paternity analyses could help to understand the function of male and of female bonds, reproductive skew in the population, and ultimately to help define the mating system. For example, are male dolphins forming larger social groups siring more offspring as reported for *T. aduncus* in the Port Stephens' population (Wiszniewski et al. 2011)? Do home range size and location of the different male social clusters correlate with their breeding success?

In the case of females, it would be also of interest to monitor their calving success and how this relates with age, maternal experience, social network metrics, levels of affiliation with kin, and areas of usage. For example, are females with more social connections or centrality in the social network more successful at rising calves? Considering ecological conditions, are females inhabiting more productive areas achieving greater calving success?

Continuing monitoring of this population, accompanied by biopsy sampling of additional individuals, will open a large range of questions that could help better explain the complex patterns of associations observed in this study and assist in elucidating the evolution of complex mammalian social systems.

Implications for conservation and management

Bottlenose dolphins inhabiting nearshore and coastal environments may be affected by an interacting set of anthropogenic stressors, including: habitat degradation, vessel disturbance, indirect and direct interactions with commercial and recreational fisheries, and environmental contaminants (e.g. Read et al. 2006; Dungan et al. 2012; Pirotta et al. 2013; Todd et al. 2015; Culloch et al. 2016). Therefore, the long-term conservation of populations inhabiting these environments represents a substantial challenge for the implementation of conservation and management strategies (e.g. Perrin 1999; Chabanne et al. 2017). In highly mobile marine mammals, such as bottlenose dolphins, obtaining information about their social and genetic structure, and their spatial and ecological preferences are vital for the formulation of management strategies (e.g. Bearzi et al. 2009; Chabanne et al. 2017).

In this study, I have demonstrated that the inner area of Coffin Bay constitutes a stronghold for two similar-sized communities of southern Australian bottlenose dolphins, which differed in their association and ranging patterns. As mentioned previously, a community of dolphins can be defined as a set of individuals that is behaviourally discrete from neighbouring communities and within which most individuals are socially more connected among them than with the rest of the population (Wells et al. 1987; Krause & Ruxton, 2002). From a management point of view a community may represent a population unit of biological significance (Chabanne et al. 2017), and therefore must be managed accordingly as a separate entity if genetic and behavioural diversity is to be preserved (e.g. Smith et al. 2001). Moreover, population genetic studies conducted on this species along the southern Australian coast have revealed that the Coffin Bay inner area population is genetically separated from other populations of this species (Pratt et al. in review). Thus, I propose that the southern Australian bottlenose dolphin population inhabiting the inner area of Coffin Bay should be managed as a separate entity with two separate sub-functional units that range over distinct areas of the Bay. Considering also the highly enclosed nature and long residency time of the waters in Coffin Bay, particularly in Kellidie and Mt. Dutton Bays (Kämpf & Ellis 2014), I suggest that the communities inhabiting these two bays may be particularly more vulnerable to habitat degradation due to human activities. In this context, it is important to investigate and monitor the impacts of anthropogenic activities in Coffin Bay as well as the long term demography of each community to ensure the long term viability of these communities.

Currently, Coffin Bay is part of the Thorny Passage Marine Park. However, the effectiveness of this park in protecting Coffin Bay dolphins remains unknown due to the fact that no specific management strategies were directed towards the dolphins. Despite being considered a marine park, only 6.2% of Coffin Bay has been declared as Sanctuary Zones, with the rest of the park classified as General Managed Use Zones or Habitat Protection Zones, in which recreational and fishing activities are allowed (DEWNR 2012). Therefore, most of the areas used by dolphins in Coffin Bay are exposed to potential negative impacts from human activities, including oyster farms, water sports, tourism cruises, and recreational and commercial fisheries (DENR 2010; Saunders 2009). The results of this study, in conjunction with those reported by Passadore et al. (2017; in review) and Pratt et al. (in review), provides baseline information that is of vital importance for the implementation of management strategies focused on the conservation of this dolphin population. Finally, I would like to emphasise the need for a long-term monitoring program of this population to evaluate trends in abundance, potential changes in distribution and social patterns, and conflicts that may arise due to human population growth and area usage, which could negatively impact upon this socially complex dolphin population.

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