Ecology and social structure of southern Australian bottlenose dolphins (*Tursiops* sp.) along Adelaide's metropolitan coast

by

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Contents

Abstract

Little is known about the ecology and behaviour of southern Australian bottlenose dolphins (*Tursiops* sp.), which hinders informed decision-making concerning their conservation and management. This is particularly important considering their coastal distribution, which puts them under threat from a range of anthropogenic activities (Chapter 1). Here, I used boat surveys, photo identification methods and biopsy sampling to investigate the (1) site fidelity, residency and abundance (Chapter 2), (2) habitat use and distribution (Chapter 3), and (3) socio-genetic structure (Chapter 4) of southern Australian bottlenose dolphins in coastal waters of Adelaide, South Australia. Systematic boat-based surveys were conducted between December 2012 and August 2014, following predetermined zig-zag line transects. Surveys covered a total of 40 km of coastline and extended up to 7 km offshore, covering approximately 195 km^2 of Adelaide's metropolitan coastal waters. A total of 83 survey days were completed, with 244 distinctly marked individuals identified: 69 individuals (28%) were sighted only once and 175 (72%) were sighted on more than one occasion. In addition, 70 biopsy samples were obtained from individual animals. In Chapter two, I used the photo-identification data collected to estimate site fidelity, residency and abundance using agglomerative hierarchical clustering, lagged identification rates and capture-recapture models. Sighting rates and agglomerative hierarchical cluster analysis categorized individuals into specific groups of site fidelity, with 119 occasional visitors, 96 seasonal residents and 29 year-round residents. Lagged identification rates indicated that these dolphins used the study area regularly from year to year following a model of emigration and re-immigration. Abundance estimates obtained from multi-sample closed capture-recapture models ranged from 95 individuals (S.E. ± 45.20) in

winter 2013 to 239 (S.E. ± 54.91) in summer 2014. In Chapter three, I identified areas of high probability of occurrence in relation eco-geographical variables using an ensemble modelling approach that combined results from three modelling techniques (generalised linear models, generalised additive models, and maximum entropy). Seasonal variation in habitat use along the metropolitan coast appears to be influenced by water depth and benthic habitat. Further, core feeding areas of dolphins overlapped considerably with areas of high probability of occurrence. Thus, I suggest that prey availability is an important driver influencing the seasonal variation in dolphin distribution along Adelaide's metropolitan coast. In Chapter four, I use generalized affiliation indices and social network analysis to investigate social cohesion, intrapopulation community structure and potential drivers of associations between individuals. I demonstrate that individuals are subdivided into two socially and spatially segregated communities, comprising a northern shallow-water community and a southern deep-water community. Community membership also appears to be influenced by genetic relatedness, but patterns differed between females and males. While females had a significantly greater genetic relatedness within communities than between communities, this was not the case for the males and suggests that other factors may be of more importance for them. Altogether these findings suggest that southern Australian bottlenose dolphins along Adelaide's metropolitan coast exhibit fission-fusion social traits similar to other coastal bottlenose dolphin populations. I then discuss how this information can be used to inform the conservation and management of bottlenose dolphins along the coastal waters of Adelaide (Chapter 5). The varying levels of site fidelity, residency, and identification of dolphin 'hotspots', highlights the importance of Adelaide's metropolitan coast as a habitat for these dolphins. Management strategies should be implemented, to restrict frequent interactions with

recreational fishing, boating and other water activities. As these bottlenose dolphins also appear to spend considerable time outside the study area, future research, conservation and management efforts of this population must take into account anthropogenic activities within Adelaide's metropolitan coast and its adjacencies in Gulf St Vincent.

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.

Signed...

Date..

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Publications submitted during duration of candidature, permits, and funding

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Chapter 1. General Introduction

1.1. The importance of ecological and behavioural studies for conservation management

Knowledge about the ecology and behaviour of a species is fundamental for conservation, and to guide effective and informed management decisions (Caro 1998, Sutherland 1998). Ecological and behavioural studies can provide information on demography and life history traits, and an understanding of the way in which species respond to different ecological circumstances. These include environmental changes (Guisan & Zimmermann 2000, Krebs & Davies 2009), changes in prey availability or predation risk (Funston et al. 1998, Lima 1998), and anthropogenic impacts (Knowlton & Graham 2010, Sih 2013). All of these factors contribute to the survival and reproduction rates of populations and species, emphasising its importance to conservation (Caro 1998, Sutherland 1998). Hence, quantifying ecological and behavioural traits, including site fidelity, abundance, distribution, habitat use and social interactions, are important for developing appropriate management strategies for species conservation.

1.1.1. Site fidelity and abundance

Site fidelity is defined by how often individuals return to use a particular location (Switzer 1993), while abundance studies are concerned with how many individuals there are within an area, population, or species (Begon 1979). Determining the site fidelity and abundance of a species and/or their populations can be used to evaluate the extent of potential threats and assess potential risk of extinction. For example, the high site fidelity of individuals to a relatively small area may increase their risk to local

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threats (*e.g.* Warkentin & Hernández 1996, Gonzalvo et al. 2014). Alternatively, individuals that display lower levels of site fidelity may not be as readily exposed to a local threat and hence at lower risk. In this scenario, conservation efforts should target those individuals that are more susceptible to threats, which are generally those that exhibit high site fidelity. However, some individuals with low site fidelity may be at more risk to threats due to their naivety and inability to recognise and respond to potential threats (Lima & Dill 1990, Griffin et al. 2000). In terms of abundance, population size is regarded as one of the most important parameters used to define the conservation status of a species (Burgman & Lindenmayer 1998). Conservation efforts often prioritise species with smaller population sizes, as they are typically more vulnerable to disturbances, threats and environmental stochasticity (Caughley 1994, Margules & Pressey 2000). However, species with larger abundances can still be at risk from threats and overexploitation, and are often recognized as fundamental to ecosystem functioning (Gaston and Fuller 2008). Conservation efforts of non-threatened species should therefore not be disregarded (Gaston and Fuller 2008). Abundance estimates can also be quantified over temporal scales, where they can provide an understanding of population trends, and therefore increase the ability of managers to detect any significant changes (Primack 2006).

1.1.2. Habitat use

Understanding how individuals use their environment is also important for their conservation and management. Habitat use is a term used to describe correlations with specific habitat features (Bergin 1992), and can be analysed using species distribution modelling (SDM), a tool that uses a range of biotic and abiotic factors to predict species distributions (Franklin 2010). SDM provides researchers with an understanding of what may be important and influence the distribution of a species

throughout its range, and allow researchers to formulate maps of species distributions and to identify biologically important areas or critical habitats (Franklin 2010). This information is particularly important in areas of high human use, as SDM allows researchers to determine the extent of a species distribution that overlaps with human activities. Conservation efforts can then be prioritized in areas where a species may be most at risk. Advances in SDM techniques now also allow projections of species distributions into the future (Thuiller 2003, Thuiller et al. 2009), and provide a method to assess the potential impacts of environmental changes, information that is critical under the current threat of global climate change.

1.1.3. Social structure

Social structure can be described as the patterns of social interactions and relationships among individuals (Whitehead 2008). The way in which individuals form social interactions and relationships can provide fitness advantages (Silk 2007), and can influence both genetic structure (Sugg et al. 1996) and the transmission of information and diseases (Krause & Ruxton 2002, Lusseau & Newman 2004). Thus, social structure can directly influence the survival and reproductive success of individuals, which can in turn influence the long-term viability and persistence of social groups, communities or a population. Intrapopulation community structure can even provide an understanding of population responses to environmental, social and anthropogenic factors, particularly where communities are spatially segregated (Krause & Ruxton 2002). Thus, defining social structure, determining how and why individuals interact and form social relationships, is also important when designing management strategies for conservation (Sutherland 1998).

1.2. Human impacts on coastal ecosystems and inshore delphinids

Information on the ecological and behavioural characteristics of a species, such as their site fidelity, abundance, habitat use and social structure, can be used to evaluate the potential effects of human activities on species and/or populations. This is particularly important in areas largely impacted by threatening processes, such as the marine environment (Gray 1997, Soule & Orians 2001, Primack 2006). In the marine environment, no area remains unaffected by human activities (Halpern et al. 2008), which has led to its rapid deterioration, through habitat degradation, overexploitation, marine pollution and eutrophication, and exotic species introductions, all exacerbated by climate change effects (Hixon et al. 2001, Peterson & Estes 2001). In particular, coastal marine ecosystems are most vulnerable to anthropogenic activities, due to increasing human population growth and urban developments in coastal areas. This has led to the degradation and modification of at least 20% of coastal marine areas in the world (Burke et al. 2001). As a result, marine organisms that use coastal areas, including marine mammals, are at higher risk than those that do not, with all global hotspots of marine mammal species extinction risk distributed along coastlines (Davidson et al. 2012).

Among marine mammals, inshore and coastal species of delphinids are at high risk from threatening processes, including habitat degradation, pollution, tourism, boat strikes, bycatch in fisheries, and entanglements with marine debris, among others (*e.g.* Smith & Smith 1998, Jefferson et al. 2009, Stockin & Orams 2009). For example, the near shore distribution of the endemic Hector's (*Cephalorhynchus hectori hectori*) and Maui's dolphins (*C. h. maui*) throughout New Zealand puts individuals at risk of

fisheries-related mortalities, and has led to significant population declines (Hamner et al. 2012, Slooten & Davies 2012), and uncertainty about the fate of their populations and species (Currey et al. 2012). Humpback dolphins (*Sousa* spp.) are also susceptible to toxicity from pollution and entanglements in fishing nets, which is of concern considering their small population sizes and high site fidelity to relatively small areas throughout their range, making them particularly vulnerable to population declines (Karczmarski 2000, Parra et al. 2006, Cagnazzi et al. 2013). Despite this, approximately 35% of delphinid species remain data deficient (Reeves et al. 2003). Obtaining baseline information on the ecology and behaviour of delphinid populations will enhance the ability of governments and wildlife management agencies to develop appropriate conservation measures, inform policy, and to mitigate the cumulative impacts of anthropogenic activities on dolphins. Systematic research efforts have been used to inform the conservation of a number of delphinid species, including humpback dolphins (*Sousa* spp.) (Karczmarski et al. 1998, Hanf et al. 2016, Parra & Cagnazzi 2016), common dolphins (Bearzi et al. 2003), and bottlenose dolphins (*Tursiops* spp.) (Ingram & Rogan 2002, Bearzi et al. 2009, Smith et al. 2016), but are lacking for many at-risk coastal species and populations.

1.3. Study species and site

Bottlenose dolphins (*Tursiops* spp.) are cosmopolitan small to medium sized delphinids that are distributed around the entire Australian coastline (Ross & Cockcroft 1990). In southern Australia, only two species of bottlenose dolphins are present; the common bottlenose dolphin (*T. truncatus*) and an inshore coastal species (*Tursiops* sp.) (Kemper 2004). It was previously believed that the coastal species of *Tursiops* was the Indo-Pacific bottlenose dolphin (*T. aduncus*) (Kemper 2004), however recent

studies incorporating morphological and genetic evidence suggest that these animals are not *T. aduncus* and are instead the Burrunan dolphin type (*T. australis*) (Moller et al. 2008; Charlton-Robb et al. 2011). Burrunan dolphins are believed to be endemic to the inshore and coastal waters of southern Australia, including the states of Victoria, Tasmania, South Australia and possibly southern Western Australia (Möller et al. 2008, Charlton-Robb et al. 2011). The bottlenose dolphins studied in this thesis are likely to be *T. australis* due to their small body size, light colouration, small group sizes (< 30) and proximity to shore. Further, mitochondrial DNA control region sequences of all sampled dolphins clustered with *T. australis*, and not with *T. aduncus* or *T. truncatus (Chapter 4,* Appendix **Figure A1***). T. truncatus* was not observed throughout this study based on morphological differentiations (larger and more robust, with darker colouration). Furthermore, their sighting records are exclusive to deeper offshore waters. As the taxonomic status of *Tursiops* sp. in southern Australia remains under debate (Perrin et al. 2013), throughout this thesis I refer to them as the southern Australian bottlenose dolphin (*Tursiops* sp.).

Studies on southern Australian bottlenose dolphins suggest that there are two resident populations in south-east Australia, one inhabiting Port Phillip Bay, Victoria, and the other extending from Gippsland Lakes to the east coast of Tasmania (Dunn et al. 2001, Scarpaci et al. 2003, Charlton-Robb et al. 2014). These populations show year-round site fidelity (Scarpaci et al. 2000, Scarpaci et al. 2003), and are relatively small, with approximately 120 individuals estimated for Port Phillip Bay (Dunn et al. 2001), and 65 for Gippsland Lakes. This has led to the species being listed as endangered in Victoria under the Victorian Flora and Fauna Guarantee Act 1988 (Department of Sustainability and Environment 2013).

Outside of Victoria, research on southern Australian bottlenose dolphins has mainly focused on one specific region encompassing the Port River estuary and Barker Inlet (Cribb et al. 2008, Steiner & Bossley 2008), located within Gulf St Vincent (GSV), which is a large, shallow embayment situated within the central part of the South Australian coastline (Bryars et al. 2008). A resident population of approximately 30 dolphins inhabits this area year-round, but this location is also used by a large number of non-resident individuals (Steiner & Bossley 2008). The Port River estuary and Barker Inlet are located adjacent to South Australia's capital city, Adelaide, and as a result, these dolphins are situated within a highly urbanized and industrial environment. In order to mitigate potential anthropogenic threats to these dolphins, this area was proclaimed the Adelaide Dolphin Sanctuary (ADS) by the South Australian Government in 2005 (Department of Environment, Water and Natural Resources 2005). Since its establishment, studies have investigated the dolphins' reproductive parameters (Steiner & Bossley 2008), activity budgets (Steiner 2011), and habitat preferences (Cribb et al. 2008, Cribb et al. 2013). Unfortunately, these research efforts do not extend to other areas along the South Australian coast. Bottlenose dolphins do occur across the majority of GSV (Kemper et al. 2008), and have been recently found to be part of one genetic population (Pratt et al. in review). Therefore, the vast majority of this population's ecology and behaviour is largely unknown.

1.4. Threats to bottlenose dolphins along Adelaide's metropolitan coast

Bottlenose dolphins that form part of the GSV population live directly adjacent to Adelaide's metropolitan coast. Due to their close proximity to this highly urbanized

area, these dolphins are at potential risk from several anthropogenic activities, which are of further concern with a forecasted human population growth of +560,000 by the year 2040 (Department of Planning Transport and Infrastructure 2010). For example, habitat modification and degradation is of increasing concern along the Adelaide metropolitan coast due to increasing coastal developments, dredging of marinas and boat launch facilities, beach and cliff erosion, and the depletion of seagrass meadows (Edyvane 1999, Bryars 2013). The presence and condition of benthic habitats and associated invertebrate and fish species may influence the abundance, distribution, and community structure of higher level predators such as dolphins (*e.g.* Wilson et al. 1997, Rossbach & Herzing 1999, Wiszniewski et al. 2009). Dolphins may therefore be at risk from the depletion of biologically important areas, which could lead to their displacement, and/or population decline (Jefferson et al. 2009).

The Adelaide metropolitan coast, in particular, is subject to pollution discharges from power stations, treated sewage effluents, and urban storm water runoffs (Harbison 1986, Edyvane 1999). Not only do these pollutants lead to eutrophication of coastal habitats, but their toxins can also bio-accumulate. This can lead to a number of health issues, and potentially compromised immune systems in dolphins (Lavery et al. 2008, Van Bressem et al. 2009). Further, dolphins along the metropolitan coast were recently subject to an outbreak of cetacean morbillivirus (Kemper et al. 2016), with the impacts and cause for the outbreak currently unknown.

Southern Australian bottlenose dolphins are also at risk of interactions with humans, with reports of individual dolphins being intentionally shot in the region (Kemper et al. 2005). In addition, dolphins are at risk of human interactions through dolphin-targeted tourism efforts. Interactions with dolphin tourism boats have been found to cause short

and long-term behavioural impacts on southern Australian bottlenose dolphins, including in GSV (Peters et al. 2012, Filby et al. 2014). Currently in Adelaide, two tour operators are licensed to conduct dolphin swim-with tours. Research onboard one vessel has found that Adelaide's metropolitan dolphins elicit short-term behavioural responses to the boats' presence, where dolphins spend more time milling, and less time feeding, travelling and socialising (Peters et al. 2012). Unfortunately, the long-term impacts of this tourism vessel on dolphins are currently unknown.

Increases in the use of recreational boats and fishing activities along the metropolitan coast also raise concerns for the dolphins that inhabit this area. Dolphins are at risk of direct contact with recreational boats (Byard et al. 2013), while their fishing gear can cause injury or mortality through entanglements and/or ingestion (Kemper et al. 2005). A recent study has suggested that southern Australian bottlenose dolphins are likely to be most sensitive to boat disturbances when along the metropolitan coast in comparison to other coastal areas within South Australia (Cribb & Seuront 2016). Despite this, and other potential threats, dolphin management strategies along the metropolitan coast are limited to restrictions on vessel and swimmer approach distances, but with no systematic law enforcement. The lack of information regarding the site fidelity, abundance, habitat use and social structure of this species along the Adelaide metropolitan coast hinders the implementation of informed management strategies, and highlights the need for systematic research efforts.

1.5. Methodologies

Natural markings have long been used across a range of taxa for behavioural and capture-recapture studies. Photo-identification is a technique that uses these natural markings to identify individuals, for example using nose scars in sea otters (Gilkinson et al. 2007), spot patterns on cheetahs (Kelly 2001), and tail fluke markings on humpback whales (Rasmussen et al 2007). For photo-identification of dolphins, nicks and notches in the trailing edge of the dorsal fin are predominantly used, however these can be accompanied by secondary markings such as scars and peduncle marks (Urian et al. 2015).

Photo-identification methods are advantageous as they are non-invasive, and can provide information on home ranges, residency and group structure, as well as provide estimates for population parameters such as abundance and survival. However, there are biases associated with photo-identification data, therefore this methodology requires that certain assumptions are met (Urian et al. 2015). For example, when collecting photo identification data, it is assumed that individual marks are retained and identified correctly, and that capture probabilities are homogeneous. However, the probability of recognising animals is also affected by the image quality, as poor or blurry images can mask an individual's markings and lead to misidentifications. To overcome these issues, photo-identification images are required to be of a sufficient quality, and individuals themselves are required to meet a certain level of distinctiveness (see Section 2.3.2 for more details). This approach ensures that marks of distinguishable individuals and any changes occurring to them over time can be tracked and correctly identified, which minimizes misidentification and heterogeneity in capture probabilities, for example. This methodology was implemented throughout this research.

1.6. Research aims

The overall aim of this thesis is to provide baseline information on the ecology and social structure of southern Australian bottlenose dolphins along Adelaide's metropolitan coast, South Australia. To achieve this aim, three specific objectives are addressed within three main research chapters (2-4):

Objective 1: Investigate the site fidelity, residency and abundance of southern Australian bottlenose dolphins along Adelaide's metropolitan coast.

In Chapter 2, I use dolphin sighting rates and agglomerative hierarchical cluster analysis to categorize individuals into specific groups of site fidelity. Lagged identification rates are used to determine how often dolphins use the study area, while seasonal abundance estimates are obtained from multi-sample closed capture-recapture models.

Objective 2: Investigate habitat use patterns and identify areas of ecological significance for southern Australian bottlenose dolphins along Adelaide's metropolitan coast.

In Chapter 3, I investigate the importance of specific environmental variables for dolphin distribution, and use an ensemble modelling approach to identify areas of high probability of dolphin occurrence. Further, kernel density estimation is used to identify core and representative areas by dolphin behaviour, and to investigate the importance and potential ecological function of areas of high dolphin occurrence.

Objective 3: Determine association patterns and intra-population community structure, and the potential influences of sex and genetic relatedness on the social

structure of southern Australian bottlenose dolphins along Adelaide's metropolitan coast.

In Chapter 4, I use generalised affiliation indices, social network analysis, ranging patterns and genetic analysis to investigate population level and sex specific association patterns, define intra-population community structure, and assess the potential influence of environmental, social and genetic factors on bottlenose dolphin community structure along Adelaide's metropolitan coastal waters.

Lastly, in Chapter 5, I summarise the main findings, and provide an overview of the ecology and behaviour of southern Australian bottlenose dolphins along Adelaide's metropolitan coast. I also discuss how the information from the three previous chapters can be used to inform the conservation and management of southern Australian bottlenose dolphins along Adelaide's metropolitan coastal waters, and provide avenues for future research.

For contributions of my supervisors and other researchers to each data chapter, please refer to 'Publications submitted during duration of candidature, permits, and funding' on page 13 of this thesis.

Chapter 2. Site fidelity, residency, and abundance of bottlenose dolphins (*Tursiops* sp.) along Adelaide's metropolitan coast

The following chapter has been removed due to copyright restrictions. The corresponding publication can be found using the following link: https://doi.org/10.1111/mms.12335

Chapter 3. Habitat use and distribution of southern Australian bottlenose dolphin (*Tursiops* sp.) along Adelaide's metropolitan coast

3.1. Abstract

Modelling dolphin distribution is key for understanding their ecology and for their conservation and management. Information on the distribution and preferred habitats of southern Australian bottlenose dolphins (*Tursiops* sp.) is lacking, particularly along metropolitan areas where the species is under threat from a range of anthropogenic activities. Here I use boat-based surveys and an ensemble modelling approach that combined results from three modelling techniques (generalised linear models, generalised additive models, and maximum entropy) to identify areas of high probability of southern Australian bottlenose dolphin occurrence along the metropolitan coast of Adelaide, South Australia. Furthermore, I used kernel density estimation to identify core and representative areas by dolphin behaviour and investigate the importance and potential ecological function of areas of high dolphin occurrence. The ensemble predictions of dolphin distribution performed better than their corresponding single models and I advocate its use for cetacean distribution modelling. Results indicate that water depth and benthic habitat type influenced dolphin occurrence along Adelaide's metropolitan coast. Dolphins favoured shallow, near shore areas and temperate reefs in summer; shallow, near shore areas in autumn; and deep waters further offshore in winter. Core feeding areas overlapped considerably with areas of high probability of dolphin occurrence. Thus, I suggest that prey availability is an important driver influencing the seasonal variation in dolphin

distribution along Adelaide's metropolitan coast. These predictions identify areas of high priority for dolphin conservation and the implementation of boating and fishing regulations. Continued monitoring is needed to assess potential changes in preferred habitat under increasing anthropogenic pressures.

3.2. Introduction

The need to identify critical habitats and priority conservation areas for coastal marine mammals has accelerated dramatically in recent times due to an increase in human activities in coastal areas (Halpern et al. 2008, Bulleri & Chapman 2010). These have resulted in a wide variety of anthropogenic threats to dolphins, particularly for populations that live in close proximity to urbanised cities (Jefferson et al. 2009, Pirotta et al. 2013, Pirotta et al. 2015). As urbanisation increases along the world's coastlines, identifying areas that are biologically important for coastal dolphins has become increasingly important as a tool to manage and mitigate cumulative impacts of anthropogenic activities (Ashe et al. 2010, Hoyt 2011). However, one of the challenges in identifying such areas is the lack of understanding of species distribution, preferred habitats, and the importance and ecological function of these areas (Salm et al. 2000, Hoyt 2011).

Understanding species-environment relationships is at the core of identifying areas of biological importance, and to prioritize areas for conservation, zoning design, impact assessment and resource management decisions (Guisan & Thuiller 2005, Elith & Leathwick 2009). Numerous studies have identified preferred habitats by linking dolphin presence to a variety of abiotic and biotic factors over various spatial and temporal scales (reviewed in Cribb et al. 2015). Species distribution models (SDMs) have been used widely to model species distributions (Guisan & Zimmermann 2000,

Elith & Leathwick 2009) and are increasingly being used to predict dolphin distribution and suitable habitats (de Boer et al. 2014, Ferro de Godoy et al. 2015, Marini et al. 2015). However, due to the wide array of methods, data types and modelling algorithms available, there are discrepancies among outputs of single-model techniques, and the best performing models tend to vary across studies and species (Guisan & Zimmermann 2000, Elith & Graham 2009, Marmion et al. 2009, Thuiller et al. 2009). One method to overcome these variations is to combine single-model predictions through a process known as ensemble modelling (Araújo and New 2007, Franklin 2010). Ensemble modelling often provides more robust estimates of species distributions because the combined model predictions yield higher accuracy and less bias than separate single models (Marmion et al. 2009, Grenouillet et al. 2011). While ensemble modelling has been previously employed for some marine species (*e.g.* Riul et al. 2013, Pikesley et al. 2015), to my knowledge it is yet to be used widely to model dolphin distribution (but see Moura et al. 2012, Pérez-Jorge et al. 2015).

Bottlenose dolphins (*Tursiops* sp.) are found throughout coastal waters of southern Australia (Bilgmann et al. 2007b, Möller et al. 2008, Charlton-Robb et al. 2014). This bottlenose dolphin may represent a new species endemic to southern Australia (*Tursiops australis*, Charlton-Robb et al. 2011), but its taxonomy status remains under debate (Perrin et al. 2013), and thus I refer to them here as the southern Australian bottlenose dolphin (*Tursiops* sp.). The coastal distribution of southern Australian bottlenose dolphins puts them at risk from a range of threatening processes. These threats include dolphin targeted tourism (Peters et al. 2012, Filby et al. 2014), interactions with fishing boats and gear (Byard et al. 2013), entanglements with marine debris (Kemper et al. 2005), habitat loss and degradation (Edyvane 1999), pollution (Lavery et al. 2008, Monk et al. 2014), and intentional killings (Kemper et al. 2008),

among others. The cumulative impact of anthropogenic threats over time can lead to the displacement of dolphins from an area and/or population decline (*e.g.* Lusseau 2005, Watson-Capps & Mann 2005, Bejder et al. 2006). This highlights the need to identify bottlenose dolphin preferred habitats along the southern Australian coast, particularly in areas where threats concentrate, such as South Australia's capital city, Adelaide.

Information on preferred southern Australian bottlenose dolphin habitat is lacking with studies limited to estuarine and tidal inlets of the Port River estuary and Barker Inlet in Adelaide, South Australia (Cribb et al. 2008, Cribb et al. 2013). This semi-enclosed, sheltered area is characterized mostly by shallow water, and likely provides important habitat for a small number of about 70 southern Australian bottlenose dolphins (Kemper et al. 2008, Steiner & Bossley 2008). Dolphins within this area show year-round preference for bare sand habitat, however, seagrass preference increased during summer and autumn and could be indicative of a seasonal pattern in habitat preference (Cribb et al. 2013). Water properties (*e.g.* temperature and water depth) had no significant influence on dolphin presence within this area, and Cribb et al. (2008) instead proposed an influence of prey movement on dolphin distribution. Currently, it is unknown whether seasonal habitat preferences or the influence of ecogeographical variables on bottlenose dolphins extends to Adelaide's coastal areas beyond the Port River and Barker Inlet. In contrast to the Port River, adjacent areas are characterised by an open coastal habitat in the large Gulf St Vincent (GSV), consisting of deeper waters (up to 40 m in depth) and additional habitat types. Given the differences in habitat characteristics, dolphins along Adelaide's metropolitan coast may use these areas in a different manner. A relatively high number of dolphins (244 individuals) were photo-identified within Adelaide's metropolitan coast, and the

presence of year-round and seasonal residents within this area suggests that at least some areas are important for this species, and likely provide preferred habitat (Zanardo et al. 2016).

The aims of this study were to 1) quantitatively assess the relationships between southern Australian bottlenose dolphin occurrence and ecogeographical variables along Adelaide's metropolitan coast; 2) identify their preferred habitat, and 3) investigate potential behavioural processes that may influence their distributions. Here, I identify preferred habitat as areas of high probability of dolphin occurrence, which reflects their distribution across space and time (Hastie et al. 2004). I use ensemble modelling to identify areas of high probability of dolphin occurrence through a consensus-modelling framework, and investigate whether this distribution changes across the austral seasons. To investigate the importance and potential ecological function of these preferred habitats I also calculate the percentage of core and representative behavioural ranges that overlap with areas of high dolphin probability of occurrence. The results highlight important habitats for southern Australian bottlenose dolphins along Adelaide's metropolitan coast, and the usefulness of ensemble modelling approaches in defining these areas. The information obtained in this study also enhances our general understanding about habitat selection in bottlenose dolphins. Further, it provides a robust baseline to guide the conservation and management of southern Australian bottlenose dolphins along this highly urbanised Australian coast.

3.3. Materials and methods

3.3.1. Study site and data collection

The study site is located within GSV, a relatively shallow and large inverse estuary in the central region of southern Australia's temperate coastline (Figure 1). The study area covered approximately 195 km^2 of the metropolitan coastal waters of Adelaide, including 40 km of the coast, extending up to 7 km offshore and reaching maximum depths of 25 m. Benthic habitat types within the study area include seagrass beds, temperate reefs and bare sand (Bryars 2003).
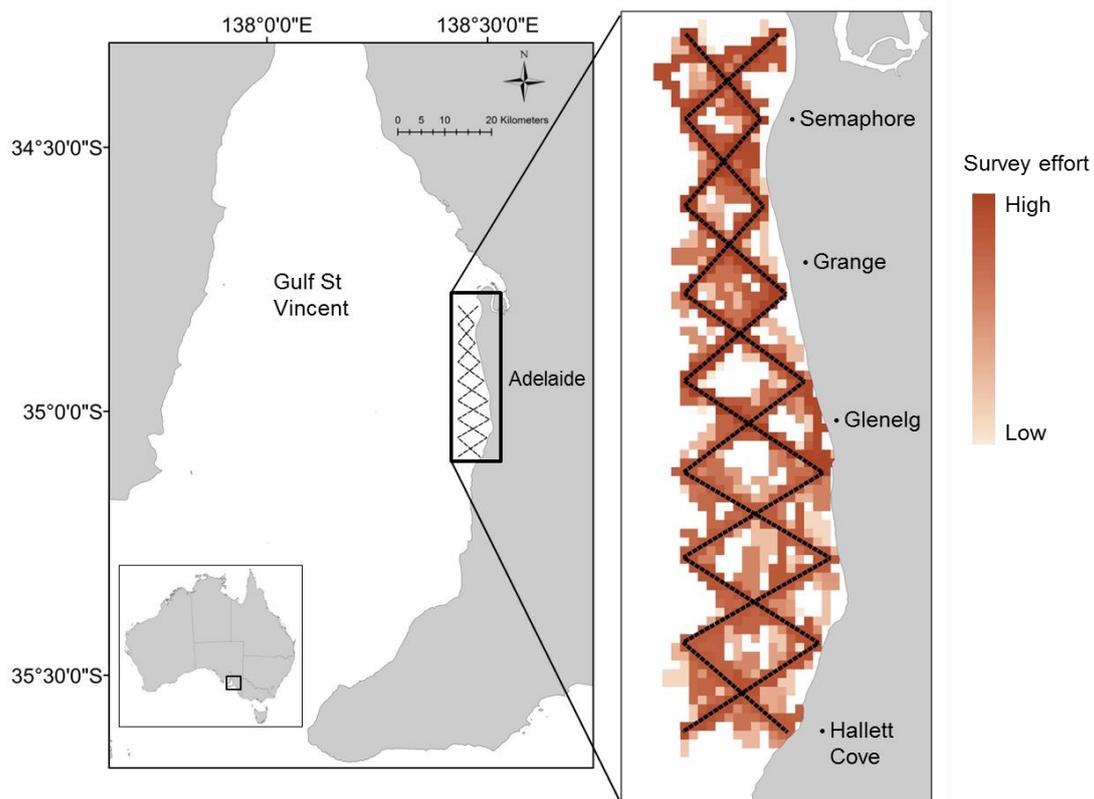
Figure 1. Study area along Adelaide's metropolitan coast, South Australia. Boat survey transects are located along the dashed line and survey effort is represented by the coloured shading.

Boat-based surveys were conducted between December 2012 and August 2014, in Beaufort sea state < 3 and swell < 1 m. No surveys were carried out in spring (September to November) due to generally poor weather conditions during this time of year. Surveys followed a predetermined zig-zag line transect layout (*ca.* 100 km) at speeds of approximately 13-17 km/hr. Observations of dolphins were made by 3-5 trained observers by naked eye and with the aid of 7x50 Fujinon binoculars. Dolphins were defined as part of the same group if they were within a 100 m radius of each other, and heading in the same direction if travelling (Irvine et al. 1981). Once a dolphin group was sighted, survey effort was ceased and the dolphins were approached to a distance of approximately 30 m to record data on location (using a hand-held Global Positioning System), time, group size, age composition (following Zanardo et al. 2016). Predominant behaviour was recorded as travelling, feeding, socialising, milling or resting (modified from Shane et al. 1986, see Appendix Table A1 for definitions). These data were recorded every 5 minutes thereafter or when there was a change in group behaviour, size and/or composition.

3.3.2. Ecogeographical predictor variables

Ecogeographical variables used to model dolphin distribution included benthic habitat type (*i.e.* seagrass beds, temperate reefs and bare sand), water depth and bathymetric slope. These variables represent proxies for other variables (*e.g.* prey availability/abundance), which are expected to influence bottlenose dolphin distribution (see Ingram & Rogan 2002). Sea surface temperature and salinity were not included in the analysis as predictor variables due to low spatial variation and resolution across the study site. Benthic habitat type and water depth data were obtained from the Nature Maps database of the South Australian Government (Department of Environment, Water and Natural Resources, available at

https://data.environment.sa.gov.au/NatureMaps/Pages/default.aspx). At present, there is no benthic habitat data available for 9% of the study area, therefore these areas (and dolphin sightings within) were excluded from analysis and masked out from presence-absence maps. I used ArcMap 10.2.2 (ESRI, Redlands, USA) to calculate bathymetric slope from bathymetric grids using the Spatial Analyst extension.

All ecogeographical variables were sampled to a 100 x 100 m resolution within ArcMap, to ensure that all grids were small enough to adequately detail ecogeographical variables across the study area and yet to be large enough to incorporate a sufficient number of presence data. Collinearity (correlation between ecogeographical variables) was investigated using Pearson's correlation coefficient (r) for all combinations of variables in R v3.1.1 (R Core Team 2014). Variables were considered correlated if $r > 0.5$.

3.3.3. Presence-absence response variables

The response variable used for species distribution modelling was the presence-absence of dolphin groups or single animals. The locations of dolphins obtained while on transect were imported into ArcMap and binary presence-absence maps were prepared for each Austral season (summer, autumn and winter) taking into account survey coverage. Survey coverage was quantified by mapping the total number of on-effort survey tracks and adding a 250 m buffer (average distance to which dolphins could be reliably observed from the boat) on either side of the tracks. Each 100 x 100 m grid within the area of survey coverage was classified as either 1 (dolphin presence) or 0 (dolphin absence). Grids were also characterised by the mean of each ecogeographical predictor variable, and land adjacent to the survey area was masked from presence-absence maps.

Dolphin presence was defined by any group or individual animal sighted whilst on survey effort. Data on species true absence, however, are difficult to obtain, particularly for mobile and wide-ranging species (Mackenzie & Royle 2005). False absences occur when a species is considered absent from a particular area, when it may in fact occur in that area. Occurrences of false absences may be due to sampling design, observer effort, and/or species detection probability (*i.e.* dolphins may be underwater and unavailable for detection) (Gu & Swihart 2004, Barbet-Massin et al. 2010). Failure to detect a species can lead to biased models and thus do not provide a true estimate of species distributions (Gu & Swihart 2004). To reduce false absences, I selected absence cells based on areas of the highest survey effort (Phillips et al. 2009). Survey effort within the area of survey coverage was quantified for each Austral season sampled by calculating the length of on-effort survey tracks within each 100 x 100 m grid cell (Macleod 2013) and ordered from highest to lowest effort. Cells with the highest survey effort and no dolphin presence for each season were selected as absence cells and were thus areas most likely to represent true absences. The number of absence cells selected for each season was the same as the number of presence cells.

3.3.4. Ensemble species distribution modelling

To investigate the distribution and preferred habitats of southern Australian bottlenose dolphins along Adelaide's metropolitan coast, I used generalised linear models (GLMs), generalised additive models (GAMs) and maximum entropy (MaxEnt) modelling algorithms. GLMs and GAMs are presence-absence modelling approaches that are non-parametric and are able to describe non-linear relationships (Hastie & Tibshirani 1990, Franklin 2010), while MaxEnt is a presence-only modelling approach that models species distributions on presence locations only (Phillips et al. 2004,

Phillips et al. 2006). These modelling algorithms perform well as SDMs (Guisan et al. 2002, Phillips et al. 2006, Franklin 2010), and provide a comparison between two dissimilar (presence-absence and presence-only) modelling approaches.

GLM, GAM and MaxEnt modelling algorithms were implemented within the Biomod2 package in R v.3.1.1 (Thuiller et al. 2009). SDMs were constructed separately for summer, autumn and winter seasons using a binomial error distribution and the logit link function. I implemented a 10-fold cross-validation method and a data split of 75/25 percent for respective model calibration and testing (Thuiller et al. 2009). The importance of the ecogeographical variables was calculated using a randomisation procedure in Biomod2 based on 10 permutation runs (Thuiller et al. 2009). This method is independent of the modelling technique, and thus provides a direct comparison between models. The procedure calculates the correlation between the standard predictions (*i.e.* fitted values) and predictions where one variable has been randomly permutated. High correlation (little difference between two predictions) indicates that the variable is not important in the model, and conversely, a low correlation indicates that the variable is important. Variables are ranked from zero to one according to the mean correlation coefficient; the variable with the highest ranking has the most influence on the model, while a value of zero assumes no influence of that variable (Thuiller et al. 2009).

SDMs based on presence absence data may lead to commission and omission errors (Guisan and Thuiller 2005, Franklin 2010). Commission errors arise when models predict species occurrence in areas where the species does not occur (false positives), while omission errors fail to predict species occurrence in areas where the species does occur (false negatives) (Guisan and Thuiller 2005). Such errors may be costly

particularly when trying to delineate critical species habitat; for example, it could be expensive to protect habitat that is not important (Franklin 2010). To evaluate SDM performance, prediction accuracy, and compare modelling methods, I used the area under the curve (AUC) metric of the receiver operating characteristics plot calculated in Biomod2. AUC is a threshold-independent measure of the ratio between the observed presence/absence values and model predictions (Fielding & Bell 1997). Values of AUC range from 0 to 1; values above 0.5 indicate that the model predictions perform better than random, and values below 0.5 indicate that the model predictions were no better than what would be expected by chance.

I then combined all three modelling approaches to generate an ensemble prediction of dolphin presence across the study area for each season (Thuiller et al. 2009). Single SDMs were weighted based on their predictive accuracy (the higher the evaluation score, the more weight given to the model) (Marmion et al. 2009); only models with AUC values above 0.5 were used to create the ensemble models. Ensemble models were then used to provide a visual output of probability of species occurrence, where values range from 0 to 1, indicating lowest to highest probability of occurrence, respectively. To include spatial context in the ensemble models, I employed a post-hoc method that recalculates the model output for each location based on the surrounding geographical area (Ashcroft et al. 2012). This method considers the amount and quality of habitat in neighbouring areas and is suitable for modelling processes that do not currently have an inbuilt mechanism that consider spatial context (*e.g.* Biomod2) (Ashcroft et al. 2012). Finally, I used AUC values to test whether the final ensemble models performed better than their corresponding single models (Marmion et al. 2009).

3.3.5. Behavioural use of preferred areas

Apart from identifying preferred habitat, understanding behaviourally (foraging adaptations, reproduction, intra-interspecific interactions) and environmentally meditated processes (prey concentration, behaviour and life history) that influence marine mammal distributions can further our understanding of the ecology of marine mammals, and improve our ability to inform conservation management (Palacios et al. 2013). However, most studies on marine mammal habitat modelling are based on correlative analyses of observed species−environment associations, and the integration of behaviour and environmental processes remains a challenge (Redfern et al. 2006, Palacios et al. 2013).

I investigated the importance and potential ecological function of areas of high dolphin presence using dolphin location and behavioural data. I used chi-square tests to assess if behaviour varied across seasons, and used kernel density estimates (Worton 1989) to identify core areas of use according to behaviour and season. To ensure a reliable representation of kernel density estimates, I restricted analysis to feeding and travelling behaviours. Socialising had to be excluded due to a small number of sightings across seasons, while milling was excluded because it is considered a transitional behaviour (Constantine et al. 2004). Kernel density estimates were calculated using the 'kernel interpolation with barriers tool' available within the Geostatistical analyst toolbox in ArcMap (following methods described in MacLeod 2014). I then extracted kernel ranges of 50% and 95% probability of occurrence (following MacLeod 2014) for feeding and travelling behaviours for each season. Kernel ranges of 50% were considered core areas of use, and 95% kernel ranges considered representative ranges (Worton 1989). Finally, to assess if behaviour may be driving patterns found in the ensemble models of dolphin presence, I calculated the

percentages of the core areas and representative ranges that overlapped with areas > 0.5 probability of occurrence (extracted from the ensemble model) for each season.

3.4. Results

3.4.1. Survey effort

A total of 83 survey days were completed (approximately 545 hours of survey effort, covering a distance of approximately 8,134 km) between December 2012 and August 2014. Survey effort varied between seasons due to restrictions from weather conditions (Table 1). Over the survey period I encountered a total of 345 dolphin groups, with numbers varying across seasons (Table 1).

Table 1. Number of survey days, number of dolphin groups encountered and number of dolphin presences used by season to model southern Australian bottlenose dolphin distribution along the Adelaide metropolitan coast between December 2012 and August 2014.

	Summer	Autumn	Winter
Total number of surveys	28	36	19
Number of dolphin groups	101	162	82
Number of dolphin presences	85	145	75

3.4.2. Presence-absence of dolphins across seasons

I found no collinearity between ecogeographical variables ($r < 0.5$ for all combinations of variables), and therefore SDMs were run with all variables. The AUC for single SDMs indicated that most models performed better than random with variation between seasons: AUC for summer SDMs ranged from 0.51 to 0.77, AUC for autumn

SDMs ranged from 0.45 to 0.77, while AUC for winter SDMs ranged from 0.44 to 0.69 (Figure 2). Ensemble models generally performed better than the single SDMs (Figure 2).
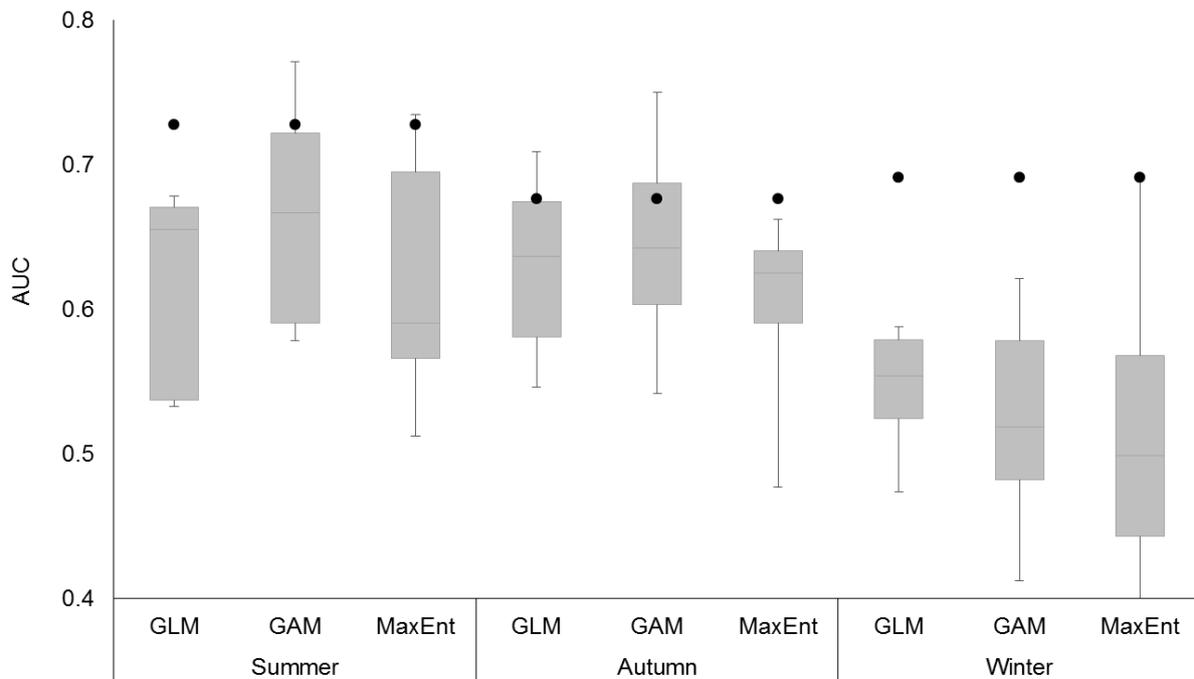
Figure 2. Box-whisker plots illustrating the differences in model accuracy (area under the curve (AUC) of the receiver operating characteristics plot) between the 10 cross-validation runs of each single species distribution model (box-whisker plot) and ensemble models (black dot) across seasons (summer, autumn and winter). GLM (generalised linear model), GAM (generalised additive model), MaxEnt (maximum entropy). AUC values above 0.5 indicate that the model predictions perform better than random.

During summer, the most influential variable for both GLM and MaxEnt were benthic habitat type (Table 2). The response curve from the GLM indicated that temperate reefs (low profile reef, macroalgae) and bare sand were important for predicting dolphin presence (Appendix **Figure A2**a). However, response curves from MaxEnt indicated that macroalgae was the most important habitat, followed by low profile reef and bare sand. The most influential variable for the GAM was water depth (Table 2),

and indicated a preference for a range of water depths (4 m, 12 m; Appendix **Figure A2**a). Using these data, the summer ensemble model predicted dolphin presence to occur predominantly over temperate reef habitat types and in shallow water depths, with a high probability of dolphin presence within the southern metropolitan waters (Figure 3).
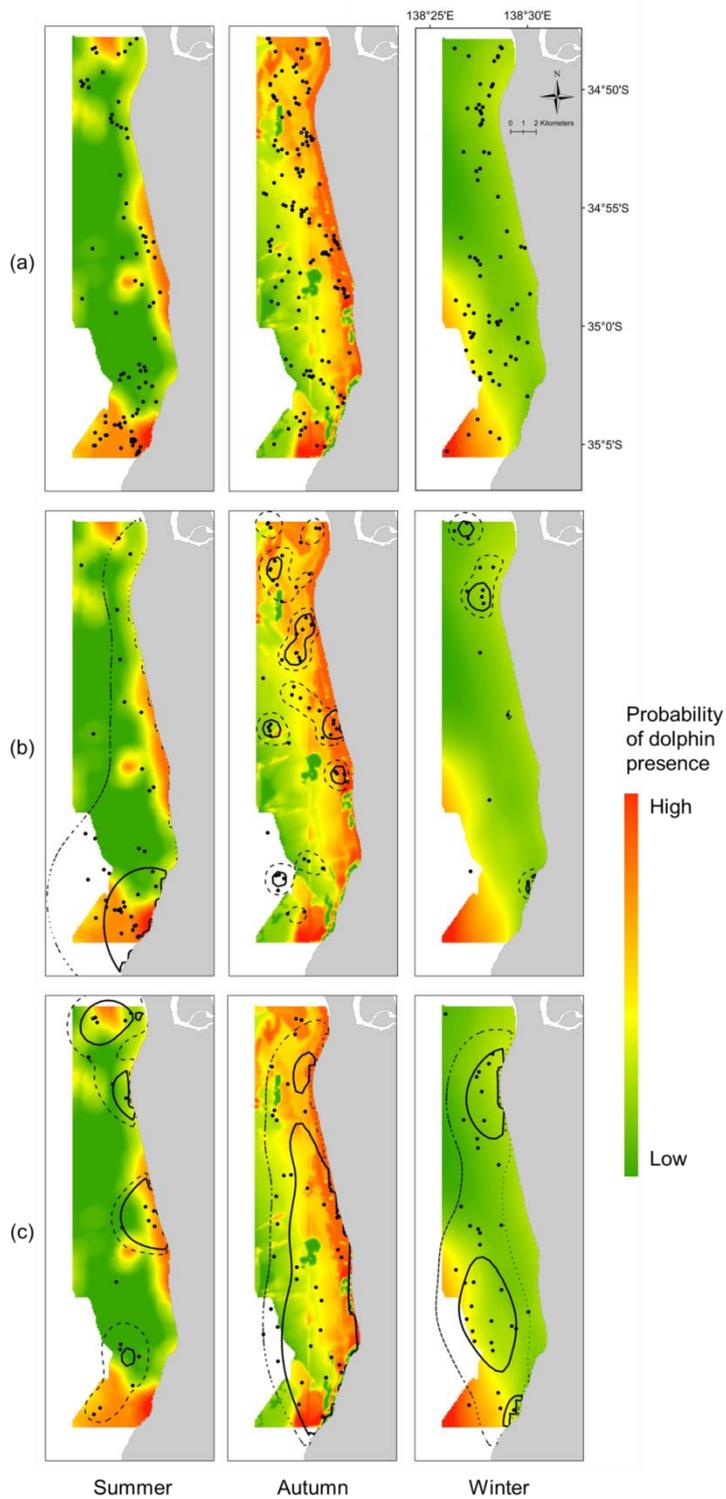
Figure 3. (a) Ensemble models of southern Australian bottlenose dolphin probability of occurrence along Adelaide's metropolitan coast during summer (December-February), autumn (March-May) and winter (June-August). Probability of dolphin occurrence is represented by the coloured shading. Solid black dots represent the location of dolphin sightings used to build the models. (b) Overlap of core areas of use (50% kernel range, solid black line) and representative range (95% kernel range, dashed

line) of dolphin feeding groups with the seasonal probability of dolphin occurrence. Solid black dots represent the locations of dolphin groups engaged in feeding behaviour. (c) Overlap of core areas of use (50% kernel range, solid black line) and representative range (95% kernel range, dashed line) of travelling groups with the seasonal probability of dolphin occurrence. Solid black dots represent the locations of dolphin engaged in travelling behaviour.

During autumn, water depth was the most influential variable for all three single SDMs (Table 2). Each model predicted a higher probability of occurrence in shallow waters (< 5m), and the probability of occurrence decreased progressively with deeper water depths (Appendix **Figure A2**b). In agreement with these single SDMs, the autumn ensemble model predicted a high probability of dolphin presence in shallow waters (Figure 3). As the probability of occurrence decreased with water depth, dolphin distribution appears to extend to a larger area of the metropolitan coast when compared to the summer ensemble model.

During winter, the most influential variable for all models was water depth (Table 2). However, in contrast to the autumn models, response curves of the winter SDMs indicated that deeper water depths (> 15 m) were more important in predicting dolphin distribution (Appendix **Figure A2**c). The winter ensemble model therefore predicted a higher probability of dolphin presence in deeper offshore waters of the study area (Figure 3).

Table 2. Importance of ecogeographical variables for southern Australian bottlenose dolphins along Adelaide's metropolitan coast over summer, autumn and winter, using three modelling algorithms: generalised linear model (GLM), generalised additive model (GAM), and maximum entropy (MaxEnt). Ecogeographical variables of greatest influence are in bold.

Variable Importance	Summer			Autumn			Winter		
	GLM	GAM	MaxEnt	GLM	GAM	MaxEnt	GLM	GAM	MaxEnt
Water depth	0.061	**0.428**	0.332	**0.858**	**0.711**	**0.553**	**0.635**	**0.414**	**0.621**
Benthic habitat	**0.710**	0.366	**0.513**	0.110	0.319	0.144	0.322	0.358	0.115
Slope	0.209	0.199	0.454	0.144	0.153	0.364	0.023	0.251	0.430

3.4.3. Behavioural use of preferred areas of occurrence across seasons

The most frequently observed behaviours were feeding, milling and travelling (respectively comprising 108, 98 and 91 groups, Figure 4). Resting was observed only once. Dolphin feeding and travelling behaviours varied significantly between seasons (feeding $x^2 = 13.23$, d.f. = 2, $p = 0.001$; travelling $x^2 = 12.11$, d.f. = 2, $p = 0.002$). Feeding groups were most predominant throughout summer and autumn, while travelling groups were most predominant throughout winter (Figure 4). Milling and socialising behaviours did not vary significantly between seasons (milling $x^2 = 3.88$, d.f. = 2, $p = 0.14$; socialising $x^2 = 2.64$, d.f. = 2, $p = 0.27$).
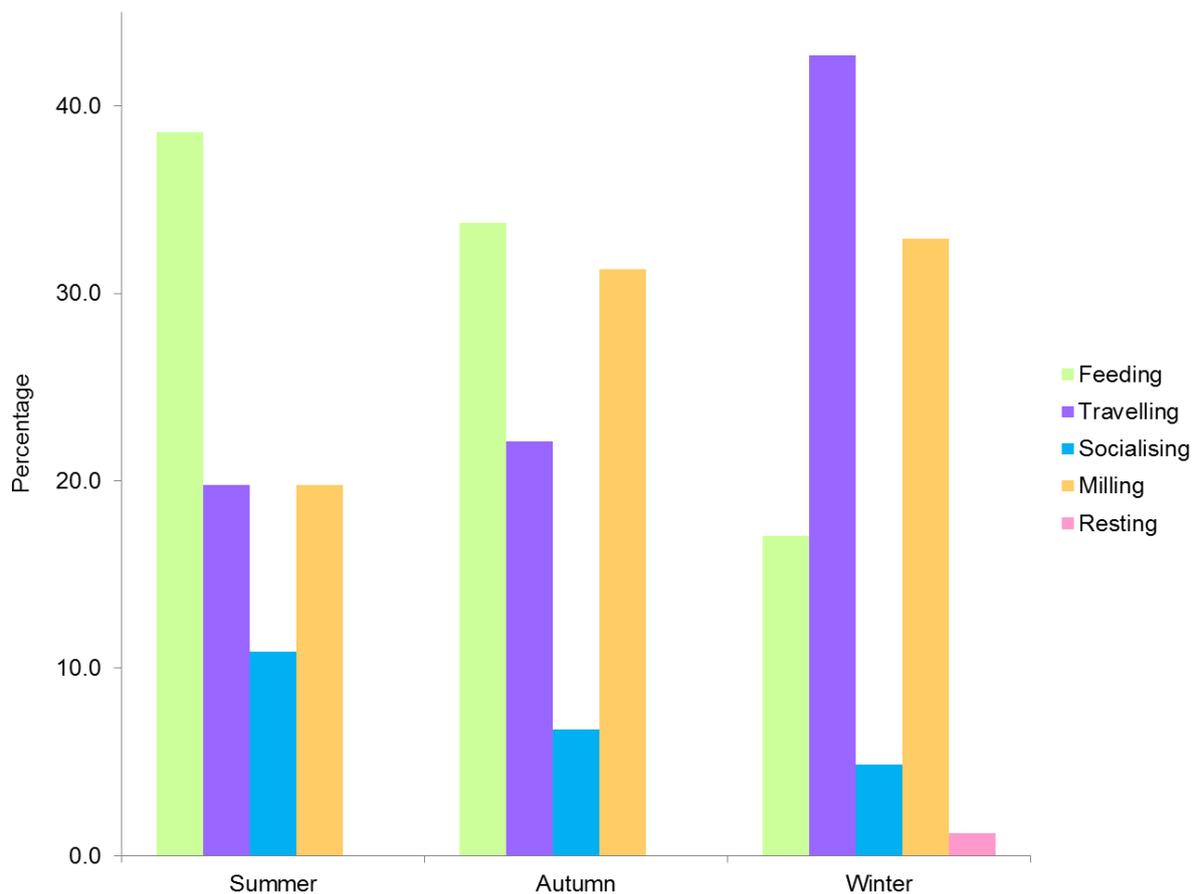
Figure 4. Seasonal number of groups according to predominant behavioural activity of southern Australian bottlenose dolphins along Adelaide's metropolitan coast between December 2012 and August 2014.

The percentages of core areas (50% kernel range) and representative ranges (95% kernel range) that overlapped with areas of high probability of dolphin occurrence are summarised in Table 3 and Figure 3. During summer and autumn, a larger percentage of core feeding areas overlapped with areas of high dolphin probability of occurrence (54% and 83%, respectively) in comparison to core travelling areas (42% and 55%, respectively, Table 3). During winter, a larger percentage of core and representative travelling ranges overlapped with areas of high dolphin probability of occurrence (56% and 36%, respectively) in comparison to core and representative feeding areas (7% and 17%, respectively, Table 3, Figure 3). These results suggest that areas of high probability of dolphin occurrence are predominantly used for feeding.

Table 3. Percentages of core (50% kernel range) and representative (95% kernel range) behavioural ranges that overlapped with areas of high probability of occurrence of southern Australian bottlenose dolphins across seasons along Adelaide's metropolitan coast.

	Feeding		Travelling	
	Kde50	Kde95	Kde50	Kde95
Summer	54	22	42	31
Autumn	83	62	55	48
Winter	7	17	56	36

3.5. Discussion

Modelling species–environment relationships can provide important insights into the ecological processes determining species distribution, with significant implications for conservation and management. Here, I show that the Adelaide metropolitan coast

provides important habitat for southern Australian bottlenose dolphins, with animals using particular areas preferentially on a seasonal basis. The ensemble model results indicated that water depth and benthic habitat type were the most important predictors of dolphin distribution, however, the relative influence of these variables changed across seasons. Overlap of core feeding areas with areas of high dolphin probability of occurrence suggests that foraging behaviour, and therefore prey distribution and availability, are likely key drivers of dolphin presence along Adelaide's metropolitan coast. Further, the results demonstrate the effectiveness of ensemble modelling approaches in reducing the predictive uncertainty of single-model techniques.

3.5.1. Ecogeographical predictors of dolphin distribution

Dolphins along Adelaide's metropolitan coast appear to favour shallower, near shore areas in both summer and autumn, and prefer deeper areas further offshore in winter. Similar seasonal variations in dolphin distribution and habitat preferences have been reported for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in Bunbury, Western Australia, and Hector's dolphins (*Cephalorhynchus hectori*) in New Zealand, and were suggested to be associated with changes in prey availability (Rayment et al. 2010, Sprogis 2015).

Previous studies on bottlenose dolphins in South Australia have suggested that the distribution patterns of dolphins in the Port River estuary and Barker Inlet in GSV were a response to prey movements (Cribb et al. 2013). In this study, core feeding areas overlapped significantly with predicted areas of high dolphin presence, suggesting that prey movements may have an impact on dolphin distribution, particularly during summer and autumn. Southern calamari (or squid, *Sepioteuthis australis*) are a predominant prey item of bottlenose dolphins in South Australia, followed by various

species of both demersal and pelagic fish (Gibbs et al. 2011). Throughout summer, numbers of squid and small fish (*e.g.* whiting (*Sillaginodes punctatus*), western Australian salmon (*Arripis truttaceus*), trevally (*Pseudocaranx* spp.), garfish (*Hyporhamphus melanochir*) and yellow-eyed mullet (*Aldrichetta forsteri*)) peak within the temperate reef habitats of the southern metropolitan coast and Fleurieu Peninsula (McGlennon & Kinloch 1997, Triantafillos 2002, Bryars 2003, Steer et al. 2007). The large congregation of prey items in reef habitats, is concurrent with the core summer feeding area, and suggests the importance of this benthic habitat type for Adelaide's bottlenose dolphins during summer.

During autumn, the summer congregations of squid and fish species tend to disseminate. Spawning squid aggregations travel northwards to the upper regions of the gulf (Triantafillos 2002), while garfish and yellow-eyed mullet are generally found within the shallow metropolitan waters, and salmon move sporadically throughout the metropolitan coast (McGlennon & Kinloch 1997, Jones et al. 2002). The diffusion of prey species along the coast during autumn may explain the more widespread distribution and habitat preference of dolphins during this season and their concentration of feeding and travelling behaviours over more than one area.

In winter, the higher probability of dolphin presence in areas further from the coast, together with the significant decrease in feeding behaviour, is likely the result of prey dispersion outside the metropolitan area. During this time, near shore waters become colder and exposed to increased water turbidity from stormwater (Kaempf 2006, McDowell & Pfennig 2013). Consequently, fewer numbers of squid are present along the metropolitan coast (Triantafillos 2002, Steer et al. 2007), and a number of fish species disperse to deeper waters and/or move to areas in southern GSV (*e.g.* garfish

and King George whiting) (McGlennon & Kinloch 1997, Jones et al. 2002, Fowler and Jones 2008). Smaller numbers of dolphins along the metropolitan coast during winter (Zanardo et al. 2016), and the higher number of observed travelling behaviours support potential movements of individuals to deeper offshore areas. Overall, I hypothesize that prey availability is a key driver of dolphin distribution along Adelaide's metropolitan coast. I recommend that futures studies investigate diet and feeding ecology of southern Australian bottlenose dolphins within GSV, to better elucidate the influence of prey on dolphin distribution, behaviour and preferred habitats.

Prey availability may also interact with other synergistic factors, including predation risk (Heithaus & Dill 2002, Hastie et al. 2004) and water temperature (Bräger et al. 2003), which may also influence seasonal variations in dolphin distribution and preferred habitat. White sharks (*Carcharodon carcharias*) are a known predator of dolphins in South Australia (Bruce 1992). Sightings of white sharks occur more frequently over spring and summer, with greater numbers observed in northern GSV and fewer along the metropolitan coast (Huveneers & Drew 2014, Huveneers et al. 2014). Typically dolphins avoid predatory sharks (Heithaus 2001); for example *T. aduncus* in Shark Bay, Western Australia, avoid foraging in shallow waters when predation risk is high, and only return to these areas when shark numbers are lower (Heithaus & Dill 2002). Thus, in summer, southern Australian bottlenose dolphins may move to shallower waters closer to shore to lower predation risk. Conversely, in winter, when shark observations are not as frequent in GSV, dolphins may be able to use areas further offshore due to a lower risk of white shark predation.

Sea surface temperature also correlates with the distribution of a number of cetacean species (see Bräger et al. 2003). Observations of dolphin populations across seasons

have documented fewer sightings, or a change in distribution and habitat use during colder winter months (Barco et al. 1999, Maze and Wursig 1999, Chilvers et al. 2003). Colder water temperatures may influence individuals directly through thermoregulation and energetic demands; for example, when temperatures move below 20°C, dolphins require a higher energetic intake to build blubber stores (Ross and Cockcroft 1990). Alternatively, indirect influences of cold temperatures may result from effects of temperatures on the distribution of prey and predators (discussed above) (Scott et al. 1990, Barco et al. 1999). Within GSV, highest temperatures (~25°C) occur towards the end of summer, and lowest temperatures (~12°C) occur towards the end of winter (Kaempf 2006). During these winter months, sea surface temperatures are colder along near-shore shallow areas than within the middle of the Gulf (Kaempf 2006). Dolphins along the Adelaide metropolitan coast may make use of the warmer middle waters during winter as a means to reduce the need for high energetic demands and/or to follow the distribution of their prey.

3.5.2. Effectiveness of ensemble modelling approaches

The results from this study support the effectiveness of ensemble modelling approaches in reducing the predictive uncertainty of single-models. I found some discrepancies in the importance of ecogeographical variables between single SDMs, and I was able to overcome these issues using ensemble modelling. Model improvements are typically higher for species with smaller ranges along geographical or environmental gradients (Grenouillet et al. 2011). Hence, dolphin preference for a restricted range of ecogeographical variables during winter (deeper waters) may explain the higher improvement of the winter ensemble model. I encourage the use of ensemble modelling for future studies assessing cetacean distribution and habitat use as this method can be used to provide a more robust representation of preferred

habitats, which is essential to implement strategies for species conservation and management.

3.5.3. Implications for conservation management

Coastal dolphins living in close proximity to urbanised cities are at risk from anthropogenic threats from increasing activities and developments (Jefferson et al. 2009). Such anthropogenic pressures are known to affect dolphin behaviour and distribution (Heithaus & Dill 2002, Lusseau 2005, Bejder et al. 2006). In the Adelaide metropolitan coast and adjacent areas, anthropogenic activities intensify throughout summer, with increased numbers of recreational fishing, boating, and other water activities (*i.e.* kayaking, jet skiing), as well as an increase in dolphin swim-with tourism. This peak in anthropogenic activities coincides with the largest estimates of dolphin abundance along the metropolitan coast (Zanardo et al. 2016). The combination of increased anthropogenic activities and larger dolphin numbers puts individuals at increased risk from these threats. Of particular concern during summer is the southern metropolitan area, where anthropogenic activities are likely to overlap with this seasonal 'hotspot' of dolphin occurrence, and potentially cause disturbances. For example, tourism boats that use the area altered the short-term behaviour of dolphins and led dolphins to spend more time milling, and less time feeding, travelling and socialising (Peters et al. 2012).

Our study indicates that the southern metropolitan waters are a predominant feeding area in summer. Furthermore, most socialising behaviours, including mating and newborn calves, were observed throughout summer (Figure 4). Therefore, the increased occurrence of tourism and recreational boats within the southern metropolitan area over summer may have a negative impact on dolphin feeding and

socialising, including reproductive behaviours. Disturbances to foraging behaviour may result in the dolphins' inability to meet nutritional requirements, while disturbances to mating and mothers with newborn calves may affect the reproductive rates of a dolphin population (Lusseau 2004). In the long term, this has been shown elsewhere to lead to population declines and/or displacement of dolphins from important habitat areas (Lusseau 2005, Watson-Capps & Mann 2005, Bejder et al. 2006).

Currently, the management of on-water anthropogenic activities on coastal dolphins in South Australia is limited to restrictions on vessel and swimmer approach distances. Additional management strategies included the establishment of the Adelaide Dolphin Sanctuary (ADS) within the Port River estuary and Barker Inlet (Department of Environment, Water and Natural Resources 2005). Management strategies within the ADS include the monitoring of dolphins through land and water surveys, vessel speed restrictions and engagement with the community to reduce marine debris and inhibit dolphin provisioning. Unfortunately, these management strategies do not extend to other areas of the South Australian coast, leaving the vast majority of the urban coast under-regulated. Threats to southern Australian bottlenose dolphins are likely to increase in the future, with proposed coastal developments (Department of Planning, Transport and Infrastructure 2010) and plans to establish additional boat-based marine and dolphin tourism experiences in South Australia (National Parks South Australia 2016). This highlights the need to implement additional management strategies for dolphins along the South Australian coast, particularly Adelaide's metropolitan coast.

Based on the results from this study, I recommend that seasonal management strategies within Adelaide's metropolitan coast be considered. I recommend that

macroalgae reef habitats in the southern metropolitan area, which were defined as the core summer feeding area for the dolphins, be protected during summer months. Specifically, recreational and tourism boats should be restricted from this area throughout summer to decrease dolphin-boat interactions, limit disruptions and provide protection within this important dolphin feeding habitat, and potential mating and calving area. Fishing limitations within the area could also enhance fish assemblages in the reef habitat and thus continue to provide an adequate food source for metropolitan dolphins over the long term. Additionally, in autumn when dolphin distribution is more widespread, I recommend the implementation of boat speed restrictions along the metropolitan coast. Due to their preference for shallow waters during autumn, speed restrictions should be implemented within areas less than 2 km from shore to mitigate dolphin-boat interactions. These seasonal restrictions should be implemented until additional information is obtained about the long-term impacts of dolphin-boat interactions in South Australia. Hence, continued monitoring is needed to investigate the potential impacts of boat presence and fishing effort on dolphins within Adelaide's metropolitan coast, and to assess the implications of these on the dolphin population considering the increase in anthropogenic pressures as well as future global climatic changes.

3.6. Acknowledgements

Chapter 4. Socio-genetic structure of southern Australian bottlenose dolphins (*Tursiops* sp.) along Adelaide's metropolitan coast

4.1. Abstract

Defining intrapopulation community variation among group living mammals can provide an understanding of population responses to environmental, social, and anthropogenic factors. Here, I use generalized affiliation indices and social network analysis to investigate social cohesion and intrapopulation community structure in southern Australian bottlenose dolphins (*Tursiops* sp.) inhabiting Adelaide's metropolitan coast, South Australia. I further use genetic data from known individuals to investigate potential correlates of sex and genetic relatedness on associations and community structure. Generalised affiliation indices indicated that southern Australian bottlenose dolphins do not associate at random but have preferred associates, particularly among females. Based on these association patterns, the population was divided into two socially and spatially segregated communities; a northern shallow-water community and a southern deep-water community. Social network metrics were similar between the two communities and temporal stability of associations was both characterized by rapid disassociations and casual acquaintances, indicative of a fission-fusion system. Genetic relatedness analysis indicated that dolphins, particularly females, were on average more related within than between communities. I suggest that the social and spatial segregation of these two dolphin communities likely arose due to a combination of ecological and social factors. Increased survey efforts within and beyond the study area are now needed to define the boundaries of

these dolphin communities, and to further elucidate drivers of the differential social structures.

4.2. Introduction

The formation of groups is common in a variety of animals, including reptiles (Duffield & Bull 2002), fish (Balshine et al. 2001), birds (Covas & Griesser 2007) and mammals (Silk 2007). In mammals, a combination of ecological and social factors, demography, and life history traits underpin group living (Kappeler et al. 2013). These animals are more likely to form groups when the benefits of being in a group outweigh the costs (Krause & Ruxton 2002). Benefits of group living may include increased foraging efficiency and protection from predators, while costs may include increased competition for food resources and space, vulnerability to predator detection, and increased exposure to infections (Rubenstein & Wrangham 1986, Krause & Ruxton 2002). Within groups, the social interactions and relationships among individuals can provide fitness advantages (Silk 2007), influence genetic structure (Sugg et al. 1996), and the transmission of information and diseases (Krause & Ruxton 2002, Lusseau & Newman 2004). Where individuals associate with kin, they may also benefit from inclusive fitness gains (Hamilton 1964). Thus, social structure can influence survival and reproductive success of individuals, and hence population persistence. Defining social structure, determining how and why individuals interact in groups and form social relationships, is therefore important when designing management strategies for conservation (*e.g.* Smith et al. 2016).

The formation of social groups will not only differ between species, but also differ between populations of a species, based on the extent of ecological and social influences (Clutton-Brock & Harvey 1978). Similarly, heterogeneous environments

within population boundaries may promote intrapopulation group structure, or community structure. Communities are groups or clusters of individuals that interact more frequently among themselves than with the rest of the population (Girvan & Newman 2002, Krause & Ruxton 2002, Leskovec et al. 2009). The formation of communities is common among mammals, such as in primates (Goodall 1986), sheep (Coulson et al. 1999), kangaroos (Best et al. 2013), elephants (Wittemyer et al. 2005), and dolphins (Wiszniewski et al. 2009). Communities typically arise when individuals display site fidelity to an area, which can provide opportunities for social interactions and relationships to develop among individuals (Hinde 1976, Ramos-Fernández et al. 2006, Wolf & Trillmich 2007). Ecological factors that may influence community structure include the surrounding environment and its complexity, resource availability and dispersion, predation risk, and interspecific competition (Blumstein 2012). For example, in Soay sheep (*Ovis aries* L.), community formation is influenced by habitat heterogeneity and the quality of food resources (Coulson et al. 1999). This is more likely to lead to spatially segregated communities that range over specific habitats (Coulson et al. 1999, Wolf et al. 2007, Mourier et al. 2012). However, communities may develop independent of environmental factors. Social factors that may influence community structure include homophily and or philopatry, where preferred associations can arise among individuals of the same sex, behavioural attributes and similar reproductive states (Hinde 1976). Individuals may also preferentially associate with closely related individuals, or unrelated individuals, depending on the role of kin selection. Social preferences may develop irrespective of spatial separation; for example, eastern grey kangaroos (*Macropus giganteus*) show strong social preferences with an influence of genetic relatedness within communities, despite significant community overlap (Best et al. 2013). Additionally, anthropogenic factors

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may indirectly influence community structure, particularly when human activities elicit changes to resource availability and other environmental factors (Blumstein 2012). For example, a change in food availability and distribution by trawling efforts may have led to the formation of two discrete Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) communities occupying the same area in Moreton Bay, Australia (Chilvers & Corkeron 2001). Once trawling efforts were reduced in the area, these dolphins began to form stronger associations between communities, which resulted in these individuals overtime becoming part of only one community (Ansmann et al. 2012).

Currently, there is a limited understanding of intrapopulation community variation among mammals. Defining communities can provide an understanding of population responses to environmental, social and anthropogenic factors, and provide a greater understanding of the evolutionary processes that affect social structure (Krause & Ruxton 2002). Intrapopulation community structure can potentially cause communities to exhibit small scale demographic differences (*i.e.* survival/birth rates) based on their environmental and/or social preferences (Sutherland 1996, Coulson et al. 1999), highlighting its applicability to conservation management. Therefore, there is a need for studies to focus on intrapopulation community structure. For example, community based approaches have been used to compare features of the distribution and abundance of primates, leading to conservation priorities (Ganzhorn 1999). Intrapopulation community variation can be readily assessed with social network analysis (SNA), which has become a powerful tool to investigate social structure and define communities at a range of spatial and temporal scales (Farine & Whitehead 2015), including for giraffes (VanderWaal et al. 2014), bats (Chaverri 2010), marsupials (Best et al. 2013), and odontocetes (Titcomb et al. 2015).

Odontocetes live in a wide variety of social structures from matrilineal societies in orcas (*Orcinus orca*) and pilot whales (*Globicephala melas*), to stratified social organisations in Risso's dolphins (*Grampus griseus*), and fission-fusion societies in Hector's dolphins (*Cephalorhynchus hectori*), Indo-Pacific humpback dolphins (*Sousa chinensis*) and bottlenose dolphins (*Tursiops* spp.) (reviewed in Möller 2012). The fluid fission-fusion societies of bottlenose dolphins make them a complex and interesting group to evaluate inter and intrapopulation community variation. Communities of *T. aduncus* and *T. truncatus* appear to be influenced by habitat (Rossbach & Herzing 1999, Lusseau et al. 2006, Urian et al. 2009), or are thought to result from a combination of ecological and social preferences (Chilvers & Corkeron 2001, Wiszniewski et al. 2009, Louis et al. 2015). Currently, there is no information on the community structure or overal social structure of a third putative species of bottlenose dolphin, the Burrunan dolphin (*T. australis*), likely endemic to coastal waters of southern Australia (Charlton-Robb et al. 2011). As the validity of this species is currently in debate (Perrin et al. 2013), I refer to them here as southern Australian bottlenose dolphins (*Tursiops* sp.).

Southern Australian bottlenose dolphins inhabit Gulf St Vincent, South Australia, where they form part of one genetic population (Pratt et al. in review). Study efforts have concentrated along the Adelaide metropolitan coast, where some individuals show high site fidelity (Zanardo et al. 2016). However, sightings of photo-identified individuals are known to occur in adjacent coastal areas (personal observations), therefore individual ranges may extend to the central and western parts of Gulf St Vincent. Seasonal variation in habitat use along the metropolitan coast appears to be influenced by water depth and benthic habitat (Chapter 3; Zanardo et al. 2017).

However, prey availability is also likely to be an important driver influencing their seasonal distribution and movement patterns (Chapter 3; Zanardo et al. 2017).

In this study I use newly developed generalised affiliation indices (Whitehead & James 2015), SNA, ranging patterns and genetic analysis to investigate population level and sex specific association patterns, define intra-population community structure, and assess the potential influence of environmental, social and genetic factors on community structure. Overall, I expected the social structure of southern Australian bottlenose dolphins to be representative of a fission-fusion society and resemble those of other coastal bottlenose dolphin populations and species. The high site fidelity of many individual dolphins along Adelaide's metropolitan coast (Zanardo et al. 2016) could also favour preferred associations, the formation of communities, and opportunities to associate with kin. As this is a relatively open coastline, community structure could not be facilitated by physical barriers, so communities may arise due to changes in habitat type and/or social preferences.

4.3. Materials and methods

4.3.1. Study site and data collection

Boat-based, photo-identification surveys were conducted between December 2012 and August 2014 along the Adelaide metropolitan coast, in eastern Gulf St Vincent (GSV), a relatively shallow and large inverse estuary in South Australia. Surveys followed predetermined zig-zag line transects, covering approximately 195 km^2 of the metropolitan coastal waters. Bottlenose dolphins (hereafter dolphins) were defined as part of the same group, if they were within a 100 m radius of each other, and heading in the same direction if travelling (Irvine et al. 1981). Once a dolphin group was sighted,

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they were approached to a distance of approximately 30 m to record data on location (using a hand-held Global Positioning System), time, group size (minimum, best, maximum), and age composition (following Zanardo et al. 2016). Photographs of dolphins were categorised (excellent, good or poor) based on the focus, contrast, angle and size of the dorsal fin in relation to the photo frame (Urian et al. 1999). Dolphins were then identified based on the unique and natural marks on their dorsal fins (Würsig & Jefferson 1990) and given a measure of distinctiveness. Only excellent and good quality images of distinguishable individuals were used to identify individuals (Würsig & Jefferson 1990, Read et al. 2003). For further details of survey design and photo-identification methods see Zanardo et al. (2016).

Biopsy samples of adult animals were collected remotely using the PAXARMS biopsy system (Krützen et al. 2002) or a hand-held biopsy pole for bow-riding dolphins (Bilgmann et al. 2007a). Individuals were recognised at the time of sampling through photo identification to avoid re-sampling. Biopsy samples were preserved in 20% dimethyl sulphoxide (DMSO) saturated with NaCl (Amos & Hoelzel 1991) or 90% ethanol, and later transferred to a -80°C freezer.

4.3.2. Genetic analysis

DNA was extracted from samples using a standard salting-out protocol (Sunnucks & Hales 1996). The sex of individuals was genetically determined by amplifying fragments of the ZFX and SRY genes using the polymerase chain reaction (PCR) (conditions as reported in Möller et al. 2001). Females were also identified *in situ* based on the presence of a calf within < 1 body length of an adult individual (the presumed mother) on more than three separate sightings of the same individual. Males were identified *in situ* by visual observation of the genitalia.

Individuals were genotyped at 11 polymorphic cetacean microsatellite loci: eight tetranucleotides (Tur4_80, Tur4_87, Tur4_91, Tur4_105, Tur4_111, Tur4_141, Tur4_142, Tur4_E12 (Nater et al. 2009)), and three dinucleotides (MK9 (Krützen et al. 2001), TexVet5, (Rooney et al. 1999), and EV37 (Valsecchi & Amos 1996)). PCR conditions were as reported in Pratt et al. (in review). I used MICRO-CHECKER v 2.2.3 (Van Oosterhout et al. 2004) to test for genotyping errors, presence of null alleles, stutter peaks and/or allelic dropout. Tests for departures from Hardy-Weinberg equilibrium and for linkage disequilibrium were conducted in GENEPOP v 4.2 (Raymond & Rousset 1995) based on a Markov chain method with 1,000 iterations. Bonferroni correction was applied to adjust significance levels for multiple comparisons (Holm 1979).

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

To confirm that all sampled individuals were of the southern Australian bottlenose dolphin type, we compared the sequence of a fragment of the mitochondrial DNA (mtDNA) control region (see Pratt et al. (in review) for more details and methods) to *T. australis, T. aduncus* and *T. truncatus* sequences available in the GenBank database. Phylogenetic analysis showed that the sequences of all sampled dolphins used in this study clustered with *T. australis*, and not with *T. aduncus* or *T. truncatus* (data not shown).

4.3.3. Defining associations

Associations were defined by group membership (Whitehead 2008), where dolphins defined as part of the same group were assumed associated. If an individual or group were sighted more than once during a survey, only the first sighting was included in the analysis. I further restricted analysis to groups where a minimum of 50% of individuals were identified, based on the visually estimated group size. The amount of time two individuals are associated can be a result of their true affiliation and preference for one another, but may also be driven by other structural factors such as spatial and/or temporal overlap in habitat use patterns and gregariousness (Whitehead and James 2015). Generalised affiliation indices (GAIs) is a new approach that assesses the existence and strength of true affiliations while controlling for structural factors, which can potentially lead to biased indices of association (Whitehead and James 2015). GAIs are calculated by means of a generalised linear model, where association indices are the dependent variable, and the potential predictors of association are the structural predictor variables (*e.g.* home range overlap, gregariousness, sex) (Whitehead 2015, Whitehead & James 2015). I used program SOCPROG v 2.6 (Whitehead 2009, Whitehead 2015) to estimate GAIs of dolphins in metropolitan Adelaide, including gregariousness and home range overlap as the structural predictor variables.

Sex and genetic relatedness were not considered structural predictor variables as these are variables known to affect individual affiliations in delphinids (reviewed in Möller 2011) and are of interest for testing in this study. Gregariousness was calculated within SOCPROG following Whitehead and James (2015). Areas of home range overlap between pairs of individuals were calculated in the adehabitatHR package (Calenge 2006) in R v 3.2.3 (R Core Team 2014), following the kernel-based

utilization distribution overlap index method (Fieberg et al. 2005). This provides a single measure of overlap of the 95% utilization distribution (UD) between pairs of individuals. Values range from zero (no overlap) to one (uniformly distributed and 100% overlap), but they can be >1 if both UDs are non-uniformly distributed and have a high degree of overlap. As a minimum of five sightings are required to calculate areas of home range overlap, I restricted all GAI analysis to only individuals sighted five or more times. To test which structural variables significantly influenced associations, I carried out a multiple regression quadratic assignment procedure (MRQAP) test for each predictor variable, and calculated standardized partial correlation coefficients within SOCPROG. Structural variables with a non-significant correlation were removed, while variables with a significant correlation were retained and taking into account when calculating GAIs (Whitehead and James 2015).

4.3.4. Population level and sex specific associations

I estimated mean GAI and the standard deviation of the observed associations for all individuals and by sex, and used permutation tests (Bejder et al. 1998, modified by Whitehead et al. 2005; Whitehead 2008) to assess whether individuals associate randomly or have preferred/avoided associates. To account for demographic effects (births, deaths, migration), I permuted groups within sampling periods (1 survey day) (Whitehead 2008). I ran multiple tests, increasing the number of permutations until the p-value stabilized (Bejder et al. 1998), in this case 2,000. Individuals were identified as having preferred or avoided associations when the standard deviation of the observed associations is significantly higher than the randomly permuted dataset (Whitehead 2009). I also ran permutation tests to test for a significant difference in the average genetic relatedness between pairs of females, males, and opposite-sex (see methods below).

4.3.5. Social and spatial segregation of communities

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

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

4.3.6. Community level association patterns

To examine potential differences in the association patterns between communities identified in the previous analysis, I used three different approaches implemented in

SOCPROG: (1) association indices and tests for preferred/avoided associations, (2) network metrics, and (3) lagged association rates. Firstly, I estimated mean GAI and ran permutation tests to assess preferred/avoided associations (see methods above) within and between communities. Second, I calculated four network metrics: strength (measure of gregariousness, the sum of an individual's association indices), eigenvector centrality (sum of an individual and its neighbours' centralities), clustering coefficient (measure of associations of an individual's neighbours), and affinity (measure of how well an individual's associates are themselves associated) (Whitehead 2008). These network metrics were compared to the expected values if individuals had no association preferences, using 1,000 permutations (Lusseau et al. 2008). I also assessed whether these network measures significantly differed between identified communities using randomisation tests in PopTools v 3.2 (Hood 2011). Third, the temporal stability of associations within and between communities was assessed using lagged association rates (LARs) (Whitehead 1995). LARs are the probability that if two individuals are associated within a given time, they will still be associating some time lag later. The LAR for each community was compared to the null association rate, which is the expected value if there are no preferred associations over time (Whitehead 1995). Standard errors were obtained using the jackknife procedure. I fitted eight exponential models of temporal stability to the observed LAR data, and used the quasi-Akaike information criterion (QAIC), which corrects for overdispersion, to select the best fit model (Whitehead 2007).

4.3.7. Genetic relatedness and sib-ship relationships within and between communities

To determine the best estimator for quantifying genetic relatedness, I simulated a dataset with known allele frequencies in COANCESTRY v. 1.0.1.5 (Wang 2011). The

triadic likelihood estimator (Wang 2007) provided the highest correlation with the true values (Wang 2011) (data not shown) and was therefore used to estimate pairwise relatedness between individuals. Genetic analyses were only carried out for those individuals used in the association analysis (*i.e.* sighted ≥ five times). I tested whether the average relatedness of individuals within communities was significantly higher than between communities, and tested for a difference in the average relatedness of same sex pairs within and between communities. Permutation tests were carried out in COANCESTRY, with 10,000 bootstraps. Furthermore, I inferred kinship relationships using pairwise likelihood methods in COLONY v 2.0 (Jones & Wang 2010), and tested for a difference in the proportion of sib-ship relationships (full-sib, half-sib, non-sib) within and between communities using a randomization test of independence.

4.4. Results

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

4.4.1. Population level and sex specific associations

MRQAP tests indicated a significant correlation of associations with gregariousness ($r = 0.426$, $p < 0.001$) and home range overlap ($r = 0.181$, $p < 0.001$), and therefore both structural variables were retained and used to calculate GAIs. The mean GAI for all individuals sighted ≥ 5 times was -0.278 (± 0.962). A significantly higher standard

deviation of the observed associations compared to random indicated preferred and avoided associations among these individuals (observed S.D. = 0.084, random S.D. = 0.073, $p < 0.001$).

When analyses were carried out within and between the sexes, the mean GAI was highest amongst females (-0.135 ± 1.102) than amongst males (-0.440 ± 1.161) and between-sex associations (-0.328 ± 0.917). I found evidence for preferred/avoided associations amongst females (observed S.D. = 0.090, random S.D. = 0.081, $p < 0.001$), while marginally non-significant results were obtained for males (observed S.D. = 0.105, random S.D. = 0.099, $p = 0.069$) and between-sex associations (observed S.D. = 0.071, random S.D. = 0.069, $p = 0.052$). Overall, the mean genetic relatedness between females (R = 0.081) was significantly higher than between males (R = 0.051) ($p < 0.05$).

4.4.2. Social and spatial segregation of communities

When constructing the network of associations, the modularity index was maximised when individuals were clustered into two communities (Q maxima = 0.36, Figure 5a). Core and representative kernel ranges indicated that members of the same community had similar geographical ranges, with no overlap in their core ranges and little spatial overlap (9%) between the representative ranges of both communities. This geographical separation between communities appears to coincide with differences in depth ranges in the north and south of the study area, at a depth of approximately 9 m. As GSV is a relatively shallow gulf (maximum depth of 37 m), I classed the communities as 'northern shallow-water' and 'southern deep-water' (Figure 5b). The northern shallow-water community (NSWC) consisted of 57 individuals (including 18

females and 9 males), while the southern deep-water community (SDWC) consisted of 70 individuals (including 15 females and 8 males).
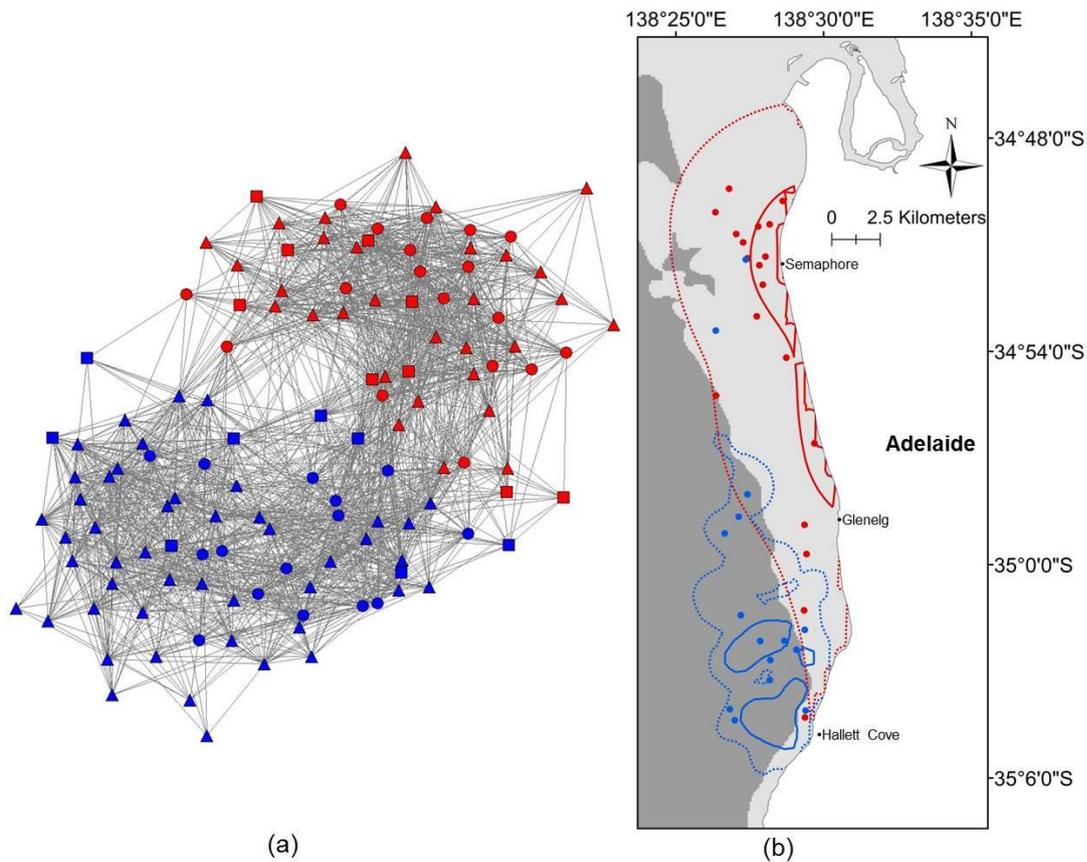
Figure 5. (a) Social network of southern Australian bottlenose dolphins along Adelaide's metropolitan coast. Each individual is represented by a node, and associations are represented by the grey lines. Only individuals sighted five or more times were included. Node colours denote community (red = northern shallow-water community, blue = southern deep-water community), while node shapes denote sex (female = circle, males = square, unknown sex = triangle). (b) Ranges of two communities of southern Australian bottlenose dolphins along Adelaide's metropolitan coast, South Australia. Contours represent 50% core kernel range (solid contour line), 95% representative kernel range (dashed contour line). Red and blue colourations correspond to the northern shallow-water and southern deep-water communities, respectively. Grey shading represents the 9 m depth contour (light grey ≤ 9 m, dark grey ≥ 9 m).

4.4.3. Community level association patterns

Within communities, the mean GAI was highest for the NSWC (0.16 ± 1.30) than for the SDWC (-0.05 ± 1.05). Results indicated that preferred and avoided associations were present within and between communities (NSWC: observed S.D. = 0.013, random S.D. = 0.105, $p < 0.001$; SDWC: observed S.D. = 0.102, random S.D. = 0.096, $p = 0.001$; NSWC-SDWC: observed S.D. = 0.044, random S.D. = 0.042, $p < 0.05$). As expected, there was a larger proportion of preferred associations within communities (NSWC: preferred = 0.085, avoided = 0.019; SDWC: preferred = 0.042, avoided = 0.005) than between communities (preferred = 0.003; avoided = 0.007).

4.4.4. Community level network metrics

For the NSWC all four network measures showed no significant differences from random (Table 1). For the SDWC eigenvector centrality was significantly lower than expected by chance ($p < 0.001$, Table 4). Between the two communities, the NSWC had non-significantly higher measures of strength, clustering coefficient and affinity, while the SDWC had a significantly higher ($p < 0.001$) measure of eigenvector centrality.

Table 4. Network analysis statistics, calculated using generalised affiliation indices (GAI) and averaged over two communities of southern Australian bottlenose dolphins along Adelaide's metropolitan coast. Random values are the mean of values with no individual preferences (expected values from permuted matrices). An asterisk indicates a significant difference from a random network.

	Strength	Eigenvector centrality	Clustering coefficient	Affinity
Northern shallow-water				
Class mean	0.07 ± 1.98	0.04 ± 0.02	1.01 ± 3.41	-0.17 ± 10.87
Random	0.02 ± 1.43	0.03 ± 0.02	-7.04 ± 150.21	-0.39 ± 25.97

Southern deep-water				
Class mean	-0.04 ± 1.42	0.09 ± 0.06 *	0.51 ± 10.48	-1.62 ± 6.19
Random	-0.01 ± 1.08	0.10 ± 0.06	-2.92 ± 65.99	-2.96 ± 98.01

4.4.5. Temporal stability of communities

Lagged association rates within and between communities remained above the null association rate (expected value if there are no preferred associations), indicating non-random associations both within and between communities (Figure 6). However, associations were stronger within communities, as the LARs remained higher compared to between communities (Figure 6). I found similar temporal variability in association patterns within and between communities, where the best fitting model for each LAR consisted of 'casual acquaintances and rapid disassociations' (Figure 6, Appendix Table A2). This model is consistent with social systems in which associations are short-lived, but where individuals still form preferred associations (Whitehead 2008). The SDWC also showed some support for a second model that consisted of 'two levels of casual acquaintances' (see Appendix Table A2). Overall, this model of temporal stability supports a fission-fusion social system.
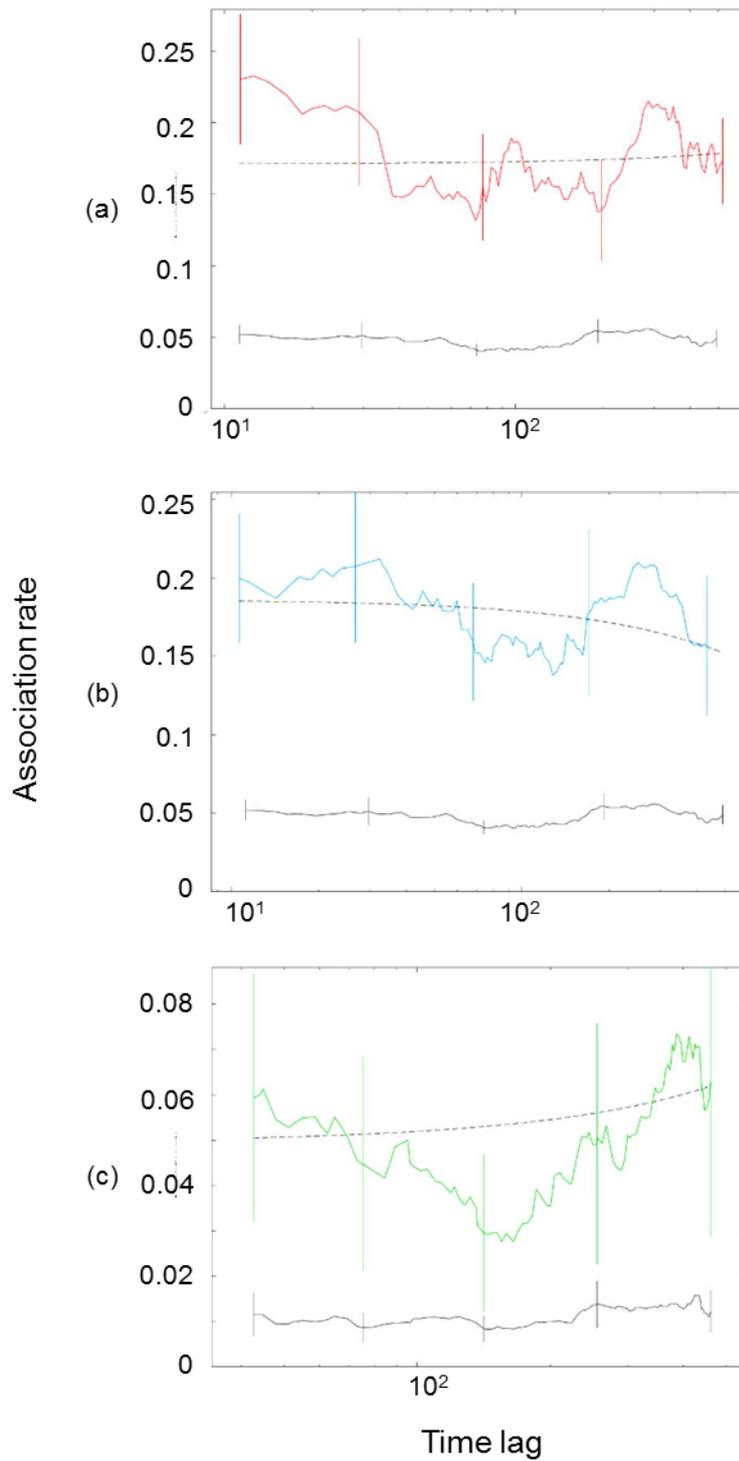
Figure 6. Lagged association rates (solid coloured line), model of best fit (dotted line), and null association rates (solid black line) for the (a) northern shallow-water community, (b) southern deep-water community, and (c) between communities of southern Australian bottlenose dolphins along Adelaide's metropolitan coast. S.E. was calculated using jackknife procedures.

4.4.6. Genetic relatedness and sib-ship relationships within and between communities

The mean pairwise relatedness of individuals within communities was significantly higher than between communities (within R = 0.075, between R = 0.056, $p < 0.001$, Table 5). When comparisons were made separately for each sex, females exhibited significantly higher mean pairwise relatedness within than between communities (within R = 0.097, between R = 0.067, $p < 0.05$, Figure 7**Error! Reference source not found.**). Males also exhibited a slightly higher mean pairwise relatedness within than between communities, however this result was non-significant (within R = 0.063, between R = 0.043, $p = 0.89$); and a similar pattern was found for between-sex pairs (within R = 0.071, between R = 0.053, $p = 0.93$, Table 5). The proportion of sib-ship relationships also differed within and between communities. I found a significantly larger proportion of half-sib and full-sib pairs within communities than between communities, and a larger proportion of non-sib pairs between communities ($\chi 2=$ 11.92, df = 2, p < 0.05, Figure 7).

Table 5. Mean relatedness within and between communities for female (F-F), male (M-M) and opposite-sex (F-M) pairs of southern Australian bottlenose dolphins along Adelaide's metropolitan coast.

	Within cluster	Between cluster
All	0.075 (± 0.118)	0.056 (± 0.094)
F-F	0.097 (± 0.127)	0.067 (± 0.111)
M-M	0.060 (± 0.093)	0.042 (± 0.066)
F-M	0.070 (± 0.121)	0.055 (± 0.093)
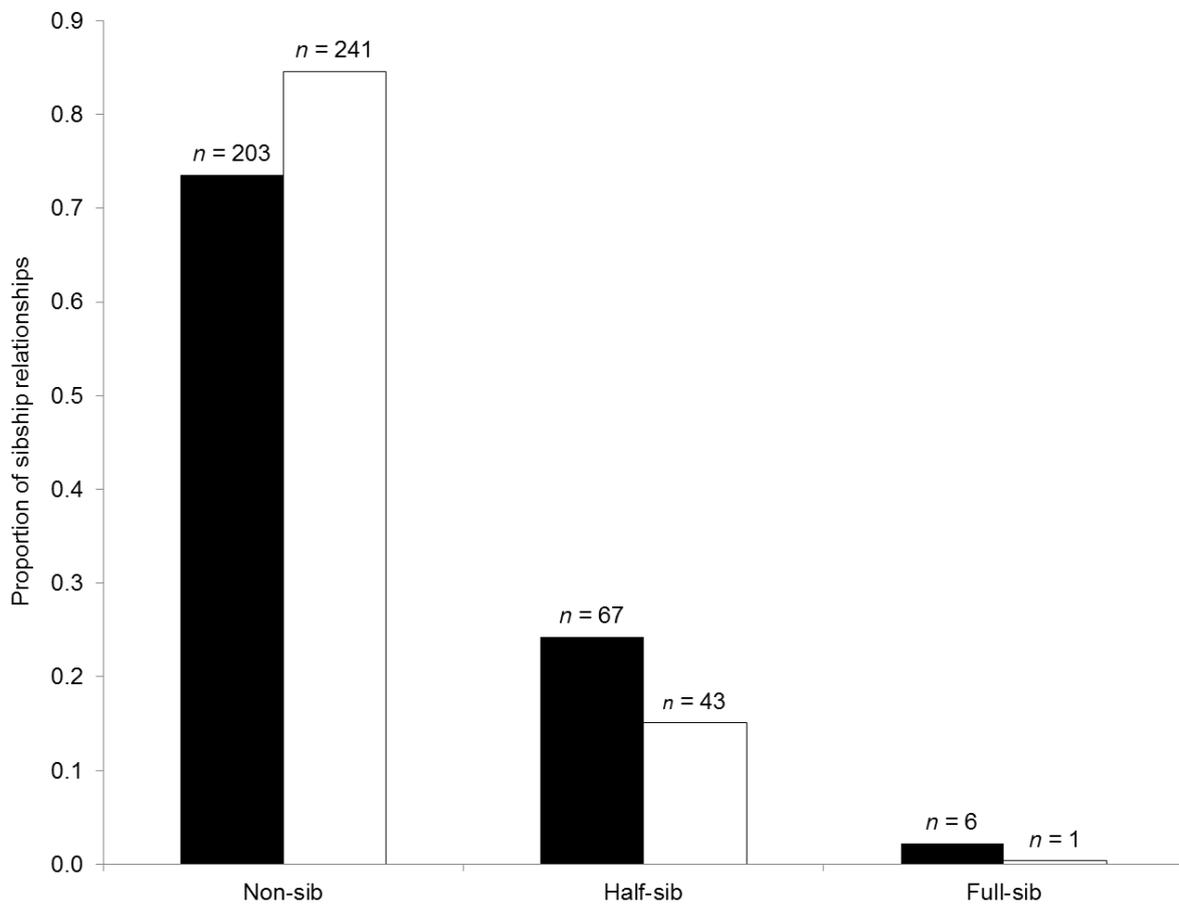
Figure 7. Proportion of sib-ship relationships between southern Australian bottlenose dolphins within (shaded) and between (unshaded) communities along Adelaide's metropolitan coast. Relationships were categorized as either 'non-sib', 'half-sib', or 'full-sib' (pairwise likelihood method, COLONY (Jones & Wang, 2010)). N-values are presented above bars.

4.5. Discussion

Despite the practicality of SNA for exploring animal social structure, there is a lack of knowledge regarding intrapopulation community structure and the factors that drive this. In this study, I used GAIs and SNA to investigate social cohesion and intrapopulation community structure in southern Australian bottlenose dolphins along Adelaide's metropolitan coast. Similar to other coastal populations and species of

bottlenose dolphins, individuals along this coast did not associate at random, but had preferred and avoided associations (Wiszniewski et al. 2009, Louis et al. 2015, Titcomb et al. 2015). Based on these association patterns, the population was divided into two socially and spatially segregated communities, comprising a northern shallow-water community and a southern deep-water community. Association patterns within communities were comparable, with little significant differences in their social network metrics and similar temporal stability of associations, suggesting similar fission-fusion social systems at community level. Genetic relatedness was on average higher within than between communities, particularly for female dolphins. These results are similar to other mammal species that show high levels of site fidelity and philopatry (Wolf & Trillmich 2007, Wiszniewski et al. 2009, Miller et al. 2010). I suggest the social and spatial segregation of these dolphin communities may have resulted from a combination of individual adaptations to ecological conditions, such as depth, benthic habitat type and prey resources, and social factors, such as preferred associates, which likely include kin.

4.5.1. Ecological and social influences on community separation

Our results demonstrate that two spatially segregated communities of bottlenose dolphins are present along the Adelaide metropolitan coast. This separation arises in a relatively open section of coast that lacks physical barriers to movement, and may therefore be influenced by other environmental factors, such as benthic habitat and resource availability. For example, in the Bahamas, separation of *T. truncatus* communities was found to be associated with changes in water depth and benthic habitat (sandy substrate in deep waters vs. seagrass meadows in shallow waters; Rossbach and Herzing 1999). Similarly, community separation of *T. aduncus* in Port Stephens, New South Wales, corresponded with a change in benthic habitat (sandy

substrate vs. muddy substrate; Wiszniewski et al. 2009), while in the northeast Gulf of Mexico, communities of *T. truncatus* were separated by shoals and oyster bars (Tyson et al. 2011). In this study, the separation of the two dolphin communities occurs over a change in bathymetry along the Adelaide metropolitan coast, with one community ranging over shallower waters (< 9 m) to the north of the study area, and the other ranging across deeper waters (9-25 m) to the south. Within this part of the Adelaide coast, the transition from shallow to deep waters also corresponds to changes in benthic habitat. The northern, inshore areas of metropolitan Adelaide lie adjacent to the Port River and Barker Inlet, and consist of estuarine, shallow waters with seagrass meadows and bare sand habitats (Bryars 2003, Bryars 2013). In contrast, the southern part of the study area is mostly characterised by temperate reefs and deeper waters that open up to the outer area of Gulf St Vincent (Bryars 2003, Bryars 2013). The separation of two communities along Adelaide's metropolitan coast may be the result of local adaptation to the different habitat types, water depths, and associated prey resources.

Prey movements do appear to influence the distribution of dolphins along the Adelaide metropolitan coast, with areas of high probability of dolphin occurrence being used predominantly for feeding (Chapter 3; Zanardo et al. 2017). The spatial and temporal predictability of resources often found in inshore environments (Gowans et al. 2008), can lead to dolphins developing specific foraging strategies characteristic of particular habitats and/or preys (Sargeant et al. 2007, Torres & Read 2009, Ansmann et al. 2015). This in turn could lead to the formation of dolphin communities, later reinforced by intrapopulation competition for food resources. Observations of specific dolphin foraging techniques, together with stable isotope analysis and assessment of fish

assemblages across habitat types would be able to confirm whether these dolphins exhibit community level differences in feeding ecology.

Irrespective of the surrounding environment, the development of foraging strategies may be dependent on local enhancement and social learning of calves from their mothers (Mann & Sargeant 2003, Weiss 2006). However, if a mother's feeding strategy is dictated by her habitat use patterns, then feeding strategies may arise through a combination of ecological and social factors. For example, northern shallow-water community individuals may have adapted to foraging amongst shallow seagrass meadows, while individuals in the southern deep-water community may have developed foraging tactics specific to the deeper temperate reef environment. Depending on prey availability and the plasticity of feeding strategies, specific feeding strategies may not extend to other areas, habitats or prey (see Torres and Read 2009) and may help explain the observed community separation.

Community separation of dolphins along Adelaide's metropolitan coast may also be, in general, driven by their preference to associate with individuals within communities, and avoidance of individuals between communities. The analyses indicated that dolphins formed non-random associations both within and between communities. There was a greater proportion of preferred associates within communities, while there were fewer preferred associates and a greater proportion of avoidances between communities. Therefore, the greater proportion of avoided rather than preferred associations between communities may facilitate social segregation between communities.

Further, the site fidelity of individuals may affect community structure and promote differences in community level social structure (Wolf et al. 2007, Wolf & Trillmich

2007). For example, the level of site fidelity displayed by individuals can affect the predictability of the social environment (Beletsky & Orians 1989) and regulate opportunities for individuals to interact and form associations (Michod & Sanderson 1985). Individuals within the Adelaide metropolitan coast show varying levels of site fidelity and can be classified into year round residents, seasonal residents or occasional visitors (Zanardo et al. 2016). A greater proportion of the northern shallow-water community are year round residents (59 %), whereas a greater proportion of seasonal residents (74 %) are predominant in the southern deep-water community (data not shown). The higher levels of site fidelity in the northern shallow-water community may increase the potential for individuals to associate, conversely, lower levels of site fidelity in the southern deep-water community may decrease the potential for individuals to associate. It is important to note that individuals from these communities have been photo-identified in adjacent coastal areas (personal observations), and it is likely that the home ranges of these communities extend to areas outside of the Adelaide metropolitan coast. Therefore, the lower levels of site fidelity and network measures in the southern deep-water community may be a reflection on survey effort only encompassing part of their home range.

Associations between kin may also contribute to the observed community separation, as mean genetic relatedness was greater within communities than between, with more sibships present within than between communities. The high levels of site fidelity exhibited by individuals along Adelaide's metropolitan coast (Zanardo et al. 2016) also likely provides opportunities for individuals to develop social relationships with kin. However, I found differences between the sexes, with greater mean pairwise genetic relatedness within communities for females than for males. This finding is consistent with other populations of Indo-Pacific bottlenose dolphins, where females associate

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more closely with kin (Möller et al. 2006, Frère et al. 2010), likely providing a means to enhance inclusive fitness gains. Female southern Australian bottlenose dolphins exhibit higher levels of philopatry than males (Bilgmann et al. 2007b) further increasing opportunities for females to associate with kin. On the other hand, the results suggest that other social factors, irrespective of kinship, may be more important in determining male associations. Male bottlenose dolphins may form alliances or coalitions to benefit from increased protection from predators and/or for enhancing access to females for reproduction (Möller et al. 2001, Wiszniewski et al. 2012). During survey efforts, I observed synchronised swimming and the herding of females by suspected males, behaviour that is indicative of male alliances (Connor et al. 2006, Connor & Krützen 2015). Increased survey effort and biopsy sampling along the metropolitan coast may further elucidate the potential influence of kinship on within-community associations of females and males.

4.5.2. Associations between members of the two communities

Despite the observed spatial separation of these two dolphin communities, some individuals were found to have preferred associations between communities. Between community associations have been documented previously for kangaroos (*M. giganteus*) (Best et al. 2013) and bottlenose dolphins (*T. aduncus*) (Wiszniewski et al. 2009), and can play an important role in maintaining connections at the population level (Lusseau & Newman 2004). The dolphins from this study are part of one genetic population that encompasses GSV (Pratt et al. in review). Therefore, an exchange of genetic information likely occurs between the northern shallow-water and southern deep-water communities, which may be facilitated by between-community associations. The slight range overlap of communities may provide individuals with the opportunity for associating with individuals of the other community. Groups of

socialising and mating dolphins were predominantly sighted within the southern metropolitan waters throughout summer (personal observations), around the area of community overlap. This area may therefore be an important breeding ground for dolphins, and provide a means to facilitate gene flow between the communities. Alternatively, individuals may change their community membership over time (see Urian et al. 2009), but this was not observed during the study period and requires long term monitoring efforts.

Overall, the results are indicative of a hierarchical fission-fusion social system. Based on their spatial ranging patterns, individuals have more opportunities to associate with individuals within communities, and therefore fission-fusion patterns may be more prevalent within communities. However, as dolphins appear to temporarily and non-randomly associate with others between communities, the dynamics of their fission-fusion may extend to higher levels of social organisation, similar to patterns found in giraffes (*Giraffa camelopardalis*) (VanderWaal et al. 2014) and white-tailed deer (*Odocoileus virginianus*) (Miller et al. 2010). In this case, individual dolphins may be members of a group, where groups are embedded in communities, and communities are embedded within the population. Additional survey efforts throughout GSV are needed to better elucidate these fission-fusion grouping patterns and hierarchical social organisation within this population.

4.5.3. Management implications

Anthropogenic activities can have significant effects on the behaviour and social structure of bottlenose dolphins (Chilvers & Corkeron 2001, Ansmann et al. 2012). For example, the presence of dolphin tourism boats along the Adelaide metropolitan coast elicits short-term behavioural changes in southern Australian bottlenose dolphins (Peters et al. 2012). While group cohesiveness appears to remain stable during short-term exposures (Peters et al. 2012), southern Australian bottlenose dolphins in Port Phillip Bay, Victoria, formed significantly larger groups after long-term boat exposure (Filby et al. 2014). Core ranges of the northern shallow-water community identified here are located directly adjacent to popular Adelaide metropolitan beaches, which show increasing levels of anthropogenic activities. Frequent interactions with recreational fishing, boating and water activities may change the grouping, fission-fusion and association dynamics of the northern shallow-water community, leading to potential negative impacts on long-term reproductive success, increased levels of displacement, and/or population decline as observed elsewhere for bottlenose dolphins (Lusseau 2005, Bejder et al. 2006). Long-term monitoring programs should be implemented to quantify potential impacts of human activities, identify short and long-term changes in community structure, and assess the resilience of the dolphins' social structure to disturbance. However, management should not only be restricted to the northern shallow-water community. Based on the results of this study, and the heterogeneous habitat of GSV, there are likely to be additional communities of southern Australian bottlenose dolphins within this Gulf. As these communities form part of one genetic population, other communities are likely to be of importance, and may act as 'source communities'. Future studies need to investigate whether dolphin communities in GSV exhibit small scale differences in survival, birth rates, mortality

and abundance (Sutherland 1996), as this could have important consequences for the management of this population over the long-term.

Overall, this study emphasises the importance and likely influences of ecological and social factors on the social structure of bottlenose dolphins. Increased survey and sampling efforts within and beyond the study area are needed to define the boundaries of the dolphin communities identified in this study, and to further elucidate ecological, social and anthropogenic drivers of intrapopulation community variation. Such information is critical for effective population management, and will enhance our understanding of the evolution of complex fission-fusion societies in odontocetes and other mammals.

4.6. Acknowledgements

Chapter 5. General Discussion

Information on a species ecology and behaviour is essential for conservation efforts and informing management regimes. The general lack of information on southern Australian bottlenose dolphins (*Tursiops* sp.) hinders informed decision making regarding their management. This species is of particular importance due to their likely endemism to southern Australia, and potential risk from a number of threatening processes due to its coastal distribution. This thesis provides critical baseline information on the ecology of southern Australian bottlenose dolphins along Adelaide's metropolitan coast, the most rapidly developing urban area in South Australia (SA). I used boat-based surveys, photo identification methods and biopsy sampling to investigate their site fidelity and abundance (Chapter 2), habitat use (Chapter 3) and social structure (Chapter 4). Here, I briefly summarize the main findings of the three previous chapters, review the implications of these results in view of the different threatening processes faced by these dolphins in SA, and identify how and where southern Australian bottlenose dolphins are most likely at risk along Adelaide's metropolitan coast. I then provide guidelines for their future management and avenues for future research, to further our knowledge and for providing better-informed management strategies for southern Australian bottlenose dolphins in SA.

5.1. The importance and seasonal use of the Adelaide metropolitan coast by southern Australian bottlenose dolphins

The varying levels of site fidelity, residency, and identification of dolphin 'hotspots' of occurrence, highlights the importance of the Adelaide metropolitan coast as a habitat for southern Australian bottlenose dolphins. Despite the large number of dolphins

categorised as 'occasional visitors', some individuals were identified as 'seasonal' or 'year-round residents' to Adelaide's metropolitan coast (Chapter 2). Further, it appears that bottlenose dolphins use the study area regularly from year to year (Chapter 2), and display seasonal changes in their abundance (Chapter 2), distribution and preferred habitats (Chapter 3). The seasonal variation in abundance and preferred habitats is likely associated with changes in prey availability (Chapter 3), and may contribute to the social community structure observed in this population (Chapter 4).

During summer, a larger number of individuals were present along the metropolitan coast compared to other seasons (Chapter 2). These individuals were concentrated within shallow, near shore areas, and temperate reefs (Chapter 3). Core summer feeding areas overlapped significantly with predicted areas of high dolphin occurrence; therefore, it is likely that dolphins are using the Adelaide metropolitan coast throughout summer as a main feeding ground. However, based on the ranging patterns of the northern shallow-water and southern deep-water dolphin communities (Chapter 4), members of these communities likely feed in different areas over the summer. During summer, the core (50% kernel range) feeding area in the southern metropolitan waters predominantly overlaps with the ranges of dolphins of the southern deep-water community (Chapter 4), while the representative (95% kernel range) feeding area predominantly overlaps with the ranges of dolphins of the northern shallow-water community. Therefore, it appears that during summer members of the southern deep-water community concentrate their feeding efforts over temperate reef habitats, while the northern shallow-water community feed preferentially over larger areas of seagrass.

Abundance estimates of dolphins in autumn and summer were similar, with slightly smaller numbers in autumn (Chapter 2). During autumn, dolphins showed a preference for shallow, near shore areas, but in contrast to summer, their distribution and core feeding areas were more widespread and scattered along the metropolitan coast. Such spatial patterns of occurrence may be the result of diffusion of prey species (Chapter 3). Autumn preferred areas and feeding hotspots predominantly overlapped with the ranging patterns of the northern shallow-water community (Chapter 4). Therefore, during autumn, the northern shallow-water community appears to be taking advantage of prey availability within its range. As few autumn feeding areas overlapped with the ranging patterns of the southern deep-water community, individuals of this community may be feeding in areas outside of the metropolitan coast, perhaps further south, but this hypothesis requires survey efforts outside the study area to discern.

During winter, abundance estimates were at their lowest (Chapter 2), and dolphins showed a preference for deeper, offshore waters, with a significant decrease in feeding behaviour, and increase in travelling behaviour (Chapter 3). This change in distribution and behaviour may reflect the movement of prey to areas north or south of the metropolitan coast, or to areas further offshore. For example, members of the northern shallow-water community have been photo-identified in adjacent coastal areas to the north (personal observations), therefore other areas within Gulf St Vincent (GSV) may be of more importance to dolphins of this community during the winter months. Similarly, deep waters outside of the study area may also be of greater importance to the southern deep-water community members during this season. Despite winter hotspots overlapping with the known range of the southern deep-water

community, there was a higher probability of dolphin occurrence along the southern limits of the study area (Chapter 3).

Overall, these results demonstrate that the metropolitan coast is an important feeding ground (Chapter 3) for two social communities of southern Australian bottlenose dolphins (Chapter 4). As these two communities occupy specific and distinct regions of the metropolitan coast (Chapter 4), this section of the coast may be of different importance to these communities. In particular, the larger number of individuals identified within the southern deep-water community, in spite of its smaller range patterns within the study area, highlights the importance, and possibly high productivity of this southern part of the metropolitan coast for bottlenose dolphins.

5.2. Potential impacts of threatening processes on southern Australian bottlenose dolphins

Increasing human activities and developments in coastal areas have resulted in a wide variety of threatening processes that may impact upon dolphins, particularly for populations that live in close proximity to urbanised cities (Jefferson et al. 2009, Pirotta et al. 2013, Pirotta et al. 2015). The coastal distribution of southern Australian bottlenose dolphins puts them at risk from a range of threats, including habitat degradation, pollution discharges, and interactions with dolphin tourism and recreational fishing boats (Chapter 1). These threats heighten along metropolitan coasts, due to increasing population growth and coastal developments (Bulleri and Chapman 2010, Bryars 2013). Based on the results from previous chapters, I discuss potential impacts of these threats to dolphins along Adelaide's metropolitan coast.

5.2.1. Habitat modification and degradation

The distribution and habitat use of bottlenose dolphins along Adelaide's metropolitan coast appears to be influenced by their surrounding marine environment (Chapter 3). Therefore, modifications to the metropolitan coast, from dredging of marinas and boat launch facilities, beach and cliff erosion, disturbance of boat anchors, eutrophication and marine debris (Edyvane 1999, Bryars 2013), could affect the distribution and preferred habitats of the dolphins, particularly if important habitats (*i.e.* temperate reefs and seagrasses) deteriorate. In the long-term, this could potentially lead to their displacement from the metropolitan coast as observed for bottlenose dolphins elsewhere (*i.e.* Milford Sound, New Zealand (Lusseau 2005) and Shark Bay, Western Australia (Watson-Capps and Mann 2005, Bejder et al. 2006)). As the segregation of the two dolphin communities identified also coincides with changes to bathymetry and benthic habitat (Chapter 4), environmental changes may also affect the social structure of these dolphins along Adelaide's metropolitan coast, but this requires further investigation to elucidate.

Habitat modifications and depletions may also indirectly affect dolphins through prey availability. Modifications to the metropolitan coast, such as increased nutrients, turbidity and sedimentation by stormwater effluent, as well as overfishing, may deplete prey or cause prey displacement (Bryars 2003). This could further elicit changes to dolphin distribution, habitat preference, abundance and social structure. Based on the results from this thesis, it appears that dolphins are more likely to be at risk from anthropogenic activities during summer and autumn, when they show a preference for shallower, near shore waters (Chapter 3). During this time, modifications to coastal habitats may have a greater impact on members of the northern shallow-water community, as this community exhibits ranges directly adjacent to the majority of Adelaide's metropolitan beaches (Chapter 4).

5.2.2. Pollution and disease outbreaks

Due to the highly urbanised environment, the Adelaide metropolitan coast is subject to higher levels of pollution discharges than other coastal areas in SA (Harbison 1986, Edyvane 1999). Coastal pollution discharges put dolphins at risk of toxicity, with southern Australian bottlenose dolphins showing the greatest concentrations of metals and selenium in comparison to other delphinid species in South Australia (Lavery et al. 2008). In particular, stranded dolphins from GSV have significantly greater concentrations of bone lead, liver mercury and selenium, in comparison to stranded dolphins from other areas in SA (Lavery et al. 2008). Recent tests have also found that dolphins from the Port River estuary and Barker Inlet have high levels of perfluorooctane sulfonate (PFOS) and perfluorooctanoic acid (PFOA) (Environment Protection Authority, unpublished data), however the effects of such pollutants remain unknown. The high site fidelity and residency of many dolphins along the Adelaide's metropolitan coast put them at increased risk of these high pollutant levels. This is particularly an issue if pollutants bio-accumulate, which can affect the long-term health, reproductive success and survival of individuals (Reddy et al. 2001, Schwacke et al. 2002). Environmental pollutants and the build-up of toxins can also lead to compromised immune systems (Lavery et al. 2008; Van Bressem et al. 2009). This is of particular concern considering the 2012-13 outbreak of cetacean morbillivirus in South Australia, which affected mostly southern Australian bottlenose dolphins (Kemper et al. 2016). This outbreak resulted in the death of at least 41 individuals, with most strandings occurring along Adelaide's metropolitan coastline (Kemper et al. 2016). This, however, is a research area that requires further investigation.

5.2.3. Dolphin tourism

During summer, tourism efforts predominantly occur in the southern metropolitan area, and overlap with the summer feeding hotspots, as well as the ranging patterns of both the northern shallow-water and southern deep-water dolphin communities. Furthermore, most socialising behaviours, including mating, were observed throughout summer (Chapter 3), and most occurred within the southern metropolitan area. Interactions with dolphin tourism boats cause short behavioural impacts of dolphins along Adelaide's metropolitan coast, where dolphins spend more time milling, and less time feeding, travelling and socialising (Peters et al. 2012). Therefore, the increased survey effort of this tourism vessel within the southern metropolitan area over summer may have a negative impact on dolphin feeding and socialising behaviours for members of both communities. Disturbances to foraging behaviour may result in an inability to meet nutritional requirements, while disturbances to mating efforts may affect the overall reproductive success of a dolphin population (Lusseau 2004). In addition, tourism threats to southern Australian bottlenose dolphins are likely to increase in the future, with proposed coastal developments (Department of Planning, Transport and Infrastructure 2010), and plans to establish additional boat-based marine and dolphin tourism experiences in SA (National Parks South Australia 2016). In the long-term, the presence of tourism boats may elicit a learned change in dolphin behaviour and/or social structure. For example, in Port Phillip Bay, Victoria, southern Australian bottlenose dolphins increased their avoidance of tour operations over time and formed significantly larger groups after long-term tour boat exposure (Filby et al. 2014). Similar responses in metropolitan Adelaide could heighten disturbances to biologically important feeding and socialising behaviours, as suggested for dolphins in other areas (Constantine et al. 2004, Lusseau and Higham 2004).

5.2.4. Interactions with recreational boats and fishing activities

In the Adelaide metropolitan coast and adjacent areas, recreational boat, fishing, and water activities (*i.e.* kayaking, jet skiing) intensify throughout summer. This peak in recreational activities coincides with the largest estimates of dolphin abundance along the metropolitan coast (Chapter 2). The combination of increased recreational activities and larger dolphin numbers puts dolphins at increased risk from direct contact with boats, and injury or mortality from fishing gear entanglements and/or ingestion as previously observed for this region (Kemper et al. 2005). Of particular concern during summer is the southern metropolitan area, where recreational activities are likely to overlap with this seasonal hotspot of dolphin occurrence, and potentially cause further disturbances to feeding and reproductive behaviours. However, studies are needed to investigate fishing hotspots and assess their extent of overlap with preferred dolphin habitat. Interactions with recreational boats and fishing activities are also of concern during the months of autumn. Despite slightly lower dolphin abundances (Chapter 2), and less recreational activities during this time, dolphin distribution is more widespread and closer to shore (Chapter 3). This puts individuals at greater risk of vessel traffic to/from boat ramps and marinas, and also puts individuals at risk from near shore water activities. During this study, dolphins were found to be circled and harassed by jet skis and kayaks in areas less than 200 m from shore (personal observations). The impact of these interactions may lead to individual avoidance of jet skis and/or other vessels, and, if continually harassed over the long-term, could result in the abandonment of biologically important behaviours or areas (Goodwin and Cotton 2004, Steckenreuter et al. 2012). Commercial fishing activities also occur within GSV, but do not operate within the boundaries of this study area. Despite this, individuals identified along the Adelaide metropolitan coast may be at risk

of interactions with commercial fishers (*e.g.* the scalefish fishery (McLeay et al 2015)) when they are in areas adjacent to the Adelaide metropolitan coast. Further information is needed to assess the potential impact of commercial fishing on southern Australian bottlenose dolphins.

5.3. Conservation and management recommendations

Currently, the general management of anthropogenic activities that may impact upon coastal dolphins in SA is limited to restrictions on vessel, swimmer and aircraft approach distances, provisioning, noise, and lights. Additional management strategies include the establishment of the Adelaide Dolphin Sanctuary (ADS) within the Port River estuary and Barker Inlet (Department of Environment, Water and Natural Resources 2005). Management strategies within the ADS include the monitoring of dolphins through land and water surveys, vessel speed restrictions, and engagement with the community to reduce marine debris and inhibit dolphin provisioning. Unfortunately, these management strategies do not extend to other areas of the South Australian coast, leaving the vast majority of the urban coast under-regulated. Here, I use the information obtained from this study to recommend management strategies for dolphins along Adelaide's metropolitan coast.

5.3.1. Long-term monitoring of dolphins along Adelaide's metropolitan coast

The Adelaide metropolitan coast is an important habitat for southern Australian bottlenose dolphins, and the high site fidelity of these individuals makes them increasingly vulnerable to local anthropogenic threats. Given their potential endemism to southern Australia (Möller et al. 2008, Charlton-Robb et al. 2011), and endangered status of some populations along their range (Department of Sustainability and

Environment 2013), it is of high management priority to monitor and maintain their natural abundance and habitat quality along this section of the coast. The development of a systematic, long-term photo identification and monitoring program will increase the ability of managers to detect trends in dolphin abundance, distribution, habitat use and social structure over time. This information will be crucial to assess the impacts of anthropogenic activities and future disease outbreaks, which is highly important considering that the number of threats is likely to increase with further human population growth. Long-term monitoring efforts should remain consistent or similar to the survey design of this study, to facilitate comparisons, and expand to areas outside of the metropolitan coast to provide information on population dynamics (see *5.4.1.1*). Once a long-term monitoring program is established, it can be used in combination with population viability analysis (see *5.4.1.2* below) to determine the long-term persistence of bottlenose dolphins in metropolitan Adelaide.

5.3.2. Amendments to South Australia's marine protected areas

MPAs are designed to restore and protect marine species and habitats, and promote biodiversity (Edgar et al. 2014). In South Australia, 19 marine parks have been established (Department of Environment Water and Natural Resources 2012); three of these marine parks are within GSV, including eight sanctuary zones, which prohibit fishing activities and the removal of plants and animals. Additional MPAs in GSV include the ADS, being specifically developed as a marine mammal protected area (Department of Environment, Water and Natural Resources 2005). Despite the concentration of human activities along the Adelaide metropolitan coast, no MPAs are located in this area, with the ADS bordering the northern part of the study area, and the closest state marine park (Encounter Marine Park) located approximately 5 km south of the study area.

Managers should consider the extension of the ADS to encompass sections of the Adelaide metropolitan coast. A resident population of approximately 30 dolphins inhabits the ADS year-round, but is also used by a large number of non-resident individuals (Steiner & Bossley 2008). Strong connectivity of dolphins between the ADS and the Adelaide metropolitan coast is highly likely, with individuals sighted in both areas (personal observations). As dolphin numbers within the ADS continue to remain small (Cristina Vicente, personal communications), animals along the Adelaide metropolitan coast and greater GSV may act as a source. Therefore, the long-term sustainability of dolphins within ADS may be dependent on the continued presence of individuals outside of the ADS boundaries. Extension of the ADS to areas along the Adelaide metropolitan coast would ensure that a more pertinent number of dolphins are protected. Specifically, the ADS should encompass important dolphin habitats, defined by the areas of high probability of dolphin presence, which includes near shore shallow waters, and the southern metropolitan waters. ADS objectives prioritize the need to obtain information on the ecology and behaviour of dolphins (Department for Environment and Heritage 2008), which can be achieved through the implementation of a long-term monitoring program, as recommended above. Other objectives of the ADS are to protect key dolphin habitat and improve water quality (Department for Environment and Heritage 2008), which would aid the rehabilitation of depleted seagrass meadows off Adelaide, and overall, increase the habitat quality and prey availability within these important dolphin habitats.

Alternatively, the Encounter Marine Park could be extended north to encompass the macroalgae reef habitat in the southern metropolitan area. This section of the marine park should constrain recreational and tourism boats from entering this area throughout summer in order to decrease dolphin-boat interactions, limit disruptions

and provide protection within this important dolphin feeding habitat. A marine park within this southern metropolitan area can enhance the quality of the marine environment, promote invertebrate and fish assemblages, and thus continue to provide adequate food resources for metropolitan dolphins and other animals over the long-term.

If extensions of MPAs are not feasible, I recommend the implementation of boat speed restrictions along the metropolitan coast. Currently, speed restrictions are in place for vessels that are within the vicinity of marinas, boat ramps, jetties, and for personal watercraft (*i.e.* jet skis) operating within 200 m of the metropolitan shore. However, due to the preference of dolphins to be in shallow waters during summer and autumn, I recommend that speed restrictions be extended to cover areas less than 2 km from the metropolitan shore to mitigate dolphin-boat interactions.

5.3.3. *Public awareness and education about dolphins and Adelaide's metropolitan coast*

Dolphin conservation strategies will benefit from community awareness and education (Hoyt 2011), including the local coastal communities and the greater Adelaide metropolitan population. The ADS currently undertakes community engagement projects, with an established 'Action Group', whose mission is to assist protecting the ADS dolphin population and the habitat that sustains them. However, these practices are mostly specific to the ADS boundaries and local suburbs, and should be expanded to the greater metropolitan coast. Public members that use Adelaide's metropolitan coast need to be made aware of (1) the ecological importance of the area for southern Australian bottlenose dolphins, (2) the benefits and importance of conservation and

management strategies for the marine environment and its inhabitants, and (3) ways in which they can help protect and sustain coastal local environments.

Management strategies should strive to educate the public about marine mammal regulations and conservation measures, by providing them with a sound knowledge of:

- the importance of Adelaide's metropolitan coast for this population of southern Australian bottlenose dolphins;

- the speed limits, where applicable and their reasons;

- the rationale for the southern metropolitan being a restricted zone during summer;

- the distance to keep from dolphins, and its importance;

- the impacts of rubbish and fishing gear on dolphins and other marine organisms, and ways to minimize marine debris.

In order to achieve this, public education should come in the form of: (1) signage along the coastline and handouts of brochures that contain detailed information on the marine mammal regulations, including when and where dolphins are most likely to be at risk; (2) engagement through media outlets and community events, such as public forums and school talks; and (3) water patrols to enforce regulation, particularly during peak and holiday seasons.

For linking public education about dolphins to other marine bodies in SA, information on Adelaide dolphin conservation and management could be added to already established signs and/or brochures, for example, those that have been developed by SA Marine Parks, the ADS, or other community groups that promote the conservation of Adelaide's coastal waters (*e.g.* Friends of GSV). The charismatic nature of dolphins

mean that they can be used as a flagship species to raise awareness of coastal conservation and protection, prompting indirect benefits for other species (Augustowski and Palazzo Jr 2003). For example, community days could be established to support Adelaide's coastal environment and its dolphins (as a flagship species), which may include for example, beach rubbish collection days and coastal re-vegetation projects that work in collaboration. It is important that the public be encouraged to educate others around them, and to monitor and report potential threats, harassment and harm to dolphins and other protected marine organisms. Furthermore, dolphin compliance could be incorporated into water patrols currently undertaken by SA Marine Parks and by PIRSA (Primary Industries and Regions SA) fisheries officers.

5.3.4. Foster collaboration between key dolphin stakeholders in SA

Lastly, I recommend that management strategies consider improving collaborations between researchers, dolphin tour operators, local government and community groups. Currently, dolphin photo-identification catalogues are being developed in areas outside of the Adelaide metropolitan coast, however, the lack of collaborative efforts between these groups inhibits the transfer of knowledge and prevents opportunities to gain and improve important baseline information for the long-term management of the population of southern Australian bottlenose dolphins that inhabit GSV. Thus, future collaborative efforts among key stakeholders will provide essential opportunities to better understand the ecology of this dolphin population, which can enhance conservation efforts of dolphins in this Gulf and other South Australian waters.

5.4. Recommendations for future research

While information on site fidelity, abundance, habitat use, and community structure is important for dolphin conservation and management, the information presented in this thesis is limited to a relatively small study area and temporal scale. Further research is needed to enhance our understanding about the ecology of southern Australian bottlenose dolphin, test hypotheses arising from the present study, and gain information about the impacts of increasing human activities on the dolphins inhabiting Adelaide's metropolitan coast. I recommend that future research be conducted in conjunction with long-term monitoring of dolphins (see *5.3.1*) along Adelaide's metropolitan coast and adjacent areas, as outlined in order of priority below:

5.4.1. High priority research for the conservation and management of southern Australian bottlenose dolphins

5.4.1.1. Investigate the population dynamics of southern Australian bottlenose dolphins in Gulf St Vincent

The individuals identified throughout this study are likely to only represent a small proportion of the larger GSV dolphin population (Pratt et al. in review). Future survey efforts should cover a larger sampling area to provide a better understanding of abundance, distribution, habitat use, community structure, and long-range movements and connectivity across GSV. Ensemble forecasting (Thuiller 2003, Thuiller et al. 2009) using data from these larger scale surveys has the potential to identify areas of high dolphin presence outside of the metropolitan coast, and may provide specific locations to target for future survey efforts. Additionally, a larger number of genetic samples across this populations' range, will provide a more comprehensive understanding of genetic/genomic variation, gene flow, philopatry and dispersal, and allow better-informed management strategies.

5.4.1.2. Assess the population viability of southern Australian bottlenose

dolphins in Gulf St Vincent

Population viability analysis (PVA) is a tool used in conservation biology to evaluate a populations' extinction likelihood or projected population growth under current or predicted conditions and threats (Boyce 1992, Reed et al. 2002). Thus, PVA is an essential tool to discern the most effective management strategies, and should be an integral part of any species management plan (Reed et al. 2002). This study highlights the importance of Adelaide's coastal habitats to southern Australian bottlenose dolphins and the potential risks from anthropogenic threats faced by the dolphins given their habitat preferences; however, the extent of these threats remains unknown. Establishment of long-term dolphin monitoring programs (see *5.3.1*) within GSV will generate robust information on dolphin demographic parameters, habitat use, and life history. These long-term monitoring datasets can be used for PVA to provide a reliable interpretation of the future viability of the southern Australian bottlenose dolphin population under increasing developments in GSV. However, as GSV covers a large area (*c.* 7,000 km), this task is likely to be challenging. Therefore, PVA can only be undertaken once a sound understanding of the long-range movements and connectivity of individuals across this area (see *5.4.1.1*) are known.

5.4.2. Moderate priority research for the conservation and management of

southern Australian bottlenose dolphins

5.4.2.1. Monitor health, diseases and causes of death of dolphins in South

Australia

Given that southern Australian bottlenose dolphins are threatened by a large number of anthropogenic activities, post mortems of recovered dolphin carcasses should

continue into the future. Post mortems can provide information on dolphin life history, diet, toxicology and pathology, and can be used to identify the most common causes of death, and elucidate the threats that dolphins are most susceptible to. Dolphin carcasses are usually reported by members of the public and collected by the South Australian Museum (SAM), the Australian Marine Wildlife Research and Rescue Organization (AMWRRO), or by the Department of Environment Water and Natural Resources. However, while efforts are made to collect specimens in more remote locations throughout SA, prioritization is often given to strandings within urbanized areas, particularly within the Port River estuary and Barker Inlet (personal observations). Necropsies are performed by either the SAM or AMWRRO, and while efforts are made to collect numerous biological samples (*e.g.* liver, muscle, brain), toxicological studies and other research outputs are lacking. To enhance research outputs, biological samples should be made readily available to Government, State and research institutions, who have the appropriate personnel and/or equipment for specific analysis. For example, the SAM and AMWRRO should work in collaboration with South Australia's Environment Protection Authority (EPA) to monitor water pollutant levels, and dolphin toxicity, pathogens and disease. In 2010-11, the EPA conducted a near shore Monitoring, Evaluation and Reporting (MER) program (Nelson et al. 2013). During the implementation of the MER program, 14-15 sites were visited annually along the Adelaide metropolitan coast. However, monitoring of these sites was restricted to spring and autumn months, with no effort during summer and winter. The EPA should implement a similar study but on year-round basis, which would align with the strategies of their Adelaide Coastal Water Quality Improvement Program (McDowell & Pfennig 2013). Regular coastal water monitoring, coupled with a long-term dolphin monitoring program, will provide a valuable opportunity to monitor dolphin

health, their susceptibility to diseases and environmental pollutants. Further, biopsy samples can also be used to compare contaminant loads and disease susceptibility (*e.g.* Rowles et al. 2011) between live and deceased dolphins. This is particularly important in the wake of the recent outbreak of cetacean morbillivirus (Kemper et al. 2016), for which the short and long-term impacts remain unknown.

5.4.2.2. Investigate the long-term impact of tourism and boat interactions on southern Australian bottlenose dolphins along Adelaide's metropolitan coast

Southern Australian bottlenose dolphins are most sensitive to boat disturbances along the metropolitan coast (Cribb and Seuront 2016), with dolphin swim-with tourism initiating short-term behavioural disturbances (Peters et al. 2012). Unfortunately, the long-term impacts of tourism and boating on dolphin populations in SA are currently unknown. Future studies should investigate the potential long-term impacts of southern Australian bottlenose dolphin swim-with tourism in SA, and determine whether dolphins exhibit increased avoidance and/or changes to their group structure, for example, as observed for this species in Victoria (Filby et al. 2014). Research should also target the potential short and long-term impacts of recreational boat presence and fishing effort on dolphins within Adelaide's metropolitan coast.

5.4.3. Valuable research for the conservation and management of southern Australian bottlenose dolphins

5.4.3.1. Investigate the feeding ecology of southern Australian bottlenose dolphins

This study identified that ecological factors, such as prey distribution, likely influence the distribution, preferred habitats and community structure of southern Australian

bottlenose dolphins. Futures studies should integrate multiple techniques to investigate the diet and feeding ecology of dolphins in GSV and better elucidate the influence of prey on dolphin ecology. For example, stable isotopes and stomach content analysis (*e.g.* Gibbs et al. 2011) can be used to investigate whether there are differences in the trophic level and diet between dolphins of the northern shallow-water and southern deep-water communities identified in this study (Chapter 4). BRUV (baited remote underwater video) analysis of fish assemblages throughout the study area and core feeding areas may also provide a better understanding on the importance of dolphin hotspots and elucidate any seasonal differences in diet composition driving their distribution. Information on seasonal fish distributions, diversity and abundances within the middle areas of GSV may also provide a better understanding of why dolphins move to deeper, offshore waters during winter.

5.5. Conclusions

Species conservation and management decisions are guided by information on their ecology and behaviour (Caro 1998). This thesis provided baseline information on the site fidelity, abundance, habitat use and community structure of southern Australian bottlenose dolphins along Adelaide's metropolitan coast, and highlights the Adelaide metropolitan coast as an important habitat for these dolphins. Environmental factors, such as benthic habitat, bathymetry, and prey, appear to have a strong influence on the ecology and behaviour of this species in the area, influencing the seasonal

variation in their abundance and preferred habitats, and possibly promoting intrapopulation community variation in social features. The information obtained from this study provides the baseline for a long-term monitoring program to evaluate this population's ecology and behaviour over the long-term. Future studies should extend to areas outside of the Adelaide metropolitan coast, to increase our understanding of this population and to provide better-informed population management strategies for their conservation and persistence.

Appendix

Table A1. Behavioural state definitions, modified from Shane et al. 1986

Behavioural state	Definition
Feeding	Dolphins involved in any effort to capture and consume prey as evidenced by chasing on the surface, peduncle diving and circle swimming. Prey is sometimes observed.
Traveling	Dolphins engaging in persistent, directional movement.
Socializing	Dolphins observed leaping, chasing and engaged in body contact with each other. Involves aspects of play and mating with other dolphins. Serves a social and sexual role.
Milling	Dolphins show frequent changes in heading, but stay in one general location, usually close to the surface and with apparent physical contact with one another.
Resting	Dolphins engaged in slow movements as a tight group, generally lacking the active components of the other behaviours described.

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Table A2. Models of temporal stability fitted to the observed lagged association rate (LAR) data for the northern shallow-water and southern deep-water communities, and between communities of southern Australian bottlenose dolphins along Adelaide's metropolitan coast. For description of model equations see Whitehead (2007). The model that best fitted the data according to Akaike's Information Criterion, corrected for small sample size and overdispersion (QAICc), is shown in bold. ΔQAIC indicates how well the data support the less favoured model (Burnham and Anderson 2002).

	Model equation	Model explanation	QAICc	ΔQAIC
Northern shallow-water community	a2*exp(-a1*td)	Rapid disassociates + casual acquaintances	4323	0
	a3*exp(-a1*td)+a4*exp(-a2*td)	Rapid disassociates + two levels of casual acquaintances	4327	4
	exp(-a1*td)	Casual acquaintances	7785	3462
	a3*exp(-a1*td)+(1-a3)*exp(-a2*td)	Two levels of casual acquaintances	7789	3466
	1	Closed units	142126	137803
	a1	Rapid disassociates + preferred companions	142128	137805
	a2+(1-a2)*exp(-a1*td)	Preferred companions + casual acquaintances	142130	137807
	a2+a3*exp(-a1*td)	Rapid disassociates + preferred companions + casual acquaintances	142132	137809
Southern deep-water community	a2*exp(-a1*td)	Rapid disassociates + casual acquaintances	2271	0
	a3*exp(-a1*td)+(1-a3)*exp(-a2*td)	Two levels of casual acquaintances	2272	1
	a3*exp(-a1*td)+a4*exp(-a2*td)	Rapid disassociates + two levels of casual acquaintances	2274	3
	exp(-a1*td)	Casual acquaintances	4402	2131
	1	Closed units	74548	72277

	a1	Rapid disassociates + preferred companions	74550	72279
	a2+(1-a2)*exp(-a1*td)	Preferred companions + casual acquaintances	74552	72281
	a2+a3*exp(-a1*td)	Rapid disassociates + preferred companions + casual acquaintances	74554	72283
Between communities	a2*exp(-a1*td)	Rapid disassociates + casual acquaintances	169	0
	a3*exp(-a1*td)+(1-a3)*exp(-a2*td)	Two levels of casual acquaintances	171	2
	a3*exp(-a1*td)+a4*exp(-a2*td)	Rapid disassociates + two levels of casual acquaintances	173	4
	exp(-a1*td)	Casual acquaintances	426	257
	1	Closed units	13510	13341
	a1	Rapid disassociates + preferred companions	13512	13343
	a2+(1-a2)*exp(-a1*td)	Preferred companions + casual acquaintances	13514	13345
	a2+a3*exp(-a1*td)	Rapid disassociates + preferred companions + casual acquaintances	13516	13347

Figure A1. Phylogenetic tree of bottlenose dolphin species from southern and southeastern Australia. The neighbour joining tree (50% majority-rule unrooted consensus) is based on sequences of 353 bp of the mtDNA control region, with 100 bootstrap replicates. Samples collected from metropolitan Adelaide (AD) are distinguished from samples of *Tursiops aduncus* (Tadu) and *T. truncatus* (Ttru).
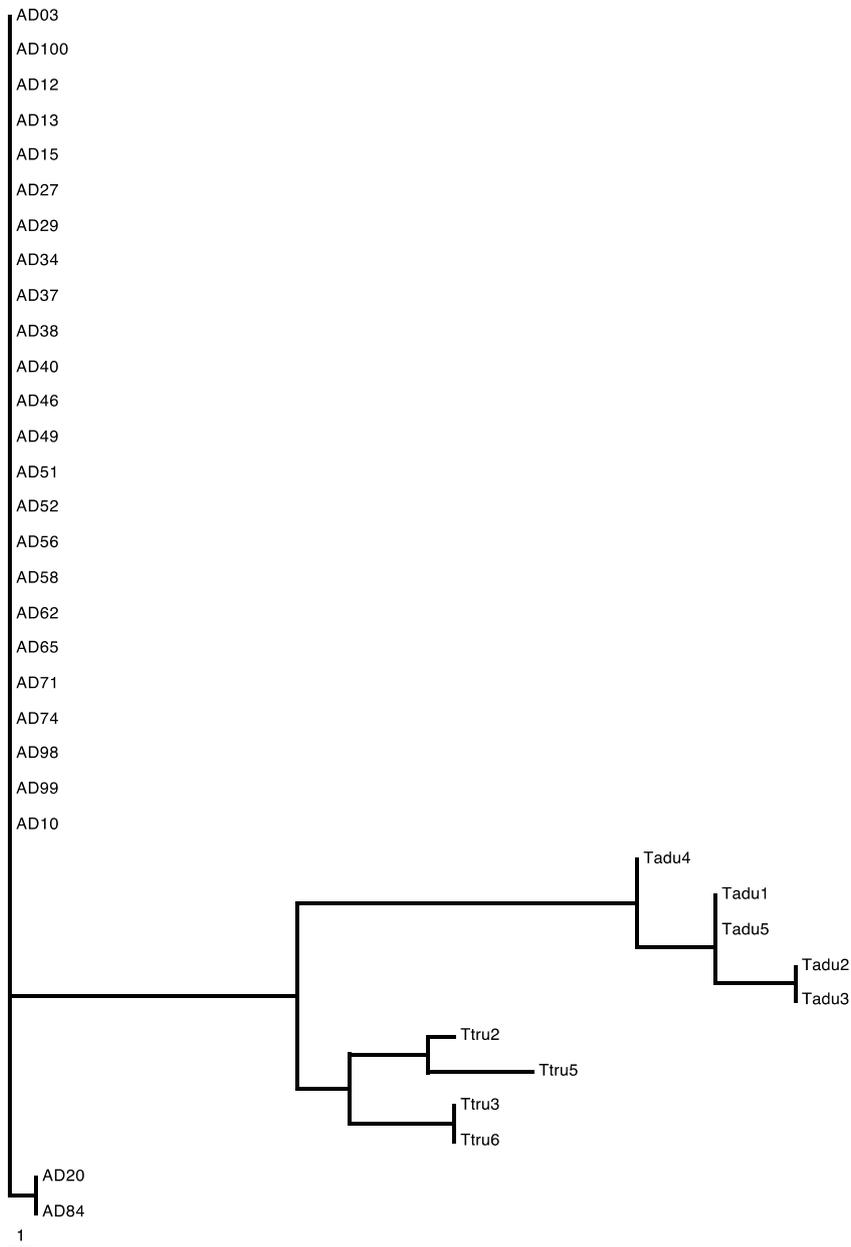
Figure A2. Summer (a), autumn (b) and winter (c) response curves of southern Australian bottlenose dolphins in metropolitan Adelaide for each Species Distribution Model (SDM) algorithm (Generalised Linear Model (GAM), Generalised Additive Model (GAM), Maximum Entropy (MaxEnt)), by ecogeographical predictor variable (water depth, benthic habitat type and slope).

(a) Summer
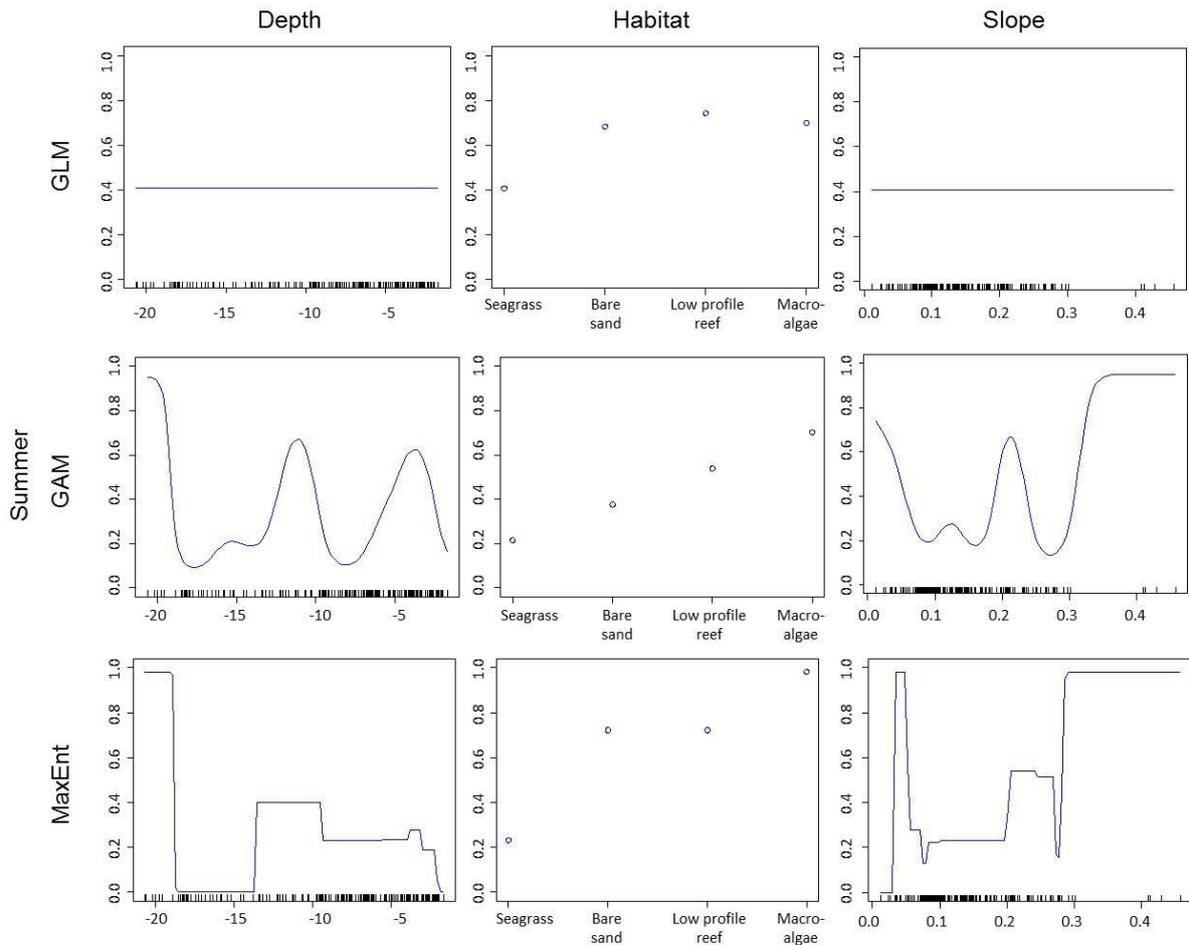
(b) Autumn
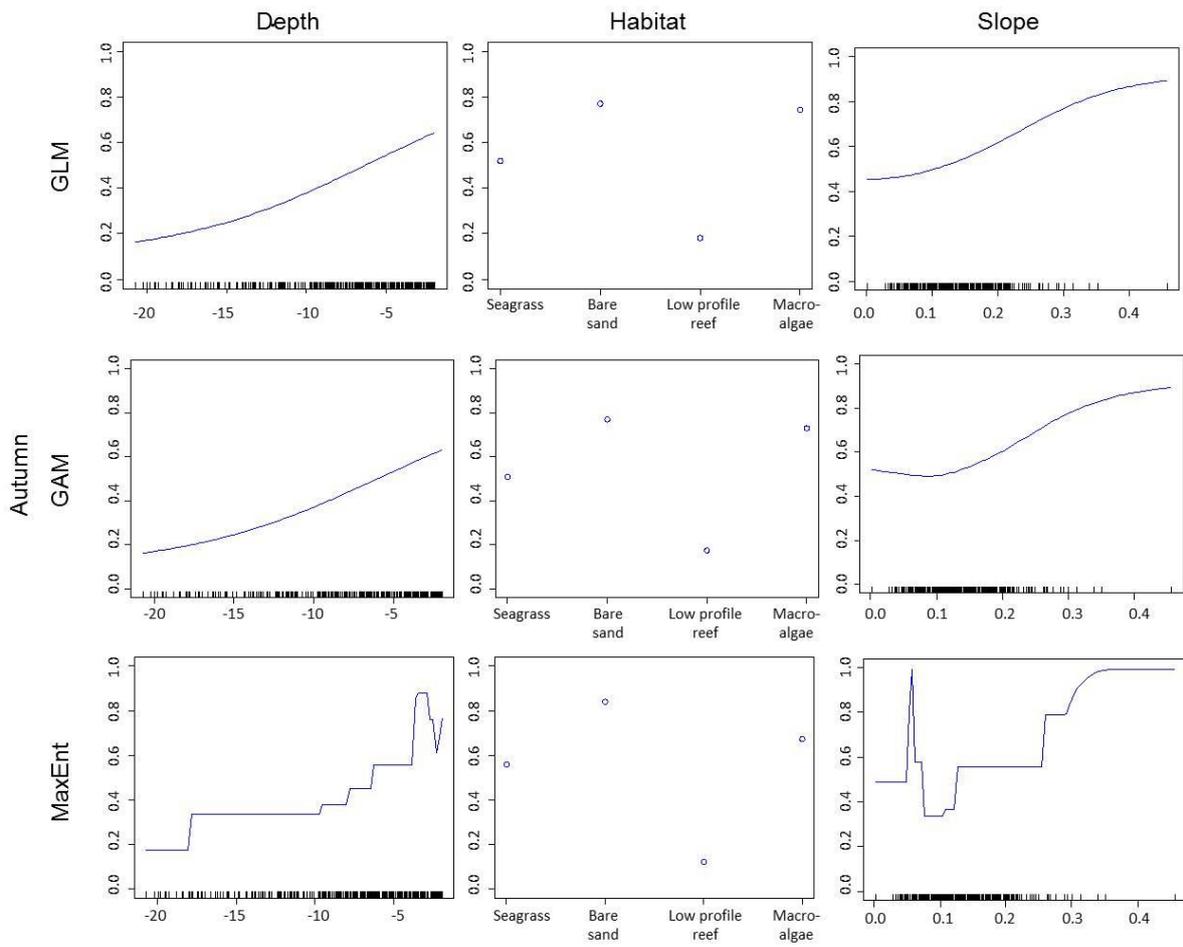
(c) Winter
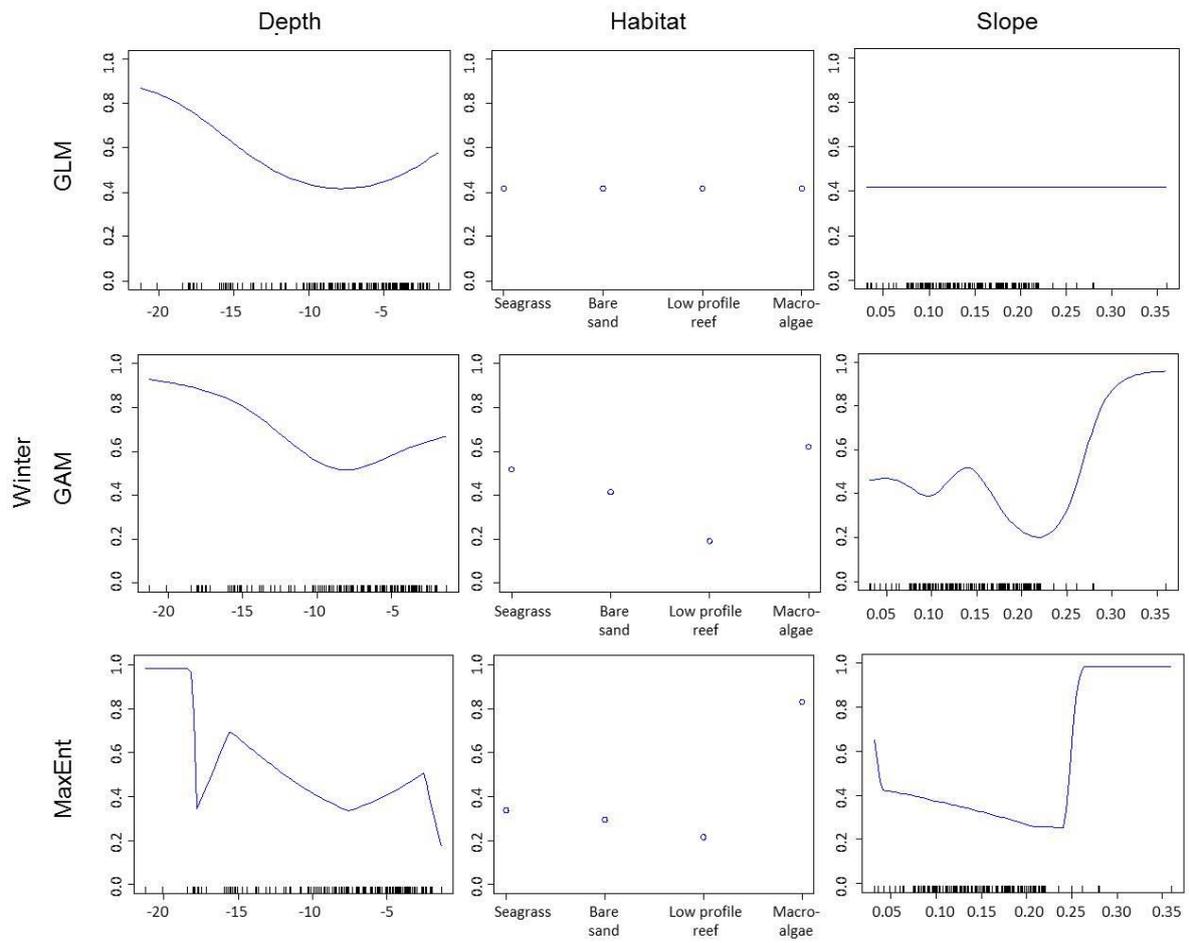
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