Demography and spatial ecology of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) inhabiting an inverse estuary in South Australia

by

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Thesis

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SUMMARY

Information on the demography and spatial ecology of coastal dolphin populations is essential to understand their ecology and inform spatial conservation planning (Chapter 1). In this study, I used boat-based surveys, photo-identification methods and biopsy sampling to investigate southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) sex-specific demographic parameters (Chapter 2); site fidelity and space use patterns (Chapter 3); identify areas of high probability of dolphin occurrence in relation to ecogeographical and anthropogenic variables, and evaluate the relevance of current sanctuary zones for their protection (Chapter 4) in Coffin Bay, Thorny Passage Marine Park, South Australia. Systematic boat-based surveys were conducted in the inner and outer areas of Coffin Bay between September 2013 and October 2015. Capture-recapture POPAN models estimated a total super-population of 306 (95% CI: 291 – 323) dolphins using the entire study area (263 km^2). For the inner area (123 km^2), Pollock's Closed Robust Design models estimated relatively constant abundance across sampling periods (marked females: 52 – 60, marked males: 46 – 52, and total: 193 – 209), high rates of apparent survival for both sexes (females: 0.99; 95% CI: 0.96 – 1.0; males: 0.95; 0.82 – 0.99), and low temporary emigration rates (0.02; 95% CI: 0.01 – 0.11) (Chapter 2). Agglomerative hierarchical clustering of individuals' site fidelity index and sighting rates indicated that the majority of dolphins within the inner area of Coffin Bay are 'regular residents' (n = 125), followed by 'occasional residents' (n = 28), and 'occasional visitors' (n = 26). A low standard distance (deviation range = 0.7 – 4.7 km, $\bar{X}$ ± SD = 2.3 ± 0.9 km) indicated that resident dolphins remained close to their main centre of use. Representative ranges of resident dolphins were small (range = 3.9 – 33.5 km^2, $\bar{X}$ ± SD = 15.2 ± 6.8 km^2), with no significant differences between males and females, and 56% of the resident dolphins seemed to have ranges restricted to a particular bay within the study area (Chapter 3). Ensemble modelling of species distribution indicated that the shallower waters of the inner area had higher probability of dolphin presence than the outer area. Important areas (> 0.6 occurrence probability) were identified in three different embayments within the inner area, in shallow waters (2 – 10 m depth) within 1,000 m of land and 2,500 m of oyster farms. Distribution patterns were relatively consistent across seasons despite the seasonality in environmental conditions and vessel traffic. Although sanctuary zones covered areas from low (0.04) to high (0.89) probability of dolphin presence, most areas with high dolphin probability of occurrence fell in multiple use areas where human activities are allowed (Chapter 4). The high year-round density of dolphins, strong site fidelity, restricted ranging patterns, and higher probability of dolphin occurrence in the inner area of Coffin Bay are likely driven and maintained by the high productivity of this system possibly coupled with low predation risks. These findings highlight the importance and conservation value of the inner area for southern Australian bottlenose dolphins, and provide the basis for guiding future monitoring and spatial conservation planning of the species within South Australia's marine parks (Chapter 5).

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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Statement of authorship

I (M.C.P.R.) am the principal contributor for each chapter. My primary supervisor, Dr Guido J. Parra (G.J.P.), and associate-supervisor, A/Prof Luciana Möller (L.M.), are co-authors of the manuscripts derived from this thesis due to their significant input, advice and guidance in study design, data analysis and manuscript writing and editing. Fernando Diaz-Aguirre (F.D.A.) is a co-author because of his contribution to data collection throughout this project, and laboratory analysis (sexing of dolphins) which I incorporated into the analysis of chapters 2 and 3.

Chapter 1:

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- Data collection and processing: M.C.P.R., F.D.A.
- Laboratory analysis: F.D.A.
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PERMITS

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CHAPTER 1: GENERAL INTRODUCTION

Human activities have had an unparalleled impact on all of Earth's ecosystems (Worm and Paine 2016); including overexploitation of natural resources, habitat loss and modification, pollution, and anthropogenic climate change (Young et al. 2016). These have greatly influenced the distribution and abundance of species and populations, and have led to major biodiversity declines and losses (Hoffmann 2010; Young et al. 2016). While the global state of biodiversity continues to deteriorate, conservation actions can still ameliorate the status of particular species and populations (Hoffmann 2010). One such action is through targeted spatial conservation in the form of reserves and protected areas. Spatial conservation planning, however, requires knowledge on species demography and distribution patterns, and how these patterns relate to environmental and anthropogenic factors (Guisan and Thuiller 2005; Franklin 2010).

Information on demographic parameters, in particular abundance, survival, and migration, are fundamental for understanding species population dynamics and for assessing species conservation status. For example, long-term data on population size allows the estimation of trends, the identification of populations at risk, and may trigger conservation actions (Taylor et al. 2007; Collen et al. 2009); however, these data are usually unavailable due to difficulties in establishing long-term monitoring programs. In these situations, short-term studies that estimate demographic parameters can provide insights on the conservation status of populations. For example, low survival rates can be indicative that a population is suffering from some type of threat (e.g., Currey et al. 2009; Mintzer et al. 2013; Azevedo et al. 2017). Furthermore, when establishing protected areas to protect populations under threat, assessments of demographic parameters are essential to keep track of management goals (Hooker et al. 2011). Additionally, knowledge on site fidelity, movement patterns, and space use of individuals and populations which are the target of conservation are also required for well-informed spatial management strategies such as protected areas.

Information on individuals' site fidelity (*i.e.* how often individuals use or return to a particular area, Switzer 1993) and ranging of animals are critical to understand how they use their environment, the relative importance of particular areas to their ecological requirements, and how localized threats may affect their growth, reproduction and survival. When individuals exhibit high site fidelity and range across relatively small areas, they tend to be more vulnerable to suffering population declines due to local threats (e.g., Gonzalvo et al. 2013; Atkins et al. 2016). On the other hand, populations with such characteristics have greater potential to be effectively managed in protected areas (e.g., Flores and Bazzalo 2004; Gormley et al. 2012; Guerra and Dawson 2016). For example, the population of common bottlenose dolphins (*Tursiops truncatus*) that inhabits Doubtful Sound, New Zealand, was suffering impacts from tourism vessels (Lusseau 2003) and exhibiting signs of decline (Currey et al. 2007). Since the creation of a small (14.1 km^2) 'dolphin protection zone' (Lusseau and Higham 2004) and the stipulations of guidelines for boat interactions, the effect of vessel impacts diminished (Elliott et al. 2011; Guerra and Dawson 2016). By contrast, species that display seasonal movements or exhibit large ranges, represent a challenge to spatial conservation planning because of the difficulties and costs of protecting large areas that include critical habitat for the species (Hyrenbach et al. 2000; Game et al. 2009; Hooker et al. 2011). Therefore, efforts towards integrating species requirements into protected area design and delineation require in-depth understanding of species site fidelity and spatial ranges, and how these may vary depending to ecological conditions (e.g., prey availability and predation risk), anthropogenic pressures and intrinsic characteristics of the population (e.g., life history traits, potential biological differences between sex).

Species that are long lived, have slow growth, late maturity and low reproductive rates are particularly vulnerable to human-caused mortality (Musick 1999; Lewison et al. 2004). Several populations with such history traits have declined to critical levels and many are currently main targets of conservation efforts, though their recovery may take decades (Musick 1999; Lewison et al. 2004). Furthermore, some long-lived species show differences between females and males attributed to their reproductive strategies, which can lead to sex-biases in their movement patterns, home ranges, social strategies and demographic parameters (Wrangham and Smuts 1979; Ruckstuhl and Clutton-Brock 2005; Skalski et al. 2010). Sex-biases within a population can have important implications for conservation and management, especially when individuals of different sex use different areas and as a result are exposed to different threats (e.g., Bruce and Bradford 2015; Sprogis et al. 2016). A typical example is the wandering albatross (*Diomedea exulans*); a long-lived species that breeds in South Georgia and exhibits a sex-bias in ranging patterns (Weimerskirch et al. 1997; Xavier and Croxall 2005). Female albatross forage in larger areas where they are exposed to higher levels of mortality due to fisheries bycatch (Xavier et al. 2004), this results in lower survival rates of females compared to males (Weimerskirch et al. 1997; Xavier and Croxall 2005). Identifying differences in ranging patterns and demographic parameters between females and males in a population, and the potential sex-biases in their threats, can contribute to better-informed conservation and management of long-lived species such as top predators.

1.1. State of marine ecosystems and top predator populations

Regionally and globally, marine ecosystems are threatened by multiple anthropogenic activities carried both on land (e.g., coastal development, runoff of pollutants and nutrients), and in the marine environment (e.g., direct extraction of resources, demersal destructive fishing, input of pollutants) (Islam and Tanaka 2004; Halpern et al. 2007; Halpern et al. 2008). Human impacts however do not act in isolation, but rather synergistically, and their effects on ecosystems are cumulative (Lotze et al. 2006). Analyses of the distribution of human impacts on marine ecosystems have identified priority areas for management intervention (Halpern et al. 2007). However, several human activities (e.g., recreational fishing, aquaculture, coastal engineering, point-source pollution) have not been considered in local and regional assessments and baseline information on species ecology and threats is still needed to better-inform decision makers and improve management of species and ecosystems (Lotze et al. 2006; Halpern et al. 2008).

Among all marine ecosystems, coastal environments are the most heavily impacted by human activities because they are exposed to both land and marine-based stressors (Halpern et al. 2008; Halpern et al. 2009). The degradation of coastal and estuarine ecosystems has been driven by human activities rather than by changes due to natural (*i.e.* non-human caused) phenomena (Islam and Tanaka 2004; Lotze et al. 2006). This degradation has increased markedly in the past 150 – 300 years, and by the 20th century the extraction of resources (e.g., food and oil) has caused global depletion of approximately 90%

of marine top predator species, including marine mammals, seabirds and marine turtles, large teleost fish and sharks (Lotze et al. 2006). In coastal areas overfishing appears to be the main driver of the 'ecological extinction' of several species (Jackson et al. 2001) because it has made coastal ecosystems and associated species less resilient and more vulnerable to other types of human impacts.

In general, an interplay of bottom-up and top-down effects regulate the functioning of marine ecosystems and the abundance of upper-trophic-level populations (Hunt and McKinnell 2006). The bottom-up effect implies that food abundance (*i.e.* primary production), which is thought to be driven by climate or nutrient load, is the limiting factor of the abundance of consumers at higher trophic levels (e.g., fish and dolphins). For example, large-scale distribution patterns of pelagic marine animals are driven by food availability, with the higher abundance of upper-trophic-level species occurring in highly productive regions such as up-welling areas (Hunt and McKinnell 2006). On the other hand, the top-down effect implies control through predation. At smaller scales predation pressure (current or historical) could be an important factor delineating local distributions of some species (e.g., marine birds and pinnipeds) (Hunt and McKinnell 2006). Marine top predators can influence marine communities directly through prey consumption and indirectly through behavioral modifications due to the risk of predation (Camhi 1998; Baum et al. 2003; Heithaus et al. 2008; Estes et al. 2011). Due to the fundamental role of marine top predators in maintaining the structure and functioning of marine ecosystems (Myers and Worm 2003; Heithaus et al. 2008), the decline in their populations can impact several trophic levels leading to a trophic cascade compromising the resilience of marine ecosystems and their capacity to recover from perturbations (Worm et al. 2006).

Marine top predators such as marine mammals, seabirds and sharks share life history traits (late maturity, low reproductive rates and long life spans) that make them extremely vulnerable to extinction risk (Camhi 1998; Robertson and Gales 1998; Bastida et al. 2007). Top predator populations have been declining worldwide at an accelerated rate due to several types of threats (Pauly et al. 1998; Estes et al. 2011). Marked declines of entire communities have occurred in marine ecosystems around the globe mainly due to industrialized fisheries, and currently only 10% of the original numbers of top predators remain (Myers and Worm 2003). For marine mammals and seabirds, bycatch is currently one of the main causes of mortality, and several of their populations have declined because of this (Robertson and Gales 1998; Hall et al. 2000; Lewison et al. 2004). Other threats to marine top predators include entanglement in marine debris, reduced prey availability, oil and chemical spills, vessel strikes, noise, novel pathogens, harmful algal blooms, pollution, and loss of critical habitat (reviewed by Notarbartolo di Sciara et al. 2016).

For marine mammals, most species considered at-risk occur in coastal areas and in highly productive regions (Davidson et al. 2012), and it is estimated that about 70% of their population declines currently go undetected (Schipper et al. 2008). Particularly, coastal and inshore dolphins are among the most threatened species because of their life history traits, disjunct distributions, limited movements, and restricted geographic ranges that tend to overlap with areas of intense anthropogenic activities (Reeves et al. 2003). Several dolphin populations inhabiting inshore and coastal waters are facing human impacts such as direct kills (e.g., Kemper et al. 2005; Ross 2006; Mintzer et al. 2013), fisheries bycatch (e.g., Northridge and Hofman 1999; Rojas-Bracho et al. 2006; Slooten et al. 2013), pollution (e.g., Schwacke et al. 2002; Hall et al. 2006), habitat degradation and destruction (Turvey et al. 2007), boat disturbance (e.g., tourism boats, Bejder et al. 2006b), aquaculture expansion and reduction of prey availability due to overfishing (e.g., Watson-Capps and Mann 2005; Cañadas and Hammond 2008). These impacts may contribute to population decline or extinction (e.g., Bejder et al. 2006b; Turvey et al. 2007; Mintzer et al. 2013; Azevedo et al. 2017). The conservation of populations which show evidence of decline rely on policy makers, as their decisions can lead to effective management actions to protect them (Rojas-Bracho et al. 2006; Slooten 2013). However, for many dolphin species there is simply not enough information on their demography and ecology to determine the status of their populations, and properly inform management decisions. For example, the IUCN Red List assessment of cetaceans, which included a total of 87 species, left most (45) of them without evaluation due to data limitations (Roman et al. 2015).

1.2. Conservation of coastal ecosystems and marine mammal populations

Although the marine environment is currently highly disturbed by human activities (Halpern et al. 2007; Halpern et al. 2008), trends in marine, coastal and estuarine degradation are still reversible (Lotze et al. 2006; Worm et al. 2006). Indeed, in some coastal and estuarine ecosystems, degradation has been reversed due to the establishment of conservation measures (Lotze et al. 2006). One type of measure is the creation of Marine Protected Areas (MPAs). MPAs have become one of the most effective tools used to manage and ensure the conservation of marine top predators such as marine mammals and their associated habitats (e.g., Hughes et al. 2003; Hooker and Gerber 2004; Worm et al. 2006; Notarbartolo di Sciara et al. 2016). For example, a meta-analysis showed that the implementation of MPAs and fishery closures increased species diversity of target and non-target species, with large increases in fisheries productivity even in areas outside the reserves (Worm et al. 2006). Besides improvements in environmental conditions, the implementation of MPAs can also lead to improved economic income due to the development of eco-tourist activities (Worm et al. 2006).

The first areas created for marine mammal conservation dates back to early 1970s, and currently there are about six hundred MPAs established to protect cetaceans (whales, dolphins and porpoises) or areas where they inhabit (Hoyt 2012). Zoning within a MPA is used to define what human activities can occur in each location, and provide different levels of protection to species and/or habitats. The categories run from multiple-use areas, where several types of anthropogenic activities are allowed, to areas of non-use or no-take (Hughes et al. 2003). Particularly for marine mammals, the establishment of ‘sanctuary zones’ (‘protection zones’, ‘fishing exclusion area’, or ‘Special Area of Conservation’) have been used to manage recreational and commercial activities (e.g., fishing and tourism activities) within critical habitats for these animals (Lusseau and Higham 2004; Hoyt 2012; Di Tullio et al. 2015).

Determining if MPAs are effective tools for conservation requires evidence showing that management goals are being achieved; these could be an increase in numbers of the target population, an improvement in prey availability, or a reduction of human-caused mortality

(Hooker et al. 2011; Hoyt 2012). Currently, increasing evidence indicates that the creation of such protected zones are also a useful tool for the conservation of coastal dolphins (e.g., Gormley et al. 2012; Cheney et al. 2014; Bossley et al. 2016). For example, a 'dolphin protection zone' was created in Doubtful Sound, New Zealand, to protect a small endangered population of common bottlenose dolphin (*Tursiops truncatus*) which was targetted by a dolphin-watching industry and was suffering impacts from vessel disturbance (Currey et al. 2007; Guerra and Dawson 2016). In this particular case, previous information on critical habitat for the population was used to delineate the 'dolphin protection zone' (Lusseau and Higham 2004). To diminish the effect of vessel impacts, the management of this zone included guidelines on how boats should interact with dolphins. Compliance made this place-based approach an effective strategy for dolphin conservation (Elliott et al. 2011; Guerra and Dawson 2016).

Even though MPAs seem to be an effective tool for the conservation of marine mammals, not all species can be protected under area-based approaches (Notarbartolo di Sciara et al. 2016). For many marine mammals it is difficult to cover a population's year-round distribution within a single MPA (Reeves 2000). However, species that form small populations occupying restricted ranges are more prone to be managed through the establishment of MPAs (Notarbartolo di Sciara et al. 2016), especially when these encompass the critical habitat of a population (Hooker et al. 2011). Therefore, to guide spatial conservation planning, knowledge on species distribution, population size, and species-habitat relationships are needed, as well as information on the distribution of threats and their potential impacts upon animal populations such as those of coastal dolphins.

1.3. South Australian coastal dolphins and MPAs

At least 47 species of cetaceans occur in Australian waters, including a minimum of 21 dolphin species (Ross 2006; Woinarski et al. 2014). All cetaceans inhabiting Australian state and territory waters are protected under the *Environment Protection and Biodiversity Conservation Act 1999* (Act 1999). Despite this 'protection', there is not enough information on the conservation status of most of dolphin species inhabiting Australian waters. Most of them are classified in the 'data deficient' category of IUCN (2017), and as 'No category assigned because of insufficient information' within the 'Action Plan for Australian Mammals 2012' (Woinarski et al. 2014).

A recent large-scale study, which related the spatial distribution of marine mammals with factors that threaten their long term survival, identified coastal areas of southern Australia among 13 global hotspots of marine mammal species extinction risk (Davidson et al. 2012). This study emphasized the importance of understanding the basic biology and ecology of at-risk marine mammal species occurring in coastal areas to assess their threats and to implement effective conservation and management solutions (Davidson et al. 2012). Unfortunately, such basic information is lacking for most species and our ability to provide science-based conservation is hindered by the paucity of biological and ecological data on dolphin populations in southern Australia.

Coastal dolphins inhabiting South Australian waters are exposed to multiple human threats. In this region, dolphins are exposed to entanglement in fishing and aquaculture equipment (Kemper et al. 2005; Hamer et al. 2008), dolphin watching activities (Peters et al. 2012), and mass mortalities caused by pathogens such as morbillivirus outbreaks (Kemper et al. 2013). Historically, bottlenose dolphins inhabiting Port Adelaide River estuary and Barker Inlet suffered from harassment and were exposed to high inputs of pollution from industry, sewage plants and storm water (Bossley et al. 2016). To protect the dolphin population inhabiting Port Adelaide River estuary and Barker Inlet, the 'Adelaide Dolphin Sanctuary' was created in 2005. Since the creation of this sanctuary, water quality improved and surveillance and education to protect the dolphins was put into place. These likely triggered better habitat conditions for the dolphins favoring a noticeable increase in their sightings within the sanctuary (Bossley et al. 2016).

Besides this sanctuary, a Representative System of MPAs with 19 multiple use marine parks was declared by the South Australian Government in 2009 (DEWNR 2012). The 'Marine Parks (Zoning) Regulations 2012' in South Australia include zones of 'general managed use' (which allows for recreational activities, including fishing), 'habitat protection' (protects sea floor, while allowing for recreational activities, including fishing, but prohibits prawn trawling), ‘sanctuary zones’ (areas of high conservation value, which allows only low-impact recreational activities such as diving, surfing and swimming, but prohibits fishing and motorized water sports), and ‘restricted access’ (prohibits public access). One of the commitments of these marine parks is to guarantee the effective conservation and management of protected species (DEWNR 2012), including all cetacean species which are protected under Australia’s ‘Environment Protection and Biodiversity Conservation Act 1999’ (Act 1999). Although South Australia’s marine parks have the potential to be an important management tool to ensure the conservation of cetaceans, the lack of information on species such as the southern Australian bottlenose dolphin (see 1.4.) at the time of their establishment prevented the inclusion of the species in their management plans.

1.4. Study species

Currently there are two widely accepted species in the genus *Tursiops*, the common bottlenose dolphin (*T. truncatus*) that inhabits both offshore and coastal waters, and the Indo-Pacific bottlenose dolphin (*T. aduncus*) that seem to prefer coastal and inshore waters (Ross and Cockcroft 1990). Recently, bottlenose dolphins inhabiting coastal waters of southern Australia were described as a new species, the Burrunan dolphin (*Tursiops australis*) based on genetic, morphological and foraging ecology evidence (Möller et al. 2008; Charlton-Robb et al. 2011; Owen et al. 2011). However, their taxonomy is still contentious (Perrin et al. 2013; Committee on Taxonomy 2016), and therefore I refer to them hereafter as southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) (Figure 1.1a).

Southern Australian bottlenose dolphins are endemic to coastal and inshore waters of Tasmania, Victoria, southern Western Australia, and South Australia (Bilgmann et al. 2007a; Möller et al. 2008; Charlton-Robb et al. 2011; Charlton-Robb et al. 2015; Pratt et al. under review). Externally, southern Australian bottlenose dolphins are characterized by a tall falcate dorsal fin, a short ‘stubby’ rostrum and a distinctive tri-band colouration (*i.e.* dark bluish-gray back; light gray flanks with a pale shoulder blaze under the dorsal fin; and whitish belly with that colouration extending up to the eye and above the flipper) (Charlton-Robb et al. 2011). The body length of an adult ranges from 2.27 to 2.78 m, and with a mean of 2.57 m it is considered smaller than *T. truncatus* but larger than *T. aduncus* (Charlton-Robb et al. 2011).

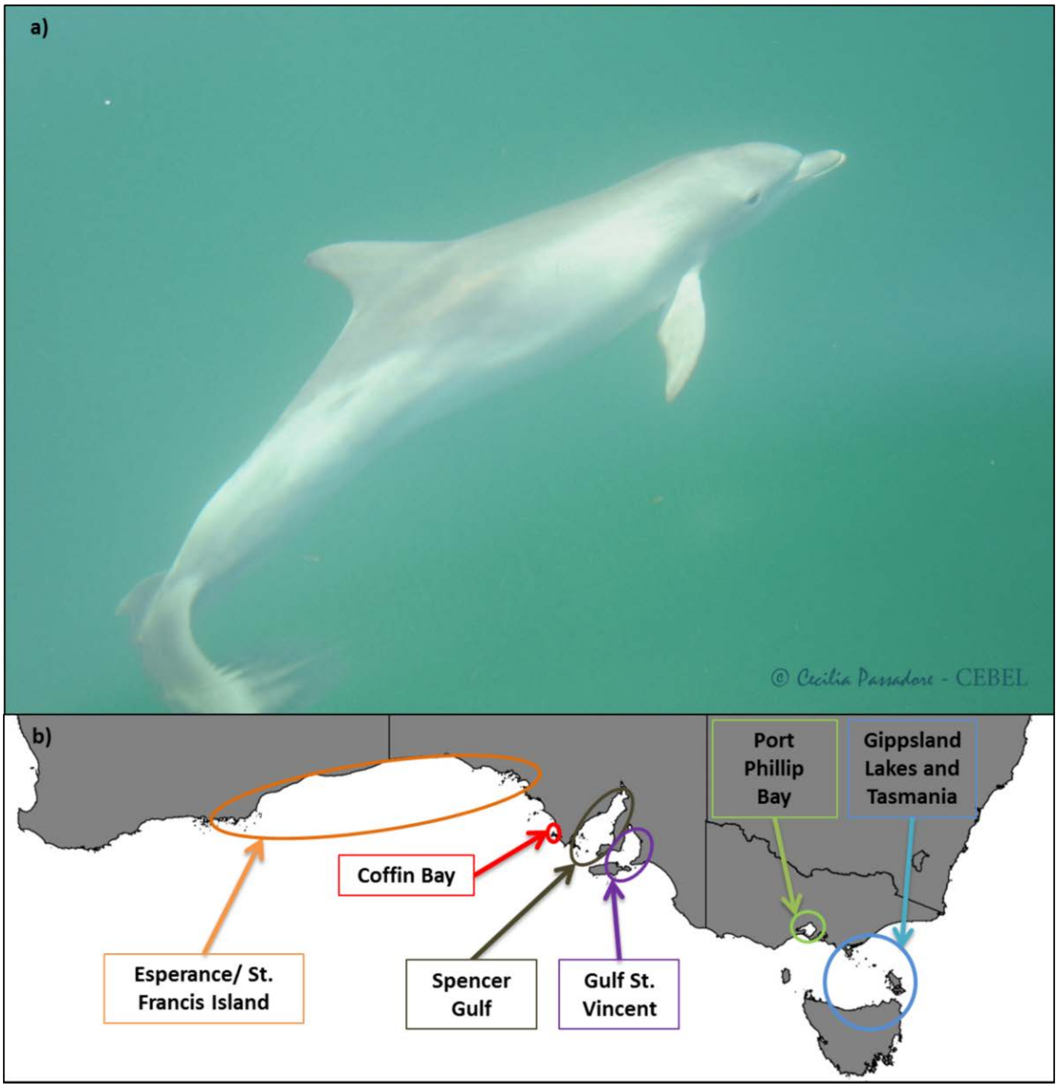

Figure 1.1. a) Southern Australian bottlenose dolphin (*Tursiops* cf. *australis*); and b) map indicating the general distribution of the six populations identified thus far in southern Australia based on mitochondrial DNA and microsatellite genetic markers (Bilgmann et al. 2007a; Möller et al. 2008; Charlton-Robb et al. 2011; Charlton-Robb et al. 2015; Pratt et al. under review).

The species tend to form small, resident and genetically differentiated populations (Charlton-Robb et al. 2015). Population structuring may be occurring at small spatial scales in relation to environmental factors (*i.e.* location of an oceanographic front, Bilgmann et al.

2007b). Based on mitochondrial DNA and microsatellite genetic markers, six populations have been identified to date in (Figure 1.1b): i) coastal waters from Esperance (Western Australia) to St. Francis Island (South Australia); ii) inshore waters of Coffin Bay (South Australia); iii) Gulf Saint Vincent (South Australia); iv) Spencer Gulf (South Australia); v) inshore waters of Port Phillip Bay (Victoria); and vi) inshore and coastal waters of Gippsland Lake (Victoria) and northern (Tasmania) (Bilgmann et al. 2007a; Charlton-Robb et al. 2011; Charlton-Robb et al. 2015; Pratt et al. under review). In general, there is little information available on the ecology of most of these populations.

The population distributed across the Gippsland Lakes and up the coast of Tasmania consist of approximately 50 – 150 individuals (Charlton-Robb et al. 2011; Charlton-Robb et al. 2015), while the population of Port Phillip Bay in Victoria is composed of about 80 – 120 individuals (Dunn et al. 2001; Scarpaci et al. 2003; Filby et al. 2014; Charlton-Robb et al. 2015). Despite the lack of knowledge about their ecology some conservation actions have been implemented in Victoria to protect them. Dolphins of Port Phillip Bay inhabiting waters near Melbourne, a highly urbanised area, face the pressures associated with major shipping port, commercial and recreational fisheries, and tourism activities (Charlton-Robb et al. 2011; Filby et al. 2014). In 1996, the Ticonderoga Bay Sanctuary Zone (ca. 2000 m^2) was established to protect this resident population from anthropogenic stressors, including commercial dolphin swim tourism (Filby et al. 2017). Currently, due to the small population size, high residency, genetic distinctiveness (Charlton-Robb et al. 2011), and restricted home ranges to areas with exposure to human threats (Hale 2002), the southern Australian bottlenose dolphin is listed as threatened under the 'Victorian Flora and Fauna Guarantee Act 1988'.

Recent studies in South Australia's waters suggest that southern Australian bottlenose dolphin may be relatively abundant in comparison to Victoria and Tasmanian waters (Taylor 2010; Zanardo et al. 2016). In Gulf St. Vincent, there is an estimate of about 30 residents and a larger number of non-resident dolphins inhabiting the inshore waters of the Port River estuary and Barker Inlet have been estimated (Steiner and Bossley 2008; Cribb et al. 2013). In the adjacent Adelaide metropolitan waters, the abundance of southern Australian bottlenose dolphins has been estimated to vary seasonally, from about 95 individuals in winter to 239 in summer (Zanardo et al. 2016). These dolphins are found in shallow nearshore areas during summer and autumn, and further offshore in deep waters during winter (Zanardo et al. 2016). This seasonal variation in dolphin distribution patterns is likely driven by prey availability along this coast (Zanardo et al. 2017). Bottlenose dolphins in South Australia feed at different trophic levels and in different habitats; they exhibit regional differences in the diet indicating niche partitioning within the same species (Gibbs et al. 2011). The diet of bottlenose dolphins in In South Australia and Victoria comprise a wide diversity of fish and squid including sand flathead (*Platycephalidae* sp.), yellow-eye mullet (*Aldrichetta forsteri*), Australian salmon (*Arripis truttacea*), garfish (*Hyporhamphus melanochir*), Australian herring (*Arripis georgianus*), red snapper (*Centroberyx* sp.), trevally (*Pseudocaranx* spp.), jacks (*Trachurus* sp.), cardinalfish (*Vincentia conspersa*), sardines (*Sardinops sagax*), silverbellies (*Parequula melbournensis*), snapper (*Pagrus aurtus*), barracouta (*Thyrsites atun*), octopus, cuttlefish (*Sepia* spp.) and squid (*Sepioteuthis australis*), among others (Gibbs et al. 2011; Filby et al. 2017). A preliminary study done in the inner area of Coffin Bay, located in the Thorny Passage Marine Park (Eyre Peninsula, South Australia), during April-June 2010 estimated a population of 266 individuals (95% CI = 231 – 300), which suggests that this may be an important area for southern Australian bottlenose dolphins (Taylor 2010). However, the short study period prevented making robust inferences on the long-term use of this area by dolphins and the demography and ecology of this population.

1.5. Study area: Coffin Bay

Coffin Bay is a small embayment (263 km^2) located within the multiple use Thorny Passage Marine Park (TPMP), Eyre Peninsula, South Australia. Coffin Bay comprises two distinctive areas, the outer area, which is exposed to the oceanographic conditions of the Southern Ocean, and the inner area, which is a shallow inverse estuary consisting of a variety of habitats (e.g., seagrass beds, subtidal sandflats, macroalgae, low reefs, ponds, shallow pools, limestone ledges) across several interconnected embayments (DEH 2004; Saunders 2009; Kämpf and Ellis 2015). Only 6.2% of Coffin Bay waters are currently classified as sanctuary zones (*i.e.* areas of high conservation value where only low-impact recreation activities are allowed, and fishing and motorized water sports are prohibited). The rest of Coffin Bay is zoned as a multiple use area where several human activities are allowed (e.g., boating, oyster aquaculture, recreational fishing, DEWNR 2012; Bryars et al. 2016).

1.5.1 Potential anthropogenic threats to dolphins in Coffin Bay

Different types of human activities occur within Coffin Bay, and some of them have the potential to negatively impact upon the dolphins and their habitat. The population of Coffin Bay consists of 500 people, but increases to approximately 4,000 people during summer and the Easter holiday due to tourist presence. Human activities occurring in Coffin Bay waters include recreational fishing, fishing charters, swimming, diving, several types of water sports and cruises to experience the work in oyster farms as well as dolphin watching (DEWNR 2012).

The inner area of Coffin Bay is home to South Australia's main Pacific oyster aquaculture industry. Studies elsewhere show that aquaculture activities can affect dolphins either directly or indirectly, having different impacts on their populations. Direct effects include alteration of dolphins' behaviour, habitat use and distribution patterns. For example, some bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia, avoid areas where pearl oyster farms were located even though the characteristics of those habitats were similar to the areas they used regularly (Watson-Capps and Mann 2005). Indirect effects of aquaculture include the alteration of dolphins' habitat and food resources, which can result in major impacts such as dolphin population declines. For instance, the increase of aquaculture tuna farms has been proposed as one of the indirect causes of the decline of short-beaked common dolphins (*Delphinus delphis*) in the Gulf of Vera due to an overexploitation of the dolphins' main prey items (*i.e.* round sardinella, *Sardinella aurita*) to feed the farmed tuna (Cañadas and Hammond 2008). Dolphin responses to aquaculture activities also seem to vary depending on the type (e.g., fish, oyster or mussel) and characteristics of the farms, as well as on how these impact the environment (Markowitz et al. 2004; Watson-Capps and Mann 2005; Kemper et al. 2006; Ribeiro et al. 2007; Pearson et al. 2012; Bonizzoni et al. 2014). Interactions with farms can also lead to entanglements of dolphins in aquaculture gear, resulting in injury or death (Kemper and Gibbs 2001; Kemper et al. 2005; Watson-Capps and Mann 2005; Kemper et al. 2006). The farming system employed in Coffin Bay uses structures that result in debris washing up on beaches (DEH 2004), including poles, baskets, rubber bands and plastic clips.

Although Coffin Bay is within the TPMP and the local human population is relatively small, even during peak tourist season, most human activities in the bay involve the use of boats (*i.e.* fishing, tourism cruises, and farming activities). Elsewhere, vessel traffic is known to affect dolphins' behaviour in the short-term (Bejder et al. 2006a; Lemon et al. 2006; Pirotta et al. 2015), cause injuries or death due to collisions (Kemper et al. 2005), and in cases of long-term disturbances lead to population declines or abandonment of habitat (Bejder et al. 2006b; Lusseau and Bejder 2007). How vessel traffic affects dolphin behaviour and the potential impacts on their population dynamics and distribution patterns in Coffin Bay remains unknown.

Understanding how aquaculture and vessel traffic may affect dolphins in Coffin Bay is important for the management of this multiple use marine park in SA. Currently, our ability to provide effective conservation measures to southern Australian bottlenose dolphins in Coffin Bay is hindered by the paucity of ecological and spatial information on the species and any associated threats.

1.6. Aims and specific objectives

The overall aim of this thesis is to provide baseline information on the demography and spatial ecology of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, Thorny Passage Marine Park (TPMP), South Australia. The specific objectives of this research are to:

1. Estimate sex-specific abundance, apparent survival and temporary emigration of the dolphin population inhabiting Coffin Bay (Chapter 2).

2. Determine individuals' site fidelity and sex-specific ranging patterns in the inner area of Coffin Bay (Chapter 3).

3. Investigate the spatio-temporal distribution of dolphins in relation to ecogeographical and anthropogenic variables, identify areas of high probability of dolphin occurrence, and evaluate the relevance of the sanctuary zones of TPMP for the dolphin population (Chapter 4).

1.6.1. Thesis structure

This thesis encompasses five chapters. Chapter 1 presents a general conceptual framework and rationale underlying the proposed objectives, as well as background knowledge on the species and general characteristics of the study area. Each data chapter (chapters 2, 3 and 4) has been prepared as a stand-alone manuscript to be published in peer-reviewed scientific journals. As a result, each chapter has a separate reference list and follows the reference style of the corresponding journal, and overlap between some sections of each chapter has been unavoidable. Chapter 2 is published (Passadore et al. 2017, *Aquatic Conservation: Marine and Freshwater Ecosystems*, Early View, DOI: 10.1002/aqc.2772), chapter 3 is published (Passadore et al. 2017, *Ecology and Evolution*, Early View, DOI: 10.1002/ece3.3674), and chapter 4 is yet to be submitted for publication (target journal *Ecography*). Tables and figures are integrated along the text of each chapter, and the supplementary information for these chapters is presented as Appendices at the end of the thesis. Chapter 5 corresponds to a general discussion and conclusions of the thesis.

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CHAPTER 2: Demography of southern Australian bottlenose dolphins living in a protected inverse estuary

2.0. Abstract

Assessments of demographic parameters are essential to understand the dynamics of wild populations, and for their efficient conservation and management. Here, sex-specific abundance, apparent survival and temporary emigration of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay (CB), South Australia, is investigated. Results are based on capture-recapture modelling of photo-identification data and molecular analyses of biopsy samples collected during boat-based surveys between September 2013 and October 2015 in the inner and outer areas of CB. The total super-population of dolphins (including calves) using the entire study area (263 km^2) was estimated with POPAN models at 306 (95% CI: 291–323), which included 71 (68–73) marked females and 57 (55–60) marked males. Seasonal estimates of abundance for the inner area of CB (123 km^2) obtained with Pollock's Closed Robust Design models remained relatively constant over the two years (marked females: 52–60, marked males: 46–52, and total: 193–209). The high density of dolphins inhabiting the inner area (seasonal range: 1.57–1.70 individuals/km^2), high apparent survival rates estimated for both sexes (females: 0.99; 95% CI: 0.96–1.0; males: 0.95; 0.82–0.99), and low temporary emigration rates (0.02; 95% CI: 0.01–0.11) indicate that the inner area of CB offers highly favourable habitat for these dolphins. High biological productivity and low predation risk may promote these demographic patterns in the inner area of CB. This study provides a robust baseline of sex-specific population demographics of southern Australian bottlenose dolphins with important implications for future research and their management and conservation in South Australia.

Keywords: Australia; bottlenose dolphin; capture-recapture; cetacean; demography; inshore; marine protected area; migration; population size; survival.

2.1. Introduction

Accurate assessments of demographic parameters, such as population size, survival, recruitment and movement patterns, are essential to understand the dynamics of wildlife populations. This ecological knowledge, as well as the identification of threats and impacts, is critical to determine species conservation status and establish well-informed management strategies. Long lived species, with late maturity and low reproductive rates, such as dolphins, are especially vulnerable to human impacts (Lewison Crowder, Read, & Freeman, 2004). Particularly, coastal and inshore dolphins are among the most threatened species because of their restricted geographic ranges, limited movements, and disjunct distributions, which tend to overlap with areas of intense anthropogenic activities (Reeves, Smith, Crespo, & Sciara, 2003). For those species with evidence of decline, the role of decision-makers is fundamental, as their decisions can lead to effective management actions that promote species conservation (e.g., Rojas-Bracho, Reeves, & Jaramillo-Legorreta, 2006; Turvey et al., 2007; Slooten, 2013). However, for many dolphin species inhabiting coastal and inshore waters there are simply not enough demography information to determine their status and inform management decisions (Roman, Dunphy-Daly, Johnston, & Read, 2015).

Demographic assessments of top level predators such as dolphins, which provide clear and measurable population-level objectives, should be included in management plans of Marine Protected Areas (MPAs) to ensure they are an effective tool for their conservation (Hooker et al., 2011). In South Australia (SA), a Representative System of 19 multiple use MPAs was declared by the South Australian Government in 2009 (DEWNR, 2012). One commitment of these MPAs is to guarantee the effective conservation and management of protected species (DEWNR, 2012), which include all cetacean species protected in Australia under the 'Environment Protection and Biodiversity Conservation Act' (Act, 1999). However, the current paucity of information on dolphin populations inhabiting SA waters prevents the implementation of well-informed conservation and management measures within these established MPAs.

Bottlenose dolphins (*Tursiops* spp.) inhabit the entire Australian coast (Ross & Cockcroft, 1990). A separate species from the common bottlenose (*T. truncatus*) and the Indo-Pacific bottlenose dolphin (*T. aduncus*) was recently described for inshore waters of southern and south-eastern Australia, the Burrunan dolphin (*Tursiops australis*) (Charlton-Robb et al., 2011). The taxonomic identity of the Burrunan dolphin is still contentious (Perrin, Rosel, & Cipriano, 2013; Committee on Taxonomy, 2016), and thus, they are referred to here as southern Australian bottlenose dolphins (*Tursiops* cf. *australis*). In Victoria, two inshore populations of southern Australian bottlenose dolphins have been studied, one in Port Phillip Bay (~80–120 individuals) and another in Gippsland Lakes (~50–150 individuals) (Dunn, Goldsworthy, Glencross, & Charlton-Robb, 2001; Scarpaci, Dayanthi, & Corkeron, 2003; Charlton-Robb et al., 2011; Charlton-Robb, Taylor, & McKechnie, 2015; Filby, Stockin, & Scarpaci, 2014). The species is listed as threatened under the 'Victorian Flora and Fauna Guarantee Act 1988' because of their small and resident population status (Dunn et al., 2001), as well as genetic distinctiveness (Charlton-Robb et al., 2011). In SA, there are records of the species in Spencer Gulf, Gulf St. Vincent, St. Francis Island and Coffin Bay (Bilgmann, Möller, Harcourt, Gibbs, & Beheregaray, 2007; Kemper, Bossley, & Shaughnessy, 2008; Möller, Bilgmann, Charlton-Robb, & Beheregaray, 2008). In Gulf St. Vincent, ~30 resident bottlenose dolphins inhabit the inshore waters of the Port River estuary and Barker Inlet (Steiner & Bossley 2008; Cribb, Miller, & Seuront, 2013), a highly urbanized area where a Sanctuary Zone was created to protect the dolphins (Adelaide Dolphin Sanctuary Act 2005). In the adjacent Adelaide metropolitan waters, dolphins show varying patterns of site fidelity and residency, with a population size varying from 95 to 239 individuals seasonally (Zanardo, Parra, & Möller, 2016). A preliminary study in Coffin Bay, a protected inverse estuary located within Thorny Passage Marine Park (Figure 2.1), suggested that this area may constitute an important habitat for the species, and should be considered a key site for conducting long-term research (Taylor, 2010).

One approach to investigate the demographic parameters of coastal and inshore dolphins is the application of capture–recapture modelling to photo-identification data (Hammond, Mizroch, & Donovan, 1990; Amstrup, McDonald, & Manly, 2010). Demographic parameters can differ among groups of individuals (e.g., males vs females, adults vs juveniles) within the same population (Skalski, Ryding, & Millspaugh, 2010) because of differences in individuals' social behaviour and ecology (e.g., movement patterns, home range) linked to their age and sex (Connor, Wells, Mann, & Read, 2000; Wells, 2014). Therefore, the integration of sex- and age-specific information into capture-recapture models allows for a more in-depth interpretation of a population's demography (Lebreton, Burnham, Clobert, & Anderson, 1992). However, due to the difficulties in sexing and aging free-ranging dolphins, only a few long-term studies have been able to integrate this information into the modelling of demographic parameters (Fruet, Daura-Jorge, Möller, Genoves, & Secchi, 2015; Sprogis et al., 2016).

In this study, photo-identification data of individual dolphins, biopsy sampling, and capture–recapture modelling is integrated to estimate sex-specific abundance, apparent survival and temporary emigration of southern Australian bottlenose dolphins in inshore waters of Coffin Bay, South Australia. The findings provide important information into sex-specific population parameters of this species, which should be used to inform its conservation and management.

2.2. Methods

2.2.1. Study area

Coffin Bay (CB) is a small (263 km^2) Wetland of National Importance located within the 2,472 km^2 Thorny Passage Marine Park (TPMP) in the lower part of Eyre Peninsula, South Australia (Figure 2.1). A narrow and long (5 km) spit of land, called Point Longnose, divides the bay into an inner (~123 km^2) and an outer area (~140 km^2) (Kämpf & Ellis, 2015; Figure 2.1). The inner area is a small inverse estuary consisting of several interconnected shallow (mean depth ~2.5 m) bays such as Port Douglas, Mount Dutton and Kellidie (DEH, 2004; Kämpf & Ellis, 2015; Figure 2.1), and a variety of habitats (e.g., seagrass beds, saltmarshes, salt creeks, low reefs, subtidal sandflats, and limestone ledges; Miller, Westphalen, Jolley, & Brayford, 2009; Saunders, 2009). The inner area is hypersaline during the austral summer, and freshwater input occurs during austral winter, mainly in Mount Dutton and Kellidie bays (Kämpf & Ellis, 2015). The outer area is characterized by shallow waters (<1 m depth) in the south and south-eastern sections, and by deeper waters surpassing 25 m in the central and most exposed part of the bay. The outer area is influenced by oceanographic features of the

Southern Ocean (DEH, 2004), with cold waters flowing from the south-east and warm and relatively low-nutrient waters coming from the west (Middleton & Bye, 2007).

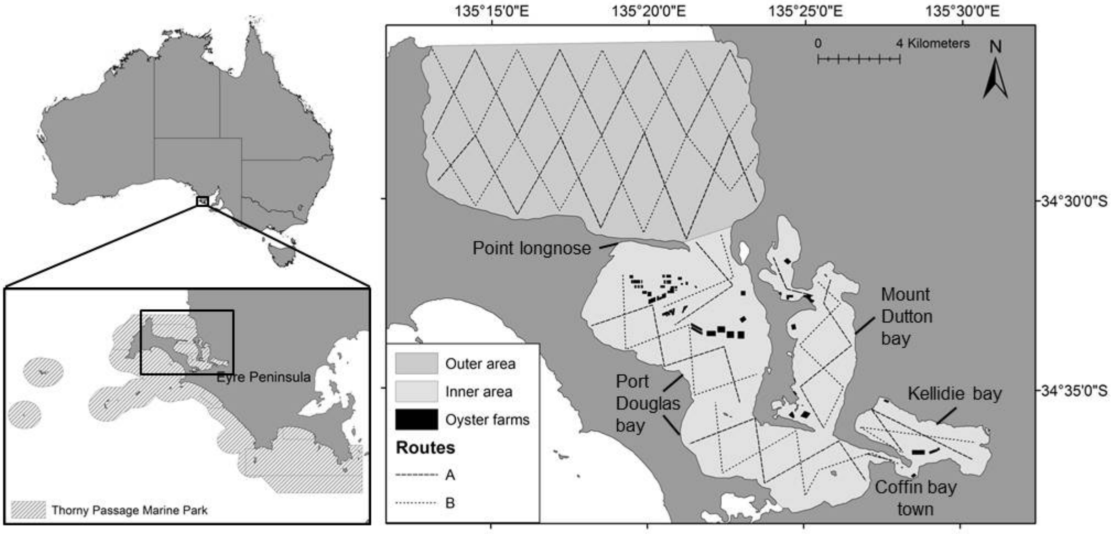

Figure 2.1. Left: Location of Coffin Bay within the Thorny Passage Marine Park, Eyre Peninsula, South Australia. Right: Study area (~263 km^2) showing the zig-zag transect layout used (Routes A and B) to cover the outer (grey) and inner (light grey) areas of Coffin Bay.

2.2.2. Data collection

Boat-based surveys for southern Australian bottlenose dolphins were conducted across the inner and outer areas of Coffin Bay during six fieldwork seasons (referred hereafter as primary sampling periods, 'P-periods') between September 2013 and October 2015 (Table 2.1).

Two different vessels were used for surveys, a 6.5 m semi-rigid inflatable with twin 80 hp outboard motors or a 7.2 m rigid aluminium vessel with twin 115 hp outboard motors. Surveys followed an 'equal spaced zigzag' transect layout designed using Distance 6.0 software (Thomas et al., 2010). Two zig-zag transect routes (Figure 2.1), with transects spaced 4 km apart, were established to ensure thorough coverage of the study area and environmental conditions (e.g., depth, distance to shore, temperature, and salinity). Each route consisted of a total transect length of approximately 124 km, with ~55 km in inner and ~69 km in outer areas. Shallow waters (<0.5 m), and the presence of oyster farms in the north-east of Port Douglas and south of Kellidie, prevented access to these areas, thus boat surveys covered 85.5 and 140 km^2 of the inner and outer areas, respectively (Figure 2.1). A single route of the entire inner and outer area took 2-4 and 2-3 days of surveys to complete, respectively. Each time a route was completed, it was considered to be a 'secondary sampling period' (hereafter 'S-period').

Surveys were undertaken during daylight hours, at an average speed of 15 km/hr and under good weather conditions (*i.e.* Beaufort state ≤3, good-average visibility, no rain or fog, swell height ≤1 m). During surveys, three to five (mode = 4) observers searched for dolphins scanning at both sides of the boat, from -5° to 90° degrees of the transect, with 7 x 50 binoculars and naked eyes. When a school of dolphins was sighted the GPS position at the transect was recorded, searching effort was suspended and dolphins were approached slowly up to a distance of 10-20 m to record data on GPS position, species identification, school size and composition (number of non-calves and calves), and to carry out photo-identification and biopsy sampling. A school of dolphins was defined as all animals seen within a radius of ~100 m (Wells, Irvine, & Scott, 1980). Dolphins in CB appear to be smaller in size in comparison to other study areas (C.P. *unpubl data*) making it difficult to distinguish among individuals' age-classes (adults, juveniles and calves) used in previous studies in SA (Peters, Parra, Skuza, & Möller, 2012; Zanardo et al., 2016). Therefore, individuals were categorized as non-calves (>1.5 m in length) and calves (≤1.5 m in length). Two experienced researchers took photographs of dorsal fins of individual dolphins using a Nikon D300s DSLR camera with a 28-300 mm zoom lens and a Canon EOS 60D with a 100-400 mm zoom lens. To minimize animal disturbance and potential effects on capture probabilities, vessel approaches to take photographs were done at slow speed and biopsy sampling started only after all the individuals within a group were photo-identified. Skin biopsy samples were obtained using a biopsy pole system for bow-riding dolphins (Bilgmann, Griffiths, Allen, & Möller, 2007), or a PAXARMS remote biopsy system specifically designed for small cetaceans (Krützen et al., 2002). At the same time dolphins were biopsied, photographs were taken to associate biopsy samples with photo-identified individuals. Samples were preserved in a 20% dimethyl sulphoxide solution saturated with sodium chloride while in the field (Amos & Hoelzel, 1990), and then frozen at -20° upon returning to the laboratory. The aim was to obtain photos of all the individuals within a school; after doing so, or when individuals were lost from sight for ≥10 minutes, researchers returned to the transect and resumed survey effort.

2.2.3. Photo-identification analysis

Individual dolphins were identified based on photographs of long lasting marks such as nicks, cuts and deformities in the edges of their dorsal fins (Würsig & Würsig, 1977; Würsig & Jefferson, 1990). All photographs taken were examined and given an overall quality ('Q1'= 'excellent'; 'Q2'= 'good'; and 'Q3'= 'poor') and distinctiveness score ('D1'= 'very distinctive', 'D2' = 'average distinctive' and 'D3' = 'Not distinctive') to minimize misidentification (based on Urian et al., 2015; see Supporting Information Table S1). The best images (right and left side, or both if available) of each individual within a school were selected by a team of research assistants. They were then assigned a new ID number or matched with the already known individuals included in the CB catalogue by two trained and experienced researchers (C. Passadore and F. Diaz-Aguirre). Only high quality photographs (*i.e.* Q1 and Q2) of distinctive individuals (*i.e.* D1 and D2) were used for analyses. Calves were included in the D3 category for analysis purposes. Data of individuals with D3 dorsal fins (including calves) were considered to determine the proportion of marked individuals in the population (see below). DISCOVERY (version 1.2.) was used to process, match, catalogue and manage all the photo-identification data (Gailey & Karczmarski, 2013).

2.2.4. Sexing individuals

DNA from biopsy samples was extracted using a salting-out protocol (Sunnucks & Hales, 1996). The sex of sampled dolphins was determined by amplification of fragments of the ZFX and SRY genes through the polymerase chain reaction (PCR) (Gilson, Syvanen, Levine, & Banks, 1998). Individuals were also considered females if they were recorded swimming accompanied by a dependent calf on ≥3 different survey days.

2.2.5. Encounter rates

Encounter rates were determined as the number of non-calf individuals photo-identified (D1 and D2) per km of transects surveyed on effort in each S-period. Marked dolphins sighted more than once within a single S-period were only counted once. Encounter rates were summarized (*i.e.* X ± SE) across all S-periods within each P-period for inner and outer areas separately to provide a standardized measure of the number of photo-identified dolphins in each area.

2.2.6. Estimates of population parameters

Capture-recapture histories of distinctive individuals were used to estimate abundance, apparent survival and temporary emigration of marked individuals using the program MARK version 7.1 (White & Burnham, 1999). An individual was considered 'captured' when it was first photo-identified, and 'recaptured' when photo-identified thereafter. Due to uneven survey coverage and differences in encounter rates between inner and outer areas (see Table 2.1); two different approaches to estimate population parameters were used. First, the POPAN formulation of the classic Jolly-Seber open population models (Schwarz & Arnason, 1996) was used, and capture-recapture histories of inner and outer areas pooled together to estimate the total number of individuals that utilised the entire study area over the study period (*i.e.* super-population, Crosbie & Manly, 1985; Schwarz & Arnason, 1996). Secondly, given the higher survey effort and dolphin encounter rates in the inner area compared to the outer area (Table 2.1), capture-recapture records of distinctive individuals found in the inner area were used to estimate abundance, apparent survival and temporary emigration under Pollock's Closed Robust Design (hereafter referred to as 'PCRD', Pollock, 1982; Kendall & Nichols, 1995; Kendall, Pollock, & Brownie, 1995; Kendall, Nichols, & Hines, 1997). To determine sex-specific demographic parameters, both datasets were sub-divided into three groups: females, males, and individuals of unknown sex (see Table 2.2).

Table 2.1. Summary of survey effort including number of survey days, number of secondary sampling periods (S-periods), average number of days apart needed to complete S-period, total transect length surveyed on-effort, number of southern Australian bottlenose dolphin schools encountered on-effort and encounter rate per primary sampling period (P) in inner and outer areas of Coffin Bay, South Australia, between September 2013 and October 2015.

Primary sampling periods (P)	Days of survey	No. of S-periods		Average number of days apart to complete S-period (± SD)		Total transect length surveyed on-effort (km)		No. of schools sighted		Encounter rate No. of marked dolphins per km of transect (± SD)	
		Inner	Outer	Inner	Outer	Inner	Outer	Inner	Outer	Inner	Outer
P1: Spring 2013	26	7	1	9.6 ± 4.9	7 ± 0	379.9	67	99	2	0.82 ± 0.45	0.37 ± 0
P2: Summer-autumn 2014	29	8	3	8.9 ± 5.6	5.3 ± 5.8	435.6	208.8	113	8	0.76 ± 0.33	0.23 ± 0.18
P3: Winter 2014	22	5	2	11.2 ± 6.2	5 ± 4.2	271	137.9	127	8	1.26 ± 0.24	0.39 ± 0.13
P4: Summer 2014-2015	20	5	1	9.6 ± 8.8	2 ± 0	271	69	70	6	0.83 ± 0.32	0.23 ± 0
P5: Autumn-winter 2015	27	7	2	8.6 ± 4.5	7 ± 7.1	382.4	137.9	144	6	1.07 ± 0.28	0.21 ± 0.16
P6: Winter-spring 2015	27	7	1	7 ± 2	2 ± 0	379.9	67	148	2	0.96 ± 0.28	0.07 ± 0
TOTAL	151	39	10	9 ± 5.2	5.1 ± 4.3	2119.8	687.6	701	32	0.93 ± 0.35	0.26 ± 0.15

Table 2.2. Summary of the capture-recapture datasets used for estimation of demographic parameters of southern Australian bottlenose dolphin in Coffin Bay, South Australia: a) capture-recapture dataset of the entire study area (inner and outer) used to build POPAN models; b) capture-recapture dataset of the inner area only, used to build Pollock's Closed Robust design models (PCRD). Table includes primary sampling periods (P-periods), time intervals (in decimal years) between P-periods, number of secondary sampling periods (S-periods) within each P-period, and number of photo-identified individuals (total, females, males and unknown sex) of southern Australian bottlenose dolphins per P-period over the 2013-2015 study period.

Primary sampling period (P)	*a) POPAN: Inner and outer area*[1]						*b) PCRD: Inner area*					
	Time intervals (year^{-10})	No. of S-periods[1]	Total	Females	Males	Unknown sex	Time intervals (year^{-10})	No. of S-periods	Total	Females	Males	Unknown sex
P1	0	1	109	34	33	42	0	7	137	50	43	44
P2	0.416	3	148	47	41	60	0.426	8	136	49	43	44
P3	0.390	2	120	47	38	35	0.393	5	147	55	49	43
P4	0.419	1	74	25	22	27	0.381	5	131	47	40	44
P5	0.271	2	104	41	25	38	0.349	7	148	57	45	46
P6	0.366	1	65	27	24	14	0.362	7	140	57	44	39
Total	---	10	220	70	57	93	---	39	179	62	52	65

[1] For POPAN models the photo-identification data obtained in each S-period was pooled by P-period, and an encounter parameter to weight the number of S-periods per P-period (p_{effort}) was tested in the model selection process.

2.2.6.1. *Super-population size, apparent survival and probability of entry for entire Coffin Bay*

POPAN models were used to estimate the super-population ($\widehat{N}_D$), apparent survival (Φ), capture probabilities (p) per P-period, and probability of entry of individuals from the super-population into the sampled population between sampling events (p_{ent}) (Schwarz & Arnason, 1996). Within a single P-period the entire study area was surveyed one to three times (S-periods) (Table 2.2); each of this S-periods consisted of a complete survey of the outer area transects plus a complete survey of the inner area transects. S-periods were separated by one to 11 days apart within a P-period ($\bar{X}$ ± SD = 7 ± 4 days, n = 4), and 79 to 135 days apart between P-periods ($\bar{X}$ ± SD = 108 ± 21 days, n = 5). For POPAN models, each S-period within a P-period was pooled to form a single capture history, for a total of six sampling P-periods. To obtain consistent per annum estimates of apparent survival the time intervals between P-periods (Table 2.2) were quantified as decimal years between their mid-dates (Tezanos-Pinto et al., 2013).

POPAN models were fit to the CB dataset, with parameters set to constant (.) or to vary with time (t), and to be equal for all individuals or dependent on individuals' sex (*i.e.* sex: *groups*, in model notation). Model building followed a step-forward process where, in each step, models were selected based on Akaike Information Criterion corrected for small sample size (AICc); the model with lowest AICc was considered the most parsimonious and was selected as the basic model for the following step (Burnham & Anderson, 2002). In the first step, models with different configurations of p were compared. To account for the varying number of S-periods per P-period, a model with encounter probabilities conditional to the number of S-periods (p_{effort}) was fitted (*i.e.* P-periods with the same number of S-periods were assigned the same capture parameter, e.g., $p_{effort1}$ to P-periods P1, P4 and P6). In the second step, models with different configuration of Φ were explored. In the third step, models with different p_{ent} were tested (see Supporting Information Table S3). As p_{ent} was set to vary between P-periods but restricted to sum one, the link function used for p_{ent} was *Multinomial logit*. For Φ and p the *Sin* link function was used, while for $\widehat{N}_D$ a *Log* link function was applied (Cooch & White, 2014). Finally, to account for model selection uncertainty (Buckland, Burnham, & Augustin, 1997), final population parameters were estimated by weight-averaging the estimates of all suitable models according to their likelihood within a set of models (*i.e.* from the models ranked by their AICc, the ones with a cumulative AICc weight ≥99.6% were averaged).

2.2.6.2. *Seasonal abundance, apparent survival and temporary emigration in inner area of Coffin Bay*

To estimate population parameters of the study population inhabiting the inner area of CB the PCRD models were used. Under the PCRD formulation, the population is considered open (*i.e.* a scenario with migration, birth and deaths) between P-periods, and assumed closed (*i.e.* no migration and no significant changes due to deaths and births) during S-periods (Kendall et al., 1997). Closed population models can be used to estimate capture probabilities (p) and abundance (N) within each P-period, and open-population models can be used to estimate apparent survival (Φ) and temporary emigration parameters (γ' as the probability of staying away from the study area given that the animal has left the area; and γ'' as the probability of emigration from the study area) between P-periods (Pollock, Nichols, Brownie, & Hines, 1990; Kendall et al., 1997). For PCRD models a total of six P-periods, with five to eight S-periods in each P-period, were included for the analysis (Table 2.2).

Huggins's parameterization method of PCRD within MARK was used to estimate N as a derived parameter (Huggins, 1991); *Sin* was set as link function and second partial derivate of the log-likelihood function for variance estimation. The PCRD model building process was the same as the one followed for the POPAN models. In the first step of PCRD model building, capture (p) and recapture probability (c) were compared using $p = c$, with parameters held as either constant (.) or varying with tim*e (t*), and affected by sex (*group*) or not, while temporary emigration ($\gamma' = \gamma'' = 0$) was ignored, and Φ set to vary with time between P-periods and by sex (*group*s*t*). In the second step, models with different Φ configurations were compared. In the third step different dolphin movement patterns were tested by including random ($\gamma' = \gamma''$) and Markovian ($\gamma' \neq \gamma''$) emigration models with or without time effects (*i.e.* varying between P-periods) on γ (Kendall et al., 1997) (see Supporting Information Table S4). Determining the occurrence of time effects on migration parameters can help detect if there are differences in immigration or emigration of individuals between seasons (P-periods). As the precision of the estimates of demographic parameters can be influenced by the effective capture probabilities per P-period (p_P), p_P was calculated as follows: p_P = 1 - (1-p_{s1})(1-p_{s2})...(1-p_{sk}), where s1, s2,... sK, are the capture probabilities of the S-periods in each P-period (Cooch and White, 2014; Rankin et al., 2016).

2.2.6.3. *Assumptions of models and goodness of fit*

Several assumptions have to be met under the POPAN and PCRD models to obtain accurate and precise estimates of the parameters. The assumptions, *goodness-of-fit* (GOF) tests and specific tests to validate assumptions for both POPAN and PCRD models, are presented in Supporting Information: Methods S1, Table S2.

2.2.6.4. *Total population sizes*

The capture-recapture models (POPAN and PCRD) estimate the abundance of the marked proportion (*i.e.* individuals with dorsal fins D1 and D2) of the population ($\widehat{N}_m$). Because these models produce estimates for each sex-group separately, total $\widehat{N}_m$ was obtained by adding the estimated $\widehat{N}_m$ per group (*i.e.* $\widehat{N}_m = \widehat{N}_{m-females} + \widehat{N}_{m-males} + \widehat{N}_{m-unknonw-sex}$). Finally, to estimate the total population size ($\widehat{N}_t$), the $\widehat{N}_m$ values were adjusted to incorporate the proportion of distinctly marked individuals (D1 and D2) individuals in the population ($\hat{\theta}$) following (Wilson, Hammond, & Thompson, 1999; Nicholson, Bejder, Allen, Krützen, & Pollock, 2012):

$$\widehat{N}_t = \frac{\widehat{N}_m}{\hat{\theta}}$$

Schools where the group size estimated *in situ* was the same as group size after processing photographs in the lab were used to estimate $\hat{\theta}$; *i.e.* where all individuals were photographed with sufficient quality (*i.e.* Q1 and Q2), including the not distinctive individuals (D3). The total number of marked individuals was divided by the total number of dolphins encountered (including calves) within these groups (Nicholson et al*.,* 2012). Standard errors and 95% confidence intervals for the total population size were determined following the "delta method" (Seber, 1982; Williams, Nichols, & Conroy, 2002):

$$SE(\widehat{N}_t) = \sqrt{\widehat{N}_t^{\,2}\left(\frac{SE(\widehat{N}_m)^2}{\widehat{N}_m^{\,2}} + \frac{1-\hat{\theta}}{n\hat{\theta}}\right)}$$

where n is the total number of dolphins from which $\hat{\theta}$ was derived. The log-normal 95% confidence intervals of the total population were calculated by either dividing or multiplying $\hat{N}_t$ by the factor C (Burnham, 1987) as follows:

$$C = exp\left(1.96\sqrt{\ln\left(1 + \left(\frac{SE(\hat{N}_t)}{\hat{N}_t}\right)^2\right)}\right)$$

$$\hat{N}_t^{\,Lower} = \frac{\hat{N}_t}{C} \text{ and } \hat{N}_t^{\,Upper} = \hat{N}_t \times C$$

2.3. Results

2.3.1. Survey effort, photo-identification and encounter rates

Over 151 days between September 2013 and October 2015, a total of 39 S-periods in the inner area (~2,120 km of transect effort) and 10 S-periods in the outer area (~688 km of transect effort) of CB were completed (Table 2.1). During surveys 733 schools of dolphins were encountered; 701 in inner, and 32 in outer areas (Table 2.1). Schools varied in size from one to 45 dolphins, with an overall mean school size (± SD) of 5.4 ± 5.8. A total of 227 distinctive non-calf individuals were photo-identified during the study period, of which 131 (58%) were exclusively recorded in the inner area, 48 (21%) in the outer area only, and 48 (21%) were seen in both inner and outer areas.

The mean encounter rate per P-period was consistently higher for inner area than for outer area (Table 2.1). The overall mean number (± SD) of marked individuals per kilometre of transect surveyed on effort was 0.93 ± 0.35 in the inner area and 0.26 ± 0.15 in the outer area. The cumulative number of all photo-identified dolphins over time (*i.e.* discovery curve), reached a plateau at approximately the third primary sampling period for both the entire CB study area and the inner area dataset (Figure 2.2). The discovery curves of photo-identified females, males and individuals of unknown sex followed a similar pattern, with ≥90% of individuals in each dataset photo-identified by the third primary sampling period (Figure 2.2).

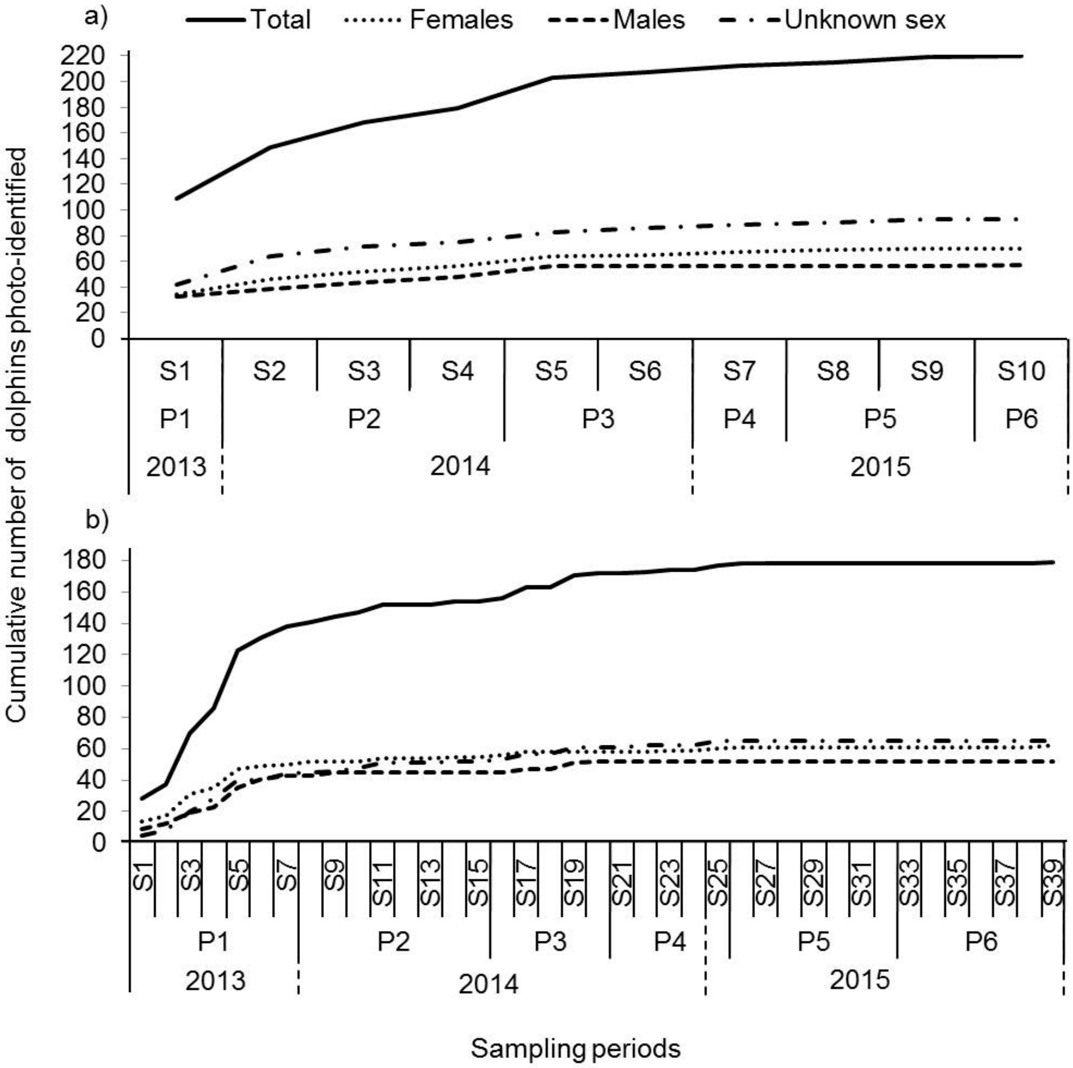

Figure 2.2. Discovery curve: cumulative number of total and sex-specific groups (*i.e.* females, males and unknown sex) of southern Australian bottlenose dolphins photo-identified (D1 and D2) across primary (P) and secondary (S) sampling periods between September 2013 and October 2015 in a) the entire Coffin Bay study area and b) inner area only. Data is pooled by S as each one represents the same amount of survey effort in km.

2.3.2. Sexing individuals

Fifty-eight females and 57 males were identified from genetic analysis of 115 biopsy samples. Additionally, 12 dolphins were identified as females based on mother-calf associations, bringing the total number of females to 70 (Table 2.2). The sex ratio of biopsied individuals was balanced, with 0.98 males per female according to DNA analysis.

2.3.3. Super-population size in Coffin Bay

The photo-identification data recorded during the 10 S-periods when all transects of inner and outer areas were completed included 220 dolphins (Table 2.2). Ten POPAN models were fitted to this dataset to estimate sex-specific super-population size and associated apparent survival (Φ), capture probabilities (p), and probability of entry (p_{ent}) (Supporting Information Table S3). The GOF test with U-CARE (Global TEST, number of groups = 3, Chi-square test, χ^2= 28.249, p = 0.7027, d.f. = 33) indicated that the assumptions of homogeneous capture and survival probabilities were met. The derived $\hat{c}$ value at 0.86 suggested some under-dispersion in the data, thus models were compared using $\hat{c}$ = 1 output and model selection was based on AICc (Supporting Information: Methods S1, Table S2). The POPAN model with most support was the one with Φ constant but varying between sex groups, p time dependent and not influenced by sex, and p_{ent} time dependent (Supporting Information Table S3).

The sex-specific estimates of super-population (± SE) obtained by weight-averaging the POPAN models were: 71 ± 1 females, 57 ± 1 males and 101 ± 3 individuals of unknown sex (Table 2.3a), which results in a total estimate of 229 marked individuals. The total super-population size estimate, considering the overall marked proportion of individuals ($\hat{\theta}$ = 0.75), was 306 (95% CI: 291–323) dolphins for the entire CB study area over the study period, with a density of 1.16 individuals/km^2 (Table 2.4a).

Final parameter estimates obtained by weight-averaging POPAN models (Table 2.3a) indicated high and similar apparent survival estimates for females and males (Φ = 0.98), while for the unknown sex group survival was relatively low (Φ = 0.67). The averaged estimates of recapture probabilities reflected the survey effort with lower (0.37–0.38), intermediate (0.56–0.58) and higher (0.75) recapture probability values obtained for P-periods with one, two and three S-periods, respectively. The averaged estimates of probability of entry (p_{ent}) showed that half of the individuals of the super-population were captured in the first P-period; from that to the second P-period the remaining 40% of the super-population entered the sampled population; and by the third P-period almost all individuals of the super-population had already been photo-identified (Table 2.3a). This pattern matches the plateau reached in the discovery curve by the third P-period (Figure 2.2).

2.3.4. Inner area population parameters

The 39 S-periods completed in the inner area comprised 179 distinctive dolphins (Table 2.2). Most of the PCRD models' assumptions were satisfied (see Supporting Information Methods S2), however, there was evidence of transience for males (TEST 3.SR: Chi-square test, χ^2 = 11.3110, df = 1, p = 0.0008) and unknown-sex groups (TEST 3.SR: Chi-square test, χ^2 = 11.6814, df = 3, p =0.0086). The GOF with 'median $\hat{c}$' approach in MARK showed that the global Cormack-Jolly-Seber model fitted to the inner area dataset had some over-dispersion ($\hat{c}$ = 1.35, sampling SE = 0.037). Therefore, models were adjusted using $\hat{c}$ and model selection was based on QAICc values. A total of 13 PCRD models were fitted to the data to estimate sex-specific population parameters of the dolphins encountered in the inner area (Supporting Information Table S4). The two models used for obtaining weight-averages of population parameters had the same configuration of survival ($\Phi_{(group*.)}$) and capture ($p_{(s*t)}=c$) probabilities but differed in the movement parameter, one with Markovian emigration ($\gamma' \neq \gamma''$) and the other with no movement ($\gamma' = \gamma'' = 0$) (Supporting Information Table S4).

Seasonal estimates of the marked proportion of the population ($\widehat{N}_m$) showed that the numbers of females, males and unknown-sex individuals remained relatively constant during the two years study period (Table 2.3b). The total number of marked dolphins obtained by adding the seasonal abundances by sex varied slightly, from 145 (CI 95%: 132–158) to 161 (135–187) (Table 2.4b). Considering the proportion of marked individuals per P-period, which ranged from 0.71 to 0.80, the total population of dolphins using the inner area of CB varied from 193 (171–217) dolphins in spring 2013 (P1) to 209 (191–228) in autumn 2015 (P5), with derived seasonal densities of 1.57–1.70 individuals/km^2 (Table 2.4b).

The estimated annual survival of dolphins of known sex in the inner area was similar to that of the total area (Table 2.3), with slightly higher estimates for females (Φ = 0.99) than for males (Φ = 0.95), and lower for unknown sex individuals (Φ = 0.79; Table 2.3b). The movement parameters were not affected by sex (Table 2.3b), and the weight-averaged estimates resulted in an almost null probability of emigration (*i.e.* γ'': X ± SE = 0.02 ± 0.02) and a low probability of staying away from the study area given that the animal has left the area (*i.e.* γ': X ± SE = 0.3 ± 0.27). These values highlight a high residency of dolphins in the inner area. Capture probabilities varied between S-periods from 0.10 to 0.59 ($\bar{X}$ ± SD = 0.35 ± 0.12, n = 39), while effective capture probabilities per P-period was high and varied from 0.81 to 0.97 ($\bar{X}$ ± SD = 0.92 ± 0.06, n = 6; Table 2.3b).

Table 2.3. Estimates of sex-specific (*i.e.* females, males and unknown sex individuals) demographic parameters of southern Australian bottlenose dolphins in Coffin Bay, South Australia between September 2013 and October 2015: a) POPAN parameters estimates obtained for the entire study area by weight-averaging the best models (*i.e.* that contributed 99.6% of the cumulative AICc weight; Supporting Information Table S3); b) Pollock's Closed Robust design (PCRD) parameters estimates obtained for the inner area of Coffin Bay only by weight-averaging the best models (*i.e.* that contributed with 99.6% of the cumulative AICc weight; Supporting Information Table S4).

a) POPAN: Inner and outer areas

	Parameter[1]	Females	Males	Unknown sex
Apparent survival Φ ± SE (95 % CI)	$\Phi(.)$	0.98 ± 0.05 (0.28–1)	0.98 ± 0.04 (0.17–1)	0.67 ± 0.06 (0.54–0.78)
Recapture probability p ± SE (95 % CI)	p_{P1}	Confounding (not estimable)[2]		
	p_{P2}	0.75 ± 0.04 (0.66–0.83)[2]		
	p_{P3}	0.58 ± 0.04 (0.51–0.65)[2]		
	p_{P4}	0.38 ± 0.04 (0.31–0.46)[2]		
	p_{P5}	0.56 ± 0.05 (0.47–0.65)[2]		
	p_{P6}	0.37 ± 0.06 (0.27–0.49)[2]		
Probability of entry p_{ent} ± SE (95 % CI)	$p_{ent\ \mathrm{P1\text{-}P2}}$	0.41 ± 0.06 (0.31–0.52)	0.41 ± 0.06 (0.3–0.53)	0.41 ± 0.05 (0.32–0.51)
	$p_{ent\ \mathrm{P2\text{-}P3}}$	0.1 ± 0.04 (0.05–0.21)	0.1 ± 0.04 (0.05–0.21)	0.1 ± 0.04 (0.05–0.21)
	$p_{ent\ \mathrm{P3\text{-}P4}}$	0 ± 0 (0–0)	0 ± 0 (0–0)	0 ± 0.01 (-0.01–0.01)
	$p_{ent\ \mathrm{P4\text{-}P5}}$	0 ± 0 (0–0)	0 ± 0 (0–0)	0 ± 0 (-0.01–0.01)
	$p_{ent\ \mathrm{P5\text{-}P6}}$	0 ± 0 (0–0)	0 ± 0 (-0.01–0.01)	0 ± 0 (0–0)

Marked super-population size $\widehat{N}_D$ ± SE (95 % CI)	$\widehat{N}_D$	71 ± 1 (68–73)	57 ± 1 (55–60)	101 ± 3 (95–106)
		b) PCRD: Inner area		
	Parameter[1]	Females	Males	Unknown sex
Survival probability Φ ± SE (95 % CI)	$\Phi_{(.)}$	0.99 ± 0.02 (0.96–1)	0.95 ± 0.04 (0.82–0.99)	0.79 ± 0.05 (0.67–0.88)
Temporary emigration γ″ ± SE (95 % CI)	$\gamma''_{(.)}$		0.02 ± 0.02 (0.01–0.11)[2]	
Temporary immigration γ′ ± SE (95 % CI)	$\gamma'_{(.)}$		0.3 ± 0.27 (0.03–0.84)[2]	
Effective detection probability (*dp*)	dp_{P1}		0.93[2]	
	dp_{P2}		0.94[2]	
	dp_{P3}		0.94[2]	
	dp_{P4}		0.81[2]	
	dp_{P5}		0.97[2]	
	dp_{P6}		0.96[2]	
Marked population size $\widehat{N}_m$ ± SE (95 % CI)	$\widehat{N}_{mP1}$	54 ± 6 (43–65)	46 ± 5 (37–56)	47 ± 5 (38–57)
	$\widehat{N}_{mP2}$	52 ± 2 (48–57)	46 ± 2 (42–50)	47 ± 2 (43–51)
	$\widehat{N}_{mP3}$	59 ± 2 (54–63)	52 ± 2 (48–57)	46 ± 2 (42–50)
	$\widehat{N}_{mP4}$	58 ± 5 (49–67)	49 ± 4 (41–57)	54 ± 4 (45–63)
	$\widehat{N}_{mP5}$	59 ± 2 (56–62)	46 ± 1 (44–49)	47 ± 1 (45–50)
	$\widehat{N}_{mP6}$	60 ± 2 (55–64)	46 ± 2 (42–50)	41 ± 2 (37–44)

[1] The subscripts of the parameters indicate the corresponding P-period (*i.e.* $_{P1}$, $_{P2}$, $_{P3}$, $_{P4}$, $_{P5}$ or $_{P6}$), the period for which the parameter was determined (e.g., $_{P1\text{-}P2}$: from P1 to P2), or if the parameter was held constant (*i.e.* $_{(.)}$) between P-periods.

[2] A single parameter estimate is shown as there was not sex effect in that parameter among the selected models (Supporting Information Table S3, S4), thus, the estimate is the same for females, males and individuals of unknown sex.

Table 2.4. Marked ($\widehat{\boldsymbol{N}}_{\boldsymbol{m}}$) and total ($\widehat{\boldsymbol{N}}_{\boldsymbol{t}}$) population size of southern Australian bottlenose dolphins in Coffin Bay in: a) the entire study area (inner and outer) during the period September 2013 – October 2015; b) the inner area only per primary period (P). Values of $\widehat{\boldsymbol{N}}_{\boldsymbol{m}}$ were obtained by summing the population sizes estimated for marked females, males and unknown-sex individuals of the corresponding weight-averaged POPAN and PCRD models (Table 2.3). The proportion of marked individuals ($\widehat{\boldsymbol{\theta}}$) was used to derive $\widehat{\boldsymbol{N}}_{\boldsymbol{t}}$ values, and the area size to derive the density of dolphins per km^2.

Study area	Period	Marked population size $\widehat{N}_m$ ± SE (95 % CI)	Proportion of marked individuals ($\widehat{\theta}$)	Total population size $\widehat{N}_t$ ± SE (95 % CI)	Area size (km^2)	Density (No. individuals/km^2)
a) Inner and outer	2013 – 2015	229 ± 5 (218–239)	0.75	306 ± 8 (291–323)	263	1.16
b) Inner	P1	147 ± 7 (133–161)	0.76	193 ± 12 (171–217)	123	1.57
	P2	145 ± 7 (132–158)	0.71	205 ± 13 (181–233)		1.67
	P3	156 ± 7 (143–170)	0.76	205 ± 11 (184–229)		1.67
	P4	161 ± 13 (135–187)	0.80	200 ± 18 (168–239)		1.63
	P5	153 ± 4 (144–161)	0.73	209 ± 10 (191–228)		1.70
	P6	146 ± 5 (136–157)	0.73	200 ± 10 (182–220)		1.63

2.4. Discussion

Very little is known about the ecology of southern Australian bottlenose dolphins. Knowledge about their population demography is important towards understanding their ecology and for guiding conservation and management efforts of this putative new species of bottlenose dolphin. This study provides novel information about their population dynamics by estimating sex-specific population parameters of abundance, apparent survival and temporary emigration of a population inhabiting Coffin Bay, an inverse estuary within the Thorny Passage Marine Park, South Australia. Results obtained using complementary capture-recapture modelling approaches to take into account differences in survey effort between the inner and outer areas of Coffin Bay, indicate that there is a high year-round abundance and density of dolphins, with high apparent survival for both females and males, as well as low emigration from the inner area. These findings highlight the high conservation value of this area for the species.

2.4.1. Modelling approach

In this study, the use of both POPAN and PCRD were considered as complementary approaches. POPAN models allowed the use of a reduced dataset to better understand the total number of dolphins using the entire study area; while PCRD models were used to explore seasonal variations in abundance and movement patterns in the inner area based on a larger capture-recapture dataset. Overall, most of the assumptions for both POPAN and PCRD approaches were satisfied, and the data used fitted the models well. Estimates of probability of staying away from the study area given that the animal has left the area in PCRD models for the inner area of Coffin Bay had wide confidence intervals across the study period. This is a recurrent issue of PCRD models (Kendall et al., 1995; Rankin et al., 2016) and thus its interpretation should be taken with caution. In general, wide confidence intervals around population parameters such as apparent survival and temporary emigration have been attributed to low effective detection probabilities (≤ 0.70) within primary periods (see Silva, Magalhães, Prieto, Santos, & Hammond, 2009; Hunt et al., 2017), which could cause survival and migration parameters to be correlated due to sparse data (Rankin et al., 2016). However, this was not to the case of the PCRD models as the effective capture probabilities reported here were high, leading to robust estimates of seasonal abundance, survival and temporary emigration from the PCRD models.

The records of distinctive individuals in the inner and outer area of Coffin Bay suggest that the super-population of the entire Coffin Bay comprised a majority of dolphins that seem to have used exclusively the inner area during the study period (*ca.* 60%). Individuals using both areas during the study (*ca.* 20%) could be responsible for the transience effect observed in the inner area dataset, and/or the low emigration parameters detected with PCRD models. Future research using two vessels to survey the inner and outer areas of Coffin Bay simultaneously and integrating capture-recapture multi-state models (Brownie, Hines, Nichols, Pollock, & Hestbeck, 1993) will help unravel the movement patterns of dolphins between these areas.

2.4.2. Abundance and density estimates

Differences in the sizes of study areas makes comparison of abundance estimates between studies difficult, and thus comparing density derived values is more appropriate (e.g., Shane, Wells, & Würsig, 1986; Brown, Bejder, Pollock, & Allen, 2016; Parra & Cagnazzi, 2016). Density of southern Australian bottlenose dolphins using the entire Coffin Bay between 2013 and 2015 was approximately one individual/km^2 and slightly higher in the inner area. These densities, particularly in the inner area, are higher than the dolphin densities observed for coastal Adelaide (*i.e.* 0.48–1.22 individuals/km^2, derived from Zanardo et al., 2016). Thus, Coffin Bay, and particularly the inner area, appears to be an important habitat for southern Australian bottlenose dolphins in South Australia.

Dolphin movements and habitat use are usually linked to their breeding requirements and/or to variations in the abundance and distribution of their prey and predators (e.g., Heithaus & Dill, 2002; Sprogis et al., 2016), which in turn is driven by seasonal variations in habitat conditions. The high abundance of both females and males in Coffin Bay's inner area across seasons suggests this area offers highly favourable year-round habitat conditions. Upwelling events off the adjacent continental shelf during summer-autumn months bring cold nutrient rich water into nearshore waters of Coffin Bay resulting in high productive waters (Kämpf, Doubell, Griffin, Matthews, & Ward, 2004; Kämpf & Ellis, 2015). This high productivity coupled with the high habitat diversity found within Coffin Bay (Miller et al., 2009) likely promotes a high prey availability year round. Coffin Bay is considered a regionally important nursery and feeding area for several fish species which are known prey items of bottlenose dolphins in SA (Gibbs, Harcourt, & Kemper, 2011), including sand flathead (*Platycephalidae* sp.), yellow-eye mullet (*Aldrichetta forsteri*), Australian salmon (*Arripis truttacea*), garfish (*Hyporhamphus melanochir*), Australian herring (*Arripis georgianus*), snapper (*Centroberyx* sp.) and trevally (*Pseudocaranx* spp.) (DENR, 2010). Furthermore, the shallow waters (mean depth ~2.5 m) of the inner bays, and the relatively narrow connection between the inner area and the more exposed waters of the outer area (Kämpf & Ellis, 2015), could be providing a degree of protection to the dolphins by limiting, to some extent, the access of predators such as white sharks (*Carcharodon carcharias*) to the inner area, resulting in lower predation risk. Future studies on dolphins' diet, and prey and predator abundance within Coffin Bay are needed to test these hypotheses and to better understand the ecological factors sustaining the high density of dolphins in this area.

2.4.3. Survival estimates

Apparent survival rates were high and similar across sexes (0.98 for both sexes in entire Coffin Bay, and 0.99 and 0.95 for females and males, respectively, in the inner area), indicating negligible mortality and permanent emigration of individuals of known sex during the study period. These are within the range of survival estimates of other bottlenose dolphins inhabiting coastal-estuarine waters (e.g., *T. truncatus* in Patos Lagoon, Brazil, Fruet et al., 2015; *T. aduncus* in Bunbury, Western Australia, Sprogis et al., 2016). The slight difference between annual survival rates for females and males from the inner area may be a result of the transience effect detected for the male dataset. If some males were not captured during the last P-periods in the inner area because they were in the outer area, estimates of apparent survival from PCRD models could be confounded with mortality. Given the short term sampling of this study, the long-term monitoring of this population and the continuation of demographic studies are important to confirm the accuracy of the survival estimates presented.

The lower apparent survival obtained for the unknown sex group could be the result of a combination of factors. This group may be composed by individuals that have low capture probabilities, larger home ranges, permanently emigrated, or died during the study period (Nichols, Kendall, Hines, & Spendelow, 2004). Juveniles and/or sub-adults normally have higher mortality rates than adults resulting in lower survival (see Silva et al., 2009; Fruet et al., 2015). Our discovery curve (see Figure 3.2) does not show the incorporation of new individuals in the late stages of our study period; discarding the possibility that a large proportion of the unknown sex group is composed of juveniles and/or sub-adults that became marked during the latest stages of the study period. However, individuals of unknown sex showed some evidence of transience (*i.e.* were seen in only one P-period), which may result in low capture probabilities and thus in lower apparent survival regardless of age class or sex. Future studies on Coffin Bay dolphins should attempt to improve age class determination and incorporate further classes into demographic analysis to define if there are differences in survival rates between adults, sub-adults, juveniles and calves.

2.4.4. Emigration parameters

Sex-biased dispersal is widespread among mammals, but the direction and intensity of the bias can vary broadly among species and populations (see review from Lawson Handley & Perrin, 2007). While in some coastal and estuarine dolphin populations females tend to be philopatric and males tend to disperse (e.g., *T. aduncus* in Jervis Bay and Port Stephens, Australia, Möller & Beheregaray, 2004), in others there is no sex-biased in dispersal (e.g., *T. truncatus* in Patos Lagoon, Brazil, Fruet et al., 2015). The PCRD models for Coffin Bay's inner area suggested that temporary emigration of female and male dolphins was low and not time dependent, indicating very little out movement of animals of both sexes among P-periods. This high site fidelity to the inner area of Coffin Bay and relatively low movement out of it is further supported by the high probability of an individual being in the inner area in a P-period given it was there in the previous P-period ($1 - \gamma'' = 0.98$) and the derived return rate ($1 - \gamma' = 0.7$), which shows that dolphins that temporarily emigrated from the inner area had a high probability of returning.

2.4.5. Implications for conservation

Findings of this study indicate that Coffin Bay supports a relatively high density of southern Australian bottlenose dolphins, which is among the highest recorded for this putative species. As Coffin Bay is already within one of South Australian's marine parks, the management framework to protect this abundant, resident population is already established. However, the effectiveness of the establishment of the Thorny Passage Marine Park in protecting Coffin Bay's dolphins remains unknown and there are no specific management strategies directed towards protecting this local dolphin population from potential anthropogenic impacts. Only 6.2% of Coffin Bay is currently classified as a Sanctuary Zone (*i.e.* area of high conservation value that allows only low-impact recreation activities, and prohibits fishing). The rest of Coffin Bay is classified as a General Managed Use Zone (49.4%; allows all recreational activities, including fishing), or a Habitat Protection Zone (44.3%; protects sea floor, allows all recreational activities, including fishing, but prohibits prawn trawling). Consequently, in the majority of Coffin Bay, dolphins are exposed to potentially detrimental human activities (e.g., recreational fishing, oyster aquaculture, water sports, and tourism cruises, Saunders, 2009; DENR, 2010). Long-term monitoring is therefore needed to assess population trends, evaluate impacts of potential threats, and identify critical areas for dolphins in Coffin Bay. Such monitoring in Coffin bay and in other Marine Parks across South Australia will help determine whether the current zoning is effective in contributing to this species' conservation, if re-zoning is needed, or if other specific management measures are required.

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2.6. Supporting information

Table S1: Photographic quality and scale scores, and distinctiveness classification of dorsal fins.

Methods S1: Models assumptions, validation and goodness of fit.

Table S2: Models assumptions, consequence if violated, and results of validations.

Table S3: POPAN models fitted to dolphin dataset of the entire Coffin Bay study area.

Table S4: Pollock's Closed Robust Design models fitted to dolphin dataset of Coffin Bay's inner area.

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CHAPTER 3: High site fidelity and restricted ranging patterns in southern Australian bottlenose dolphins

3.0. Abstract

Information on site fidelity and ranging patterns of wild animals are critical to understand how they use their environment and guide conservation and management strategies. Delphinids show a wide variety of site fidelity and ranging patterns. Between September 2013 and October 2015, we used boat-based surveys, photo-identification, biopsy sampling, clustering analysis and geographic information systems to determine the site fidelity patterns and representative ranges of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) inhabiting the inner area of Coffin Bay, a highly productive inverse estuary located within Thorny Passage Marine Park, South Australia. Agglomerative hierarchical clustering of individuals' site fidelity index and sighting rates indicated that the majority of dolphins within the inner area of Coffin Bay are 'regular residents' (n = 125), followed by 'occasional residents' (n = 28), and 'occasional visitors' (n = 26). The low standard distance deviation indicated that resident dolphins remained close to their main centre of use (range = 0.7 – 4.7 km, $\bar{X}$ ± SD = 2.3 ± 0.9 km). Representative ranges of resident dolphins were small (range = 3.9 – 33.5 km^2, $\bar{X}$ ± SD = 15.2 ± 6.8 km^2), with no significant differences between males and females (Kruskal-Wallis, chi^2 = 0.426, p = 0.808). The representative range of 56% of the resident dolphins was restricted to a particular bay within the study area. The strong site fidelity and restricted ranging patterns among individuals could be linked to the high population density of this species in the inner area of Coffin Bay, coupled with differences in social structure and feeding habits. Our results emphasize the importance of productive habitats as a major factor driving site fidelity and restricted movement patterns in highly mobile marine mammals, and the high conservation value of the inner area of Coffin Bay for southern Australian bottlenose dolphins.

Keywords: Spatial ecology, delphinids, *Tursiops* cf. *australis*, inshore, estuary, site fidelity, utilization distribution.

3.1. Introduction

Movement and space use patterns of individual animals affect population distribution and abundance, habitat selection, species interactions, and social and population structure, which in turn influence individual fitness (Nathan et al. 2008; Börger 2016). Studies on multiple taxa have shown that the ranging patterns of individuals (*i.e.* location and area used within a study site) and the tendency of animals to remain in the same area or return to it multiple times (*i.e.* site fidelity, Switzer 1993; White and Garrott 2012) are driven by changes in individual's needs and the distribution of conspecifics, predators and resources (Switzer 1993; Switzer 1997; Nathan et al. 2008). In low-productive landscapes/seascapes with heterogeneous habitats, individuals improve their fitness by following an opportunistic strategy of accessing the highest-quality habitats available, which result in animals showing low site fidelity and ranging across large areas (Silva et al. 2008; Edwards et al. 2009). By contrast, in landscapes/seascapes where high quality habitats are available and resources are predictable, individuals can develop high site fidelity and range in relatively small areas (Knip et al. 2012; Habel et al. 2016). Such patterns of site fidelity and space use have important implications for the conservation of animals. For example, species with high site fidelity and restricted ranging patterns are more prone to population declines due to local threats such as habitat degradation and loss (Warkentin and Hernández 1996), and human caused mortalities (e.g. due to bycatch, Atkins et al. 2016). Therefore, understanding animal patterns of site fidelity and space use is fundamental for assessing the effects of human impacts and to guide conservation and management strategies.

Marine mammals such as dolphins live in fluid, open environments with few boundaries, feed on mobile prey and have low transport costs per unit weight (Williams 1999). As a result, they are highly mobile and tend to have larger home ranges than terrestrial mammals of similar size (Tucker et al. 2014). Delphinids show a wide variety of site fidelity and ranging patterns. Some individuals may occupy large ranges while others are restricted to smaller areas; some display year-round residency patterns while others are seasonal or transient visitors (e.g., Connor et al. 2000; Parra et al. 2006; McGuire and Henningsen 2007; Silva et al. 2008; Zanardo et al. 2016; Hunt et al. 2017). This variety of site fidelity and ranging patterns is thought to be mainly linked to the spatial and temporal predictability of available food resources (Gowans et al. 2008). The socioecological model proposed by

Gowans et al. (2008) for delphinids, predicts that in areas with predictable resources dolphins should remain resident, range over relatively small areas, and form small groups to reduce intraspecific competition for food. In contrast, when resources vary in space and time, dolphins should be more transient, range widely to access sufficient resources, and form larger groups to increase foraging success and reduce predation risk (Gowans et al. 2008).

Other factors known to influence dolphin site fidelity and ranging patterns include age and sex. In some populations of bottlenose dolphins (*Tursiops* spp.), adult females display smaller ranging patterns than adult males (Urian et al. 2009; Möller 2012; Sprogis et al. 2016; Wells et al. 2017), while both sexes show similar ranging patterns during the juvenile period (McHugh et al. 2011). Sex biased dispersal in adult dolphins is typical of mammals with polygynous mating systems, where males tend to range over larger areas to increase mating opportunities with reproductive females, while females tend to be more philopatric to their natal area (Möller and Beheregaray 2004; Sprogis et al. 2016). In populations of bottlenose dolphins where both sexes exhibit a high degree of philopatry to natal areas, fitness benefits related to familiarity with associates and foraging habitats may explain such patterns, with reduced mother-offspring association after weaning diminishing mother-son inbreeding and mother-daughter resource competition (Tsai and Mann 2013).

Bottlenose dolphins are found throughout coastal and inshore waters of Australia (Leatherwood and Reeves 2012). A new species, endemic to south-eastern and southern Australia, the Burrunan dolphin (*Tursiops australis*), was recently described (Charlton-Robb et al. 2011). Their taxonomic status, however, is not fully accepted (Perrin et al. 2013; Committee on Taxonomy 2016), and thus we refer to them here as southern Australian bottlenose dolphins (*Tursiops* cf. *australis*). Only two small resident populations of southern Australian bottlenose dolphins are known to occur in Victoria (Charlton-Robb et al. 2015), while recent studies indicate that this species is relatively abundant in South Australia (Chapter 2; Zanardo et al. 2016). Capture-recapture modelling of photographic-identification (photo-ID) data and molecular analyses of biopsy samples collected in the inner area of Coffin Bay, an inverse estuary located in temperate waters of a multiple use marine park in South Australia, indicated that this area offers highly favourable habitat for both males and females of this species (Chapter 2). The demography of southern Australian bottlenose dolphins in the inner area of Coffin Bay is characterized by high year-round abundance (265; 95% CI: 253 – 278), and low temporary emigration rates (0.02; 95% CI: 0.01 – 0.11; Chapter 2). Shallow, sheltered, inverse estuaries like Coffin Bay are highly productive (Kämpf 2014); and reports of water quality indicate high nutrients loads particularly in the inner area of Coffin Bay (EPA 2014). Moreover, Coffin Bay is an important nursery and feeding area for several fish and cephalopod species (DENR 2010) that are known to constitute part of the diet of bottlenose dolphins in South Australia (Gibbs et al. 2011). Understanding the site fidelity and ranging patterns of dolphins within this area can contribute towards the development of spatial conservation measures of a significant dolphin population that is already immersed within a multiple use marine park, but for which there are no management plans.

In this study, we use photo-ID data and genetic analyses of biopsy samples of southern Australian bottlenose dolphins collected between 2013 – 2015 in Coffin Bay to: 1) determine individuals' site fidelity patterns to the inner area, 2) characterize ranging patterns of resident individuals, and 3) assess sex differences in site fidelity and ranging patterns. Considering the apparent high productivity of Coffin Bay and the high-density of dolphins inhabiting the inner area (Chapter 2), we predicted that dolphins would exhibit high degrees of site fidelity, range over relatively small areas, and males and females would show similar ranging patterns. Our results enhance our understanding of space use patterns in inshore dolphins, and contribute to better informed decision making with regard to spatial management strategies aimed at protecting marine wildlife within marine parks in South Australia.

3.2. Methods

3.2.1. Study area

Coffin Bay is located within Thorny Passage Marine Park (TPMP), in the lower part of Eyre Peninsula, South Australia (Figure 3.1). It is divided into an inner (~123 km^2) and an outer area (~140 km^2) by a narrow and long (5 km) spit of land called Point Longnose, which restricts water exchange through a narrow opening between both areas. The inner area is a small inverse estuary that consists of several interconnected shallow (mean depth ~2.5 m) bays such as Port Douglas, Mount Dutton, and Kellidie (DEH 2004; Saunders 2009; Kämpf and Ellis 2015; Figure 3.1). Evaporation rates exceeding precipitation between September and April leads to hypersaline conditions during austral summer (December to February); while in austral winter (June to August) the inverse pattern dilutes salinity leading to fresher waters mainly in Kellidie and Mount Dutton Bays (Kämpf and Ellis 2015). In most of this area tides are of approx. 1.3 m (Saunders 2009). Several types of habitat are found in the inner area including seagrass beds, subtidal sandflats, saltmarshes, salt creeks, low reefs, ponds, shallow pools and limestone ledges (Saunders 2009). The outer area extends from Point Longnose and connects the waters of the inner area with the Great Australian Bight. In the outer area the depth increases from the shoreline to more than 25 m deep in the central and most exposed section of the bay, and its oceanographic conditions are influenced by several features of the Southern Ocean including upwelling events that occur off the continental shelf enhancing its productivity during the autumn months (DEH 2004; Kämpf et al. 2004). In general, waters in the outer area have lower total nutrient loads than in the inner area; furthermore, water and habitat monitoring suggested that the inner area could be under stress from nutrient enrichment (EPA 2014).

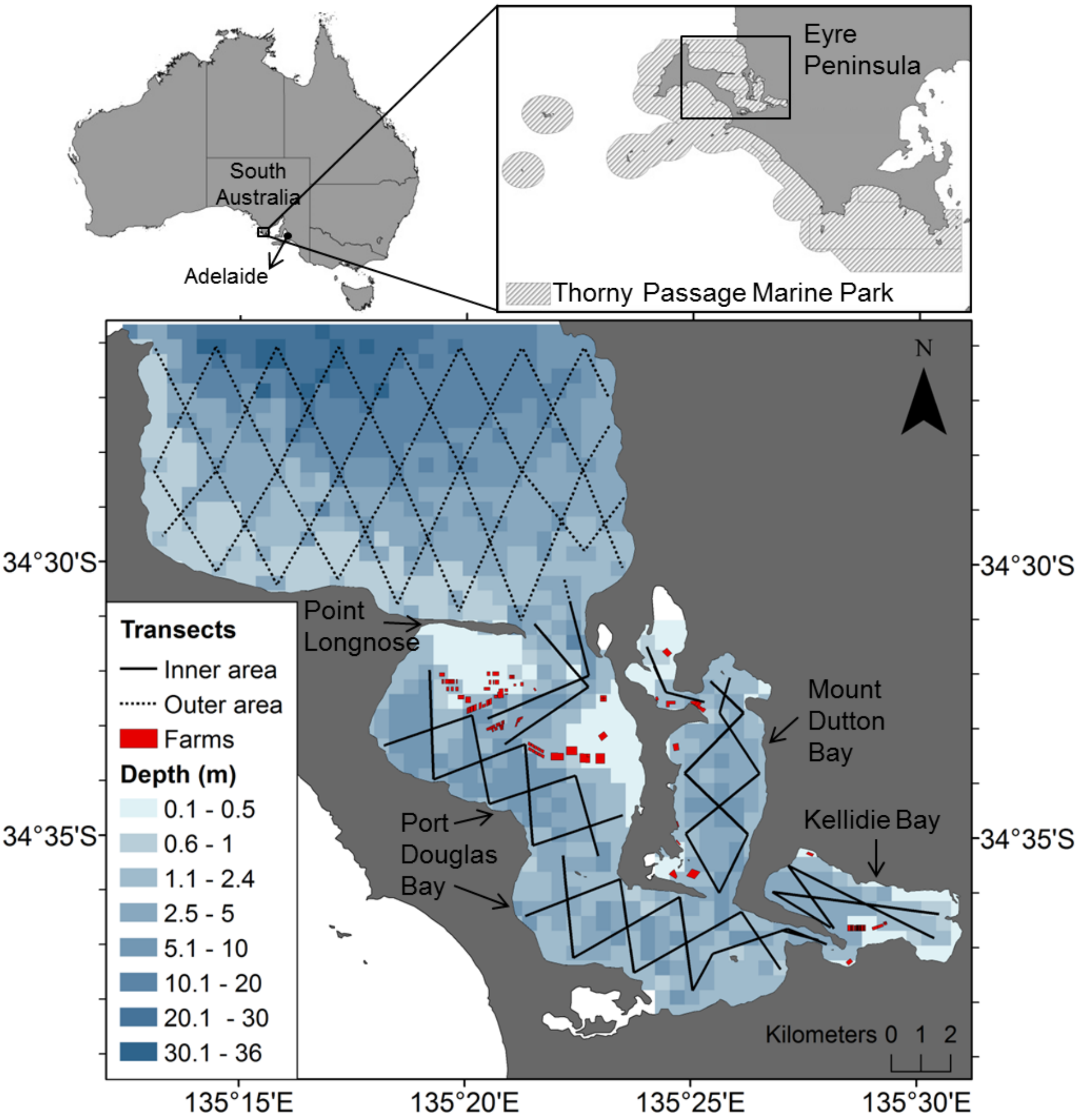

Figure 3.1. Map of the study area showing the location of Coffin Bay within the Thorny Passage Marine Park, Eyre Peninsula, South Australia. The zig-zag transect layout (solid lines) used to cover the inner area (~123 km^2) of Coffin Bay including Kellidie, Mount Dutton and Port Douglas Bays, and complementary transects (dashed lines) used to cover the outer area (~140 km^2). The location of aquaculture oyster farms (Farms) and the bathymetry of the study area is shown (depth ranges are indicated by grid colours).

3.2.2. Survey design and data collection

Boat-based surveys were conducted in Coffin Bay over six fieldwork seasons between September 2013 and October 2015 (Table 3.1). Surveys were carried out using a 6.5 m semi-rigid inflatable with twin 80 hp outboard motors, or a 7.2 m rigid aluminium vessel with twin 115 hp outboard motors. Thorough coverage of the study area was obtained following two alternative ‘equal spaced zigzag’ transect routes (Figure 3.1) designed with Distance 6.0 software (Thomas et al. 2010). Each route consisted of a total transect length of approximately ~55 km in the inner area and ~69 km in the outer area. The layout of transects maximised survey effort and ensured representative coverage of the different environmental conditions (e.g. depth, distance to shore, temperature, salinity, and habitat types) encountered within the study area. Shallow waters (<0.5 m in 20% of inner area), and the presence of oyster farms in the north-east part of Port Douglas and south of Kellidie prevented access to these areas, thus boat surveys covered 85.5 km^2 of the inner area and 140 km^2 of the outer area (Figure 3.1). A total of 2-4 days were needed to complete a single survey of the entire inner area and 2-3 days to survey the entire outer area.

Surveys were undertaken during daylight hours, at an average speed of 15 km/hr and under good weather conditions (*i.e.* Beaufort state ≤3, good-average visibility, no rain or fog, swell height ≤1 m). During surveys, three to five (mode = 4) observers searched for dolphins scanning at both sides of the boat, from -5° to 90° degrees of the transect, with 7 x 50 binoculars or with the naked eye. When a school of dolphins was sighted the global positioning system (GPS) position at the transect was recorded, searching effort was suspended and dolphins were approached slowly up to a distance of 10-20 m to record data on GPS position, school size and composition (number of non-calves and calves), and to carry out photo-ID and biopsy sampling. A school of dolphins was defined as all animals seen within a radius of 100 m (Wells et al. 1980) that were involved in similar (often the same) behavioural activities (modified from Connor et al. 1998). Distinguish among individuals’ age-classes (adults, juveniles and calves) in Coffin Bay is difficult as animals appear to be smaller in size in comparison to other study areas, thus individuals were categorized as non-calves (>1.5 m in length) and calves (≤1.5 m in length) as in Chapter 2. Only non-calves (*i.e.* adults and juveniles) were included in our analysis. Photographs of dorsal fins of individual dolphins were taken using a Nikon D300s DSLR camera with a 28-300 mm zoom lens and a

Canon EOS 60D with a 100-400 mm zoom lens. Biopsy samples were obtained using a biopsy pole system for bow-riding dolphins (Bilgmann et al. 2007), or a PAXARMS remote biopsy system specifically designed for small cetaceans (Krützen et al. 2002). In the field, biopsy samples were preserved in a 20% dimethyl sulphoxide solution saturated with sodium chloride (Amos and Hoelzel 1990), and after returning from field they were frozen at -20 °C until further analysis. We returned to the transect and resumed the survey effort once we obtained photos of all or most of the individuals within a school; or when individuals were lost from sight for ≥10 minutes.

Table 3.1. Summary of the survey effort conducted in Coffin Bay, South Australia, between September 2013 and October 2015. Information for each fieldwork season is given, including period dates, the number of months surveyed and the number of survey days on-effort. Survey effort is also shown for inner and outer area separately including: the total number of times each area was surveyed in its entirety (No. of surveys completed), the total kilometres of route surveyed (Total survey effort) and the number of southern Australian bottlenose dolphin schools encountered on-effort (No. of schools sighted).

Field-work season	Dates	No. of months surveyed	Days of survey on-effort	Inner area			Outer area		
				No. of surveys completed	Total survey effort (km)	No. of schools sighted	No. of surveys completed	Total survey effort (km)	No. of schools sighted
1	Sep. – Nov. 2013	2.5	26	7	379.9	99	1	67	2
2	Feb. – May. 2014	3	29	8	435.6	113	3	208.8	8
3	Jul. – Sep. 2014	2	22	5	271	127	2	137.9	8
4	Dec. 2014 – Jan. 2015	2	20	5	271	70	1	69	6
5	Apr. – Jun. 2015	2.5	27	7	382.4	144	2	137.9	6
6	Aug. – Oct. 2015	2	27	7	379.9	148	1	67	2
		TOTAL	151	39	2119.8	701	10	687.6	32

3.2.3. Data processing: photo-ID and sexing

Dolphins were individually identified based on photographs of long-lasting marks such as nicks, cuts and deformities in the edges of their dorsal fins (Würsig and Würsig 1977; Würsig and Jefferson 1990). To minimise misidentification, all photographs taken were examined and given an overall quality score (‘Q1’= ‘excellent’; ‘Q2’= ‘good’; and ‘Q3’= ‘poor’) based on the picture’s focus, contrast, the angle of the dorsal fin to the camera, etc. Individual’s dorsal fins were also classified into three distinctiveness categories (‘D1’= ‘very distinctive’, ‘D2’ = ‘average distinctive’ and ‘D3’ = ‘not distinctive’) according to the amount of information they presented (based on Urian et al. 2015, see full description of methodology in Chapter 2). The best images (right and/or left side) of each individual within a school were selected and were either matched with the already known individuals included in the Coffin Bay’s fin catalogue or incorporated into it with a new identification number. Only high quality photographs (*i.e.* Q1 and Q2) of distinctive individuals (*i.e.* D1 and D2) were included in the catalogue and used for analyses. Information on date and location (GPS positon) of the sighting was added to each individual’s photograph catalogued. DISCOVERY (version 1.2.) was used to process, match, catalogue and manage all the photo-ID data (Gailey and Karczmarski 2013).

DNA from biopsy samples was extracted using a salting-out protocol (Sunnucks and Hales 1996) and fragments of the ZFX and SRY genes were amplified through the polymerase chain reaction (PCR) to determine the sex of sampled individuals (Gilson et al. 1998). Individuals that were not biopsied, but were observed swimming accompanied by a dependent calf on ≥3 different survey days were also considered adult females.

3.2.4. Data analysis

Given the high density of dolphins inhabiting the inner area (1.57 – 1.70 individuals/km^2), their low temporary emigration rates (0.02; 95% CI: 0.01 – 0.11, Chapter 2), and the higher survey effort in the inner area compared to the outer area (Table 3.1; Figure S1, Supplementary material, Appendix II), we focused our spatial analyses of site fidelity and ranging patterns on individuals identified in the inner area of Coffin Bay. We used data collected in the outer area to identify individuals whose space use expanded beyond the inner area during our study period and excluded them from the spatial analysis.

3.2.4.1. Site fidelity

Three measures of site fidelity were estimated for each non-calf dolphin using information on date and location of photo-identified animals: 1) site-fidelity index, 2) survey-route sighting rate, and 3) fieldwork-season sighting rate. The site-fidelity index for each individual was calculated as the ratio between the number of recaptures and the number of survey-routes from its first capture to its last capture. An individual with a site-fidelity index of zero indicates that it was captured only once during the study period, while an individual with a site-fidelity index of one was captured in all survey routes after its first capture. The survey-route sighting rate and fieldwork-season sighting rate were calculated as the number of survey-routes and fieldwork-seasons a dolphin was identified as a proportion of the total number of survey-routes and fieldwork-seasons surveyed, respectively. In our study, survey-route sighting rate ranged from 0.026 (individuals sighted in only one surveyed route) to one (individuals sighted in all 39 surveyed routes); while fieldwork-season sighting rate ranged from 0.17 (individuals sighted in only one fieldwork season) to one (individuals sighted in all the six fieldwork seasons).

To identify clusters of individuals with similar degrees of site fidelity, the individuals' values of site-fidelity index, and survey-route sighting rate and fieldwork-season sighting rate were used in an agglomerative hierarchical clustering analysis (AHC) (Zanardo et al. 2016; Hunt et al. 2017). The AHC builds a dendrogram based on a bottom-up clustering method, which starts with each observation as an individual cluster and successively combines the clusters according to their similarity until resulting into a single final cluster (Legendre and Legendre 2012). The AHC analysis was built using Euclidean distance as the dissimilarity measure, and Ward's method (minimum variance) as the agglomerative clustering algorithm since it is considered a robust approach (Ward 1963; Singh et al. 2011). For each cluster in the dendrogram the approximately unbiased (AU) probability values (*i.e.* p-values) were obtained by generating 1,000 bootstrap resampling replications per cluster (Suzuki and Shimodaira 2006). High AU p-values indicate high confidence in the clusters, and were used to define a cut-off point along the dendrogram (a dissimilarity threshold) to obtain the most suitable number of clusters (Singh et al. 2011). To test the overall validity of the clustering, the cophenetic correlation coefficient (CPCC) was also calculated. The CPCC measures the relation between the original dissimilarity matrix and the one (cophenetic matrix) obtained after the dissimilarities are recalculated by the clustering algorithm (Sokal and Rohlf 1962). A high CPCC value (*i.e.* close to 1) indicates that the clustering is a good representation of the information contained in the original data (Bridge 1993). All the clustering analysis was done using the 'pvclust' package (Suzuki and Shimodaira 2006) in R version 3.2.3 (RCoreTeam 2015).

To explore long-term site fidelity to the inner area of Coffin Bay, we cross-checked individuals identified during our study period (2013 – 2015) with 192 distinctive individuals which were identified during a pilot study between April and June 2010 (Taylor 2010). Taylor (2010) encountered a total of 153 dolphin groups during 16 boat-based surveys which covered mainly the inner area of Coffin Bay and opportunistically the southern section of the outer area.

3.2.4.2. Site fidelity towards specific areas

Individuals' site fidelity towards specific areas within the inner area of Coffin Bay were explored by estimating the standard distance deviation (S_{XY}) as in Parra et al. (2006). The S_{XY} represents the standard deviation of the distance of each point from their mean centre, and provides a good measure of the degree to which features are concentrated or dispersed around their mean centre (Mitchel 2005). The S_{XY} was calculated only for individuals that met all the following criteria: i) were sighted in ≥ 7 different days during the study period; ii) were classified as occasional or regular residents of the study area according to the AHC analysis; and iii) were only observed in the inner area and never observed during the complementary surveys done in the outer area. The first criterion was established after determining that there was no significant relationship (ANOVA, $\alpha \leq 0.05$) between the number of locations and the size of representative ranges estimated (see below) when using 7 or more locations (ANOVA, $r(110) = 0.160$, $p = 0.09$). Since the survey effort in the outer (*i.e.* complementary) area was lower than the inner area, the latter criteria aimed to reduce the likelihood of underestimating the area used by individuals that move beyond our main study area (inner area). As some individuals were sighted multiple times during the same day, we only included their first location of each day to avoid temporal autocorrelation in the analysis.

The S_{XY} was calculated as the standard deviation of the distance of each individual dolphin location to their mean centre considering geographic coordinates in metres as follows (Mitchel 2005):

$$S_{XY} = \sqrt{\frac{\sum_{i=1}^{n}(X_i - \bar{X})^2}{N} + \frac{\sum_{i=1}^{n}(Y_i - \bar{Y})^2}{N}}$$

where X_i and Y_i are the geographic coordinates of the *i* location of an individual, $\bar{X}$ and $\bar{Y}$ are the coordinates of the mean center of all the locations of that individual, and N is the number of locations for that individual dolphin. Low values of S_{XY} indicate that the locations of an individual are limited to a small area, and thus has high site fidelity for a particular area within Coffin Bay. The S_{XY} of each individual was calculated using the spatial statistics tools of ArcGIS 10.3.1, using the Universal Transverse Mercator (UTM) Zone 35° South projection and based on the WGS 1984 datum. Difference in S_{XY} between sexes was evaluated in R version 3.2.3 (RCoreTeam 2015) with a Kruskal-Wallis test at α ≤ 0.05.

3.2.4.3. Ranging patterns

Ranging patterns were estimated for all individuals that followed the same criteria mentioned above for S_{XY} analysis. To determine the size of the area used by each individual (*i.e.* representative range) within inner Coffin Bay we used the kernel method, which estimates a probability density function that represents the utilization distribution (UD) of an individual (Van Winkle 1975; Silverman 1986; Worton 1989). As the coastline separating the system of bays and channels of Coffin Bay impose physical barriers to dolphin movements, we used the 'kernel interpolation with barriers tool' available from the Geostatistical Analyst Toolbox in Arc-GIS 10.3.1. This tool uses the shortest distance between points without intersecting the barrier (Gribov and Krivoruchko 2011), which allows accurate estimates of the dolphins' representative ranges (*i.e.* 95% kernel range, Worton 1995) area without biases imposed by the coastline (e.g., Sprogis et al. 2016; Wells et al. 2017).

The settings of the kernel interpolation with barriers analysis were kept consistent between individuals to ensure comparable results among individuals. The output grid cell size was set to 200 x 200 m, which allowed sufficient information to be included in the narrow channels and bay entrances of the study area. A first order polynomial was selected as the kernel function, and the default value of 50 was used for the ridge parameter. The bandwidth value (*i.e.* search radius that determines which surrounding location points will contribute to the kernel density) was chosen by visual inspection (Wand and Jones 1995) after running several trials with different bandwidth values (bandwidth range = 500 – 6,000; Figure S2, Supplementary material, Appendix II). If the bandwidth is too small it can generate a fragmented UD with various components and result in negatively biased home range estimates; if the bandwidth is too large the UD can be excessively smooth and the home range is overestimated (Gitzen et al. 2006; Kie et al. 2010). After visual inspection of the different trials, the bandwidth selected for the analysis was fixed at 3,000 m because the UDs obtained showed little fragmentation and were not overly smooth. The bandwidth was held constant across the plane for a fixed kernel.

Differences in representative ranges between sexes were evaluated using a Kruskal-Wallis test as for the S_{XY}. Finally, to explore individuals' space use over the long term, we plotted the location of individuals catalogued in 2010 (Taylor 2010) and checked if they fell within the representative ranges estimated in this study.

3.3. Results

We completed 39 survey-routes of the inner area of Coffin Bay between September 2013 and October 2015 (Table 3.1), covering ~2,120 km of transect on effort. A total of 701 schools of dolphins were encountered (Table 3.1) and 179 distinctive non-calf individuals were photo-identified. We determined the sex of 64% (n = 114) of the photo-identified dolphins (62 females and 52 males, Table 3.2) based on genetic analysis of 103 biopsy samples and the observation of presumed mother-calf associations for 11 individuals. The sex ratio of biopsied individuals was balanced, with 1.02 males per 1 female.

During the complementary surveys (10 survey-routes, ~688 km of transect effort) of the outer area, a total of 32 schools of dolphins were encountered (Table 1) and 96 non-calves dolphins photo-identified. Half of the photo-identified individuals in the outer area (n = 48) were also observed in the inner area, so they were excluded from the S_{XY} and representative ranges analysis. A total of 131 individuals (58% of the individuals photo-identified in the entire Coffin Bay) were found exclusively in the inner area.

3.3.1 Site fidelity

Out of the 179 non-calves individuals photo-identified in the inner area, fifteen were seen only once. The remaining 164 individuals were sighted between two and 25 survey routes in the inner area. Measures (mean ± SD) of site fidelity for all photo-identified individuals in the inner area were moderately high (site-fidelity index = 0.30 ± 0.16, survey-route sighting rate = 0.28 ± 0.15, and fieldwork-season sighting rates = 0.78 ± 0.27), indicating a large proportion of the individuals were sighted regularly in this area (Table 3.2). Individuals were seen on average during 11 (SD = 5.7) out of the 39 survey-routes. Forty six percent of photo-identified dolphins (n = 82) were seen in al fieldwork seasons surveyed, and 71% over all three years sampled. Values of the three site fidelity measures were also high and similar between females and males, indicating both sexes used the area regularly over the study period (Table 3.2).

Three main clusters of individuals were identified from the agglomerative hierarchical clustering analysis (dissimilarity threshold = 2.0) based on site fidelity measures (Figure 3.2; Table 3.3). The high value of the cophenetic correlation coefficient (CPCC = 0.77) and approximately unbiased p-values (AU p-values = 0.97 – 0.98) indicated that the dissimilarities among observations were well represented by the clusters in the dendrogram. Cluster 1 consisted of 125 individuals with relatively even numbers of males (n = 42) and females (n = 48), and the highest values of site-fidelity indices, and survey-route and fieldwork-season sighting rates (Table 3.3). These individuals were sighted on average over 13 survey routes and on five or all six fieldwork seasons; thus we consider them as ‘regular residents’ of the inner area of Coffin Bay. Cluster 2 comprised 28 individuals (5 males and 10 females) sighted in the inner area over seven survey routes on average, and in at least three fieldwork seasons; these dolphins were considered ‘occasional residents’ to the inner area. Cluster 3 consisted of 26 individuals (5 males and 4 females) sighted from one to five times and in no more than two fieldwork seasons; these were considered ‘occasional visitors’ to the inner area (Table 3.3).

Table 3.2. Site fidelity measures of southern Australian bottlenose dolphins in inner Coffin Bay including site fidelity index, survey-route sighting rate and fieldwork-season sighting rate. The mean and standard deviation (Mean ± SD), lower and upper 95% confidence intervals (CI 95%), and minimum and maximum (Min – Max) values are shown for all dolphins photo-identified and by sex (females, males and unknown sex).

	Total	Female	Male	Unknown
N	179	62	52	65
Site-fidelity index				
Mean ± SD	0.30 ± 0.16	0.34 ± 0.14	0.34 ± 0.15	0.22 ± 0.16
CI 95%	0.28 – 0.34	0.29 – 0.35	0.32 – 0.38	0.19 – 0.29
Min – Max	0 – 0.67	0.04 – 0.65	0.14 – 0.60	0 – 0.59
Survey-route sighting rate				
Mean ± SD	0.28 ± 0.15	0.32 ± 0.13	0.33 ± 0.14	0.22 ± 0.14
CI 95%	0.26 – 0.30	0.27 – 0.35	0.30 – 0.36	0.16 – 0.26
Min – Max	0.03 – 0.64	0.03 – 0.64	0.03 – 0.64	0.03 – 0.54
Fieldwork-season sighting rate				
Mean ± SD	0.78 ± 0.27	0.85 ± 0.21	0.85 ± 0.25	0.67 ± 0.31
CI 95%	0.79 – 0.87	0.88 – 0.95	0.96 – 1.04	0.70 – 0.96
Min – Max	0.17 – 1	0.67 – 1	0.67 – 1	0.17 – 1

The cross-checking of catalogues showed that at least 67% (n = 119) of the individuals photo-identified during 2013 – 2015 were previously catalogued in the pilot study of 2010 (Taylor 2010). These 119 individuals corresponded to 75% of dolphins considered members of cluster 1, 50% of cluster 2, and 42% of cluster 3. This suggests that dolphins of all clusters, including the ones considered occasional visitors, exhibit long-term site fidelity to the study area.

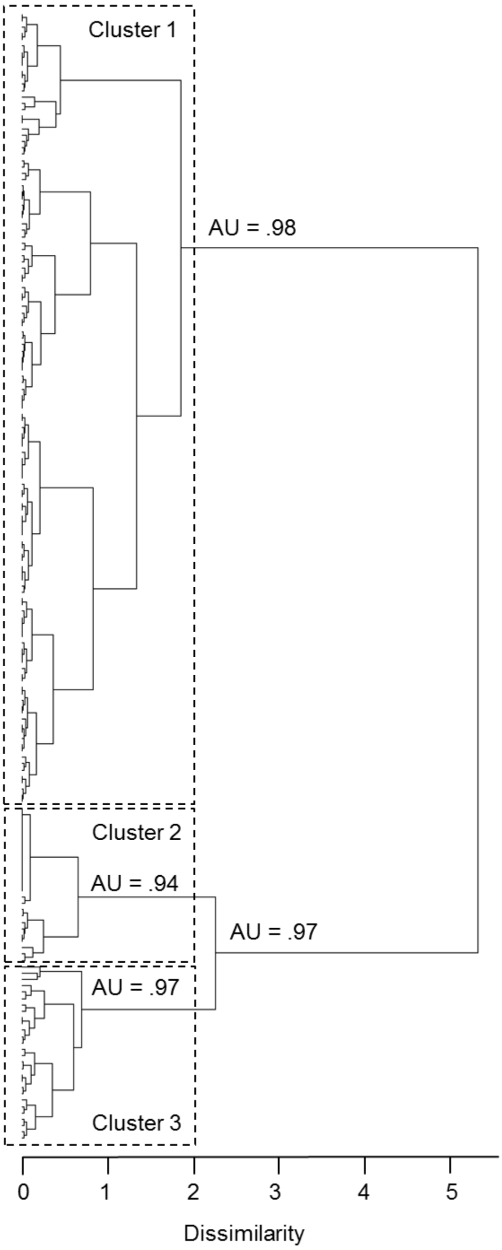

Figure 3.2. Agglomerative hierarchical clustering (AHC) dendrogram of southern Australian bottlenose dolphins in inner Coffin Bay obtained based on three measures of individuals' site fidelity: site-fidelity indices, survey-route sighting rate and fieldwork-season sighting rate. Rectangles indicate three clusters (dissimilarity threshold = 2.0): Cluster 1 ('regular residents'), Cluster 2 ('occasional residents') and Cluster 3 ('occasional visitors'). The approximately unbiased (AU) probability values of these three clusters are shown on the dendrogram.

Table 3.3. Site-fidelity indices, and survey-route and fieldwork-season sighting rates for the three clusters of southern Australian bottlenose dolphins identified in inner Coffin Bay using the agglomerative hierarchical clustering (AHC) analysis. Mean and standard deviation (± SD), lower and upper 95% confidence intervals (CI 95%), and minimum and maximum (Min – Max) values are shown for all dolphins photo-identified and by sex (females, males and unknown sex) per cluster.

	Cluster 1				Cluster 2				Cluster 3			
	Total	Females	Males	Unknown	Total	Females	Males	Unknown	Total	Females	Males	Unknown
N	125	48	42	35	28	10	5	13	26	4	5	17
Site-fidelity index												
Mean ± SD	0.36 ± 0.11	0.37 ± 0.12	0.39 ± 0.11	0.33 ± 0.11	0.23 ± 0.11	0.26 ± 0.11	0.23 ± 0.05	0.2 ± 0.12	0.03 ± 0.06	0.09 ± 0.12	0.04 ± 0.06	0.02 ± 0.03
CI 95%	0.33 – 0.37	0.31 – 0.37	0.35 – 0.41	0.28 – 0.36	0.15 – 0.22	0.19 – 0.33	0.21 – 0.25	0.15 – 0.19	-0.02 – 0.02	-0.06 – 0.14	-0.04 – 0.04	-0.02 – 0.02
Min – Max	0.13 – 0.67	0.18 ± 0.67	0.2 ± 0.67	0.13 ± 0.59	0.08 – 0.55	0.11 ± 0.44	0.15 ± 0.29	0.08 ± 0.55	0 – 0.23	0 ± 0.23	0 ± 0.14	0 ± 0.12
Survey-route sighting rate												
Mean ± SD	0.35 ± 0.1	0.36 ± 0.11	0.38 ± 0.1	0.32 ± 0.1	0.18 ± 0.06	0.2 ± 0.06	0.19 ± 0.06	0.17 ± 0.06	0.05 ± 0.03	0.05 ± 0.04	0.05 ± 0.03	0.04 ± 0.03
CI 95%	0.31 – 0.35	0.3 – 0.36	0.34 – 0.4	0.28 – 0.34	0.16 – 0.2	0.16 – 0.26	0.11 – 0.19	0.13 – 0.17	0.02 – 0.04	0 – 0.08	0.02 – 0.04	0.02 – 0.04
Min – Max	0.13 – 0.64	0.18 ± 0.64	0.21 ± 0.64	0.13 ± 0.54	0.1 – 0.33	0.1 ± 0.28	0.15 ± 0.28	0.1 ± 0.33	0.03 – 0.13	0.03 ± 0.1	0.03 ± 0.1	0.03 ± 0.13
Fieldwork-season sighting rate												
Mean ± SD	0.94 ± 0.08	0.94 ± 0.08	0.96 ± 0.07	0.93 ± 0.08	0.6 ± 0.08	0.63 ± 0.07	0.57 ± 0.09	0.58 ± 0.09	0.22 ± 0.08	0.25 ± 0.1	0.2 ± 0.07	0.23 ± 0.08
CI 95%	0.98 – 1.02	0.96 – 1.04	0.96 – 1.04	0.95 – 1.05	0.62 – 0.72	0.67 – 0.67	0.38 – 0.62	0.43 – 0.57	0.12 – 0.22	0.12 – 0.38	0.17 – 0.17	0.11 – 0.23
Min – Max	0.83 – 1	0.83 ± 1	0.83 ± 1	0.83 ± 1	0.5 – 0.67	0.5 ± 0.67	0.5 ± 0.67	0.5 ± 0.67	0.17 – 0.33	0.17 ± 0.33	0.17 ± 0.33	0.17 ± 0.33

3.3.2 Site fidelity towards specific areas

Out of the 131 non-calves individuals photo-identified exclusively in the inner area, 112 (45 females, 36 males and 31 dolphins of unknown sex) were recorded at least seven times, including 99 that were classified as ‘regular residents’ and 12 as ‘occasional residents’ by the AHC. This dataset was used for analysis of standard distance deviation (S_{XY}) and ranging patterns. For dolphins included in the spatial analysis, the mean (± SD) number of locations and the time interval between locations per individual was 14.3 ± 4.3 (Median = 14) and 56 ± 17 days (Median = 52), respectively.

The S_{XY} of individuals ranged from 0.7 to 4.7 km (Figure 3.3a), with a mean (± SD) of 2.3 ± 0.9 km (Median = 2.3 km), suggesting that dolphins had strong site fidelity to specific and relatively small areas within the inner area of Coffin Bay. The mean (± SD) S_{XY} for females (2.2 ± 0.8 km), males (2.5 ± 1.0 km) and for individuals of unknown sex (2.4 ± 0.9 km; Figure 3.3a) were similar, with no significant differences (Kruskal-Wallis, chi^2 = 3.807, df = 2, *p* = 0.149).

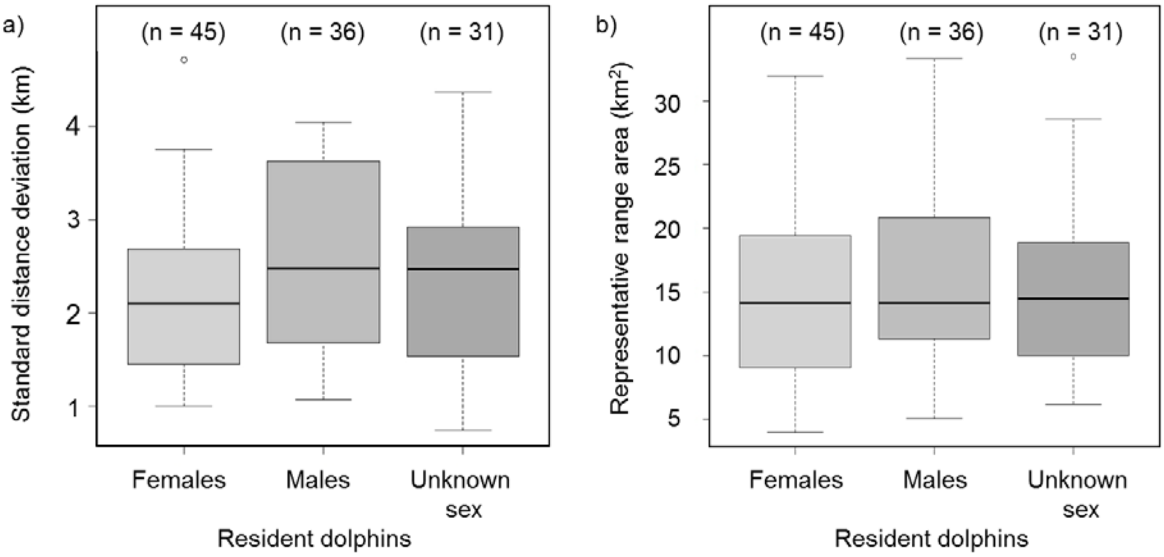

Figure 3.3. Boxplots of (a) standard distance deviation and (b) representative range area for females, males and individuals of unknown sex of southern Australian bottlenose dolphins residents to the inner area of Coffin Bay. The bold line indicates the median value, the rectangle spans from the first quartile to the third quartile, and the whiskers above and below the box show the locations of the minimum and maximum values, respectively. Circles beyond the maximum value represent the outliers.

3.3.3 Ranging patterns

Overall, representative ranges were small and restricted to particular areas. The area of an individuals' representative range (95% kernel range) varied from 3.9 to 33.5 km^2, with a mean (± SD) of 15.2 ± 6.8 km^2 (median = 14.1). The size of the representative range for females (14.7 ± 7.0 km^2), males (15.6 ± 6.6 km^2) and for individuals of unknown sex (15.4 ± 7.0 km^2; Figure 3.3b) was similar and showed no significant differences (Kruskal-Wallis, chi^2 = 0.426, df = 2, p = 0.808). The majority of females (56%) and males (55%) had representative ranges smaller than 15 km^2, with only a few individuals (9% females and 8% males) using areas larger than 25 km^2.

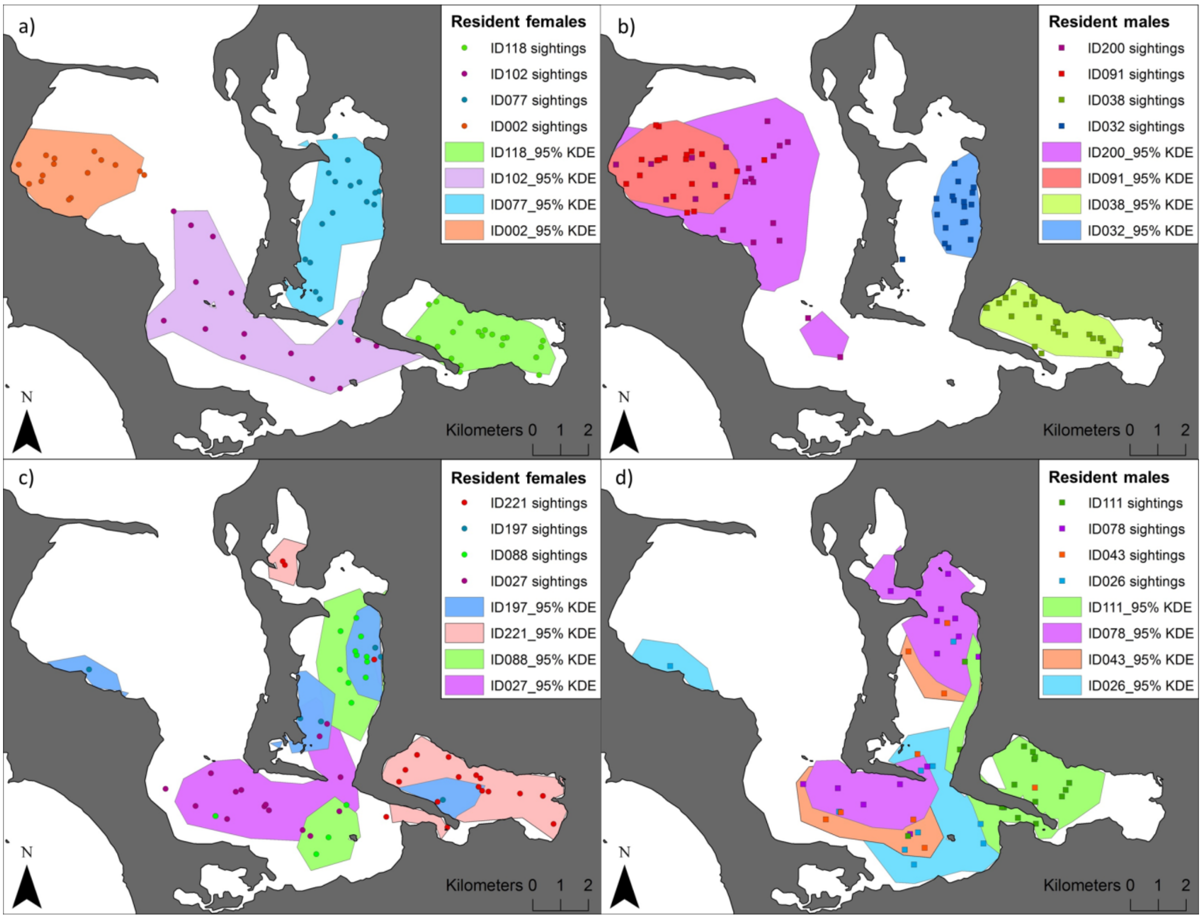

Figure 3.4. Examples of the representative ranges (95% kernel) of males and female southern Australian bottlenose dolphins encountered within the inner area of Coffin Bay between September 2013 and October 2015. Four a) females and b) males with representative ranges restricted to particular bays, and c) females and d) males with representative ranges covering multiple bays.

The representative range of 56% of the individuals (63 out of 112) was restricted to a particular bay within the inner area of Coffin Bay (see examples in Figure 3.4a, b; Figure S3, Supplementary material, Appendix II). The other 44% of individuals' representative ranges covered multiple areas within Coffin Bay (see examples in Figure 3.4c, d; Figure S3, Supplementary material, Appendix II).

Out of the 112 resident individuals included in the spatial analysis, 78 (70%) were previously photo-identified during the 2010 pilot study (Taylor, 2010). Furthermore, records from 2010 indicated that the sightings of 62 of those individuals fell within the representative ranges estimated in the 2013 – 2015 study period; while 9 individuals were observed in 2010 at less than 1 km distance from their current representative range, and the remaining 7 dolphins were seen at further distances.

3.4. Discussion

Marine mammal site fidelity and ranging patterns can provide important information about the space use patterns and relative significance of particular areas to individuals, groups and populations which are relevant for delineating conservation and management strategies for at-risk species. This study shows that the majority of southern Australian bottlenose dolphins inhabiting the inner area of Coffin Bay, South Australia, exhibit a high degree of site fidelity, with both sexes ranging over relatively small areas. Furthermore, a large proportion (56%) of individuals within the inner area appears to restrict their space use to particular embayments. High levels of site fidelity and restricted ranging patterns in dolphins are hypothesized to occur in areas where resources are spatially and temporally predictable (Gowans et al. 2008). The site fidelity and range characteristics of bottlenose dolphins reported here are concordant with theoretical models of site fidelity (Switzer 1993; Gowans et al. 2008) and our predictions based on the apparent high biological productivity of the area, the absence of sex-biases in demographic parameters and the high-density population inhabiting the inner Coffin Bay area (Chapter 2). These findings emphasize the importance of habitat quality as a major factor driving site fidelity and movement patterns in highly mobile marine mammals, and highlight the conservation value of the inner area of Coffin Bay for southern Australian bottlenose dolphins.

When comparing home range studies, caution must be taken because different methodologies (e.g. minimum convex polygon, adaptive or fixed Kernel) can produce different estimates of ranging patterns (de Faria Oshima and de Oliveira Santos 2016). Taking this into account, we found that the sizes of the representative ranges of resident southern Australian bottlenose dolphins in the inner area of Coffin Bay seem to be smaller than mean sizes reported for inshore bottlenose dolphin species elsewhere (see comparable examples in Table S1, Supplementary material, Appendix II). However, the size of the representative ranges observed in our study were within the ranges reported for other inshore delphinids inhabiting small bays (e.g. 15.22 km^2 for *Sotalia flluviatilis* in Baía Norte, Santa Catarina, Brazil, Flores and Bazzalo 2004; 13.5 km^2 for *Sotalia guianensis* in Cananéia estuary, São Paulo, Brazil, de Faria Oshima and de Oliveira Santos 2016). These bays share characteristics with Coffin Bay that may be promoting such spatial patterns; they all are shallow systems (mean depth less than 7 m), located within (or part of) marine protected areas, and are productive systems considered nursery areas of several fish species that are part of the dolphins diet (Flores and Bazzalo 2004; de Faria Oshima and de Oliveira Santos 2016; see below further references for this study). Broad-scale models of home range in mammals have shown that body size and sex are important predictor of home range size, and that 1) marine mammals tend to range over larger areas than terrestrial mammals of similar size (Tucker et al. 2014) and 2) adult males tend to have larger ranges than adult females. At finer-scales, however, there is great variability in space use patterns within and among species even when they share similar characteristics (e.g. similar body size and diet, and inhabit similar environments) (Table S1, Supplementary material, Appendix II). Such intra- and inter-specific differences in space use among bottlenose dolphins are likely driven by a combination of multiple factors acting at finer-scales rather than body size and sex alone.

The degree of site fidelity an individual has to a particular location and its ranging patterns is a reflection of extrinsic factors such as environmental conditions, habitat quality, distribution of food resources, potential mating partners and predators, intra and interspecific competition, and population density as well as intrinsic components, such as body size, individual's experience, sex and age (Switzer 1993; Switzer 1997; McLoughlin and Ferguson 2000; Saïd et al. 2009; Duncan et al. 2015). Simulations and empirical studies across different mammal species have shown that, among these factors, food availability and population density play a pervasive role in determining the size, shape and location of home ranges, with animals distributing themselves in a way that maximizes the use of spatially distributed resources while minimizing competition with conspecifics (Mitchell and Powell 2012; Duncan et al. 2015; Šálek et al. 2015; Schoepf et al. 2015). In general, these studies show that home range size decreases with 1) increasing food availability, because individuals can access food more easily and thus save energy, and 2) increasing population density, because individuals space use patterns are constrained by competitive interactions with neighbouring individuals. A high density of dolphins is found in the inner area of Coffin Bay waters (1.57 – 1.70 individuals/km^2, Chapter 2), with resident dolphins remaining close (<5 km) to their mean centre of use and showing restricted representative ranges (<35 km^2). Studies on bottlenose dolphins have shown that some populations have low fidelity and use large areas (e.g., *T. truncatus*, Ballance 1992; Defran et al. 1999), while others have strong site fidelity and small ranging patterns (*T. aduncus*, Sprogis et al. 2016; *T. truncatus*, Gubbins 2002; Ingram and Rogan 2002; Urian et al. 2009; Brusa et al. 2016; Wells et al. 2017). The latter usually occurs when dolphins inhabit sheltered and highly productive waters, such as estuaries. For example, in Bunbury, Western Australia, bottlenose dolphins (*T. aduncus*) which were more often sighted in productive sheltered habitats (*i.e.* bay, estuary and riverine waters) had smaller representative ranges than dolphins that predominately use less productive open waters (Sprogis et al. 2016). In areas with a surplus of food, increases in population density can lead to an increase in home range overlap between individuals and sharing of food resources, which can lead to intraspecific competition for food (Schoepf et al. 2015). Small and non-overlapping ranging patterns among individuals within a population may constitute a strategy to avoid competition for food resources in an area highly populated by conspecifics (Mcloughlin et al. 2000; Gowans et al. 2008; Schradin et al. 2010; Schoepf et al. 2015). Our results support the hypothesis that the apparent high productivity of the inner area of Coffin Bay likely provides enough resources for dolphins, allowing for optimal foraging efficiency within small representative ranges. Furthermore, the high density of dolphins found in the inner area of Coffin Bay (Chapter 2), and the potential intraspecific competition associated with it, might also contribute to the small ranges and spatial segregation observed among a large proportion of the resident individuals.

When dolphins have high site fidelity to an area and restricted ranging patterns they will likely become familiar with the quality of habitats and the predictability of resources, and develop social bonds with other individuals using the same area (Connor et al. 2000; Lusseau et al. 2003; Urian et al. 2009; Connor and Krützen 2015). Familiarity with resources and conspecifics together with long-lasting social bonds allows for information transfer among members of a community on the distribution of food resources and predators, contributing to maximise individuals' fitness and survival (Switzer 1993; Switzer 1997, Lusseau et al. 2003). The high site fidelity of dolphins occurring in the inner area of Coffin Bay is likely favoured by a lower predation risk compared to the outer area and coastal waters of South Australia. The inner area is characterized by shallow waters and a narrow connection with the outer area, which may restrict the access of predators to the study area. One of the main predators of dolphins in coastal waters of South Australia is the white shark (*Carchharodon carcharias*), which can occur close to shore although they seem to prefer waters of <100 m depth (Bruce et al. 2006). Additionally, the high diversity of habitats (Miller et al. 2009) and differences in environmental conditions found in Coffin Bay (Kämpf and Ellis 2015) likely result in different fish assemblages across its different embayments. A contemporary study done in autumn and spring 2015 revealed that, in fact, fish assemblage composition differs among embayments of the inner area (*i.e.* Kellidie vs. Mount Dutton vs. north of Port Douglas vs. south of Port Douglas) (S. Whitmarsh, personal communication, 14 March 2017). Consequently, individuals inhabiting each embayment may have developed different feeding habits in response to variation in habitat and associated prey resources. Such potential feeding differences and spatial segregation may also be strengthened by social structure patterns. The population of bottlenose dolphins inhabiting the inner area of Coffin Bay is socially structured, with at least two well differentiated communities occurring in different embayments, one in Port Douglas and the other in Kellidie-Mount Dutton bays (Diaz-Aguirre 2017). Further studies integrating predation risk, social structure and feeding ecology should improve our understanding of the extrinsic drivers of the high residency and fine-scale spatial structure observed for this highly mobile species in such a small area, and whether such patterns offer fitness improvements.

Determining the factors that shape site fidelity and ranging patterns of highly mobile marine species that spend most of their time underwater such as dolphins, represents a challenging field of research. Ranging patterns of dolphins have been studied using radio-tracking (Owen et al. 2002; Martin and Silva 2004), satellite-tracking (Wells et al. 1999; Wells et al. 2017) and photo-ID techniques (Owen et al. 2002; Sprogis et al. 2016) as we used here. Although radio, and especially satellite tracking approaches can provide very detailed information on animal movement and ranging patterns, usually only a few individuals from a population can be studied, resulting in ranging patterns that may not be representative of the entire population (Castro et al. 2014; Irvine et al. 2014). Photo-ID is a non-invasive mark-recapture technique that has been applied to study the fidelity and space use patterns of several species, including highly mobile marine animals such as sharks (Domeier and Nasby-Lucas 2007; Brooks et al. 2010), whales (Dorsey et al. 1990; Craig and Herman 1997) and dolphins (Gubbins 2002; de Faria Oshima and de Oliveira Santos 2016; Sprogis et al. 2016). However, one of the limitations of using photo-ID to estimate the site fidelity and ranging patterns of highly mobile species is that it can only be conducted during daylight hours in good weather conditions, and is limited to the study area and period covered by researchers. Nonetheless, a study comparing home ranges of bottlenose dolphins determined using mark-recapture data from photo- ID surveys vs radio-tracking data showed that both approaches produced very similar patterns for individuals that appeared to be year-round residents to the surveyed area (Owen et al. 2002). We acknowledge that this study carries the limitations imposed by photo-ID; our data was collected only during daytime, with some time gaps (*i.e.* 2 – 3 months) between fieldwork seasons and over a short period of time (2 years) relative to the dolphins' normal life-span (ca. 40 years). However, our previous study at the population level indicated that emigration rates from the inner area are very low (Chapter 2), and cross-checking of individuals identified during our study period (2013 – 2015) with individuals identified in 2010 (Taylor, 2010) indicated long-term site fidelity to the inner area. Furthermore, we limit our analysis to resident individuals based on their sighting patterns across the study period. Thus, we consider that our approach provides robust estimates of the space use of the resident dolphins within the inner area of Coffin Bay and a solid platform for future investigations into their site fidelity and ranging patterns.

3.4.1. Implications for conservation

Marine mammal populations exhibiting high levels of site fidelity and restricted ranging patterns are particularly susceptible to localized anthropogenic pressures such as habitat degradation and loss, entanglements in marine debris, interaction with fisheries (*i.e.* bycatch or reduction of prey availability due to overfishing), pollution, among others (Rojas-Bracho et al. 2006; Currey et al. 2007; Monk et al. 2014; Atkins et al. 2016). At the same time, such populations have the potential of being protected using area-based management measures, especially if specific strategies are established and enforced to reduce the local threats (Gormley et al. 2012; Augé et al. 2014). Although marine mammals are considered species of ecological value within the management plan for the Thorny Passage Marine Park in which Coffin Bay is located (Bryars et al. 2016), there are no strategies directed towards the protection of dolphins. The zoning in most of the Thorny Passage Marine Park, including Coffin Bay waters, allows human activities (e.g., oyster aquaculture, recreational fishing, water sports, and tourism cruises, Saunders 2009; DENR 2010) that could be negatively impacting upon the dolphins. Due to their high site fidelity and restricted ranging patterns it is likely that resident individuals inhabiting specific areas may be facing different threats. For instance, Mount Dutton and Kellidie bays are particularly vulnerable to harmful algae blooms and pollution because of their relatively slow flushing (water age of ~3 months; Kämpf and Ellis 2015), which can result in cascade effects producing mortalities of prey (e.g., PIRSA 2014) and potentially also affecting dolphins. The spatial distributions of threats to southern Australian bottlenose dolphins, however, are poorly understood. Therefore, future research is needed to map the distribution of major threats to dolphins in the area. This, together with the results presented here, should be considered in the zoning arrangements and management strategies of Thorny Passage Marine Park plan, which is scheduled to be reviewed in 2022.

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Data collection was done in accordance to the Flinders University Animal Welfare Committee under the ethics approval of project number E310. Fieldwork was done under Permits to Undertake Scientific Research (numbers: E26171-1, E26171-2, E26171-3 and MR00056-1) from the Department of Environment, Water and Natural Resources (DEWNR), and under S115 Ministerial Exemptions (MEs: 9902601, 9902660, 9902714 and 9902779) provided by Primary Industries Resources South Australia (PIRSA).

3.6. Supplementary material

Figure S1. Map of survey effort done in Coffin Bay (September 2013 – October 2015).

Figure S2. Examples of Kernel density estimates using different bandwidth values.

Figure S3. Distribution of frequency of individuals and boxplot of representative ranges in each bay.

Table S1. Examples of individual dolphins' mean size of ranging patterns in different study areas.

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CHAPTER 4: Ecogeographic and anthropogenic drivers of dolphin distribution: informing future spatial conservation planning in a marine protected area

4.0. Abstract

Information on how ecogeographic and anthropogenic variables affect species distribution is fundamental for understanding their ecology and to inform spatial conservation planning. Such spatial information is lacking for most marine top predators in South Australia's multiple use marine parks. In this study we use an ensemble modelling approach combining five different species distribution modelling methods to investigate the spatio-temporal distribution of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in relation to a variety of ecogeographical and anthropogenic variables, identify areas of high probability of occurrence, and evaluate the relevance of current sanctuary zones to the protection of dolphins within the inner and outer areas of Coffin Bay, Thorny Passage Marine Park, South Australia. The analysis is based on data collected during systematic boat-based surveys in Coffin Bay between September 2013 and October 2015. Models of dolphin distribution for the entire Coffin Bay area indicated that distance to sanctuary zones was the most important variable influencing dolphin presence. Models for the inner area, where the sanctuaries are placed and a large proportion of dolphins are year-round residents, indicated that the main drivers of distribution were water depth, and distance to land and oyster farms. Overall, areas of high probability of dolphin presence in the inner area were located in shallow waters (2 – 10 m) located within 1,000 m of land and 2,500 m of oyster farms. Despite the seasonality in environmental conditions and human activities, dolphins showed almost no temporal variability in their distribution patterns. Sanctuary zones covered areas from low (0.04) to high (0.89) probability of dolphin presence, but the majority of areas of highest probability of presence fell in multiple use areas where human activities are allowed. The areas of high dolphin presence identified here should support future spatial conservation decisions in South Australia targeting marine top predators.

Keywords: Species distribution modelling, ensemble, bottlenose dolphins**,** *Tursiops* cf. *australis*, inshore, estuary.

4.1. Introduction

Information on how different environmental and anthropogenic variables affect the distribution of species is fundamental for understanding their ecology and guiding spatial conservation planning (Franklin, J. 2010, Guisan, A. and Thuiller, W. 2005). The presence and distribution of marine top predators, such as dolphins, has been linked to a variety of abiotic and biotic factors, which are usually linked to the distribution of their prey, predators and conspecifics (Redfern, J. V. et al. 2006). Human activities such as boating, fishing activities and aquaculture can affect dolphin behaviour and ultimately also influence their distribution patterns (e.g., Bearzi, G. et al. 2016, Bonizzoni, S. et al. 2014, Lusseau, D. and Bejder, L. 2007). Species distribution models (SDM) provide a useful analytical framework to investigate the environmental and anthropogenic factors affecting species distribution and to predict their occurrence in areas where information on the environment is available (Elith, J. and Leathwick, J. R. 2009, Franklin, J. 2010, Guisan, A. and Thuiller, W. 2005). Such information can help elucidate which areas constitute potential or priority habitat for a species and where potential conflicts with human activities may occur (Guisan, A. et al. 2013).

In the marine ecosystem, coastal environments are the most heavily impacted by human activities because they are exposed to both land and marine-based stressors (Halpern, B. S. et al. 2008). Dolphins are particularly susceptible to human stressors because of their life-history traits (*i.e.* late maturity, low reproductive rate and long life span, Reeves, R. R. et al. 2003). The conservation of biologically productive places that meet the food and life history requirements of target species, can be an effective tool for managing threats to marine mammals (Notarbartolo di Sciara, G. et al. 2016). Coastal dolphin populations, especially those with high levels of site fidelity and restricted ranging patterns, are at risk due to localized pressures such as habitat degradation and loss, by-catch, prey depletion, tourism, pollution, among others (Atkins, S. et al. 2016, Currey, R. J. et al. 2007, Monk, A. et al. 2014, Rojas-Bracho, L. et al. 2006). However, the decline of dolphin numbers due to long-term disturbances have the potential to be reverted if critical habitats are identified, and management measures (including compliance) are established to diminish anthropogenic impacts within those areas (Guerra, M. and Dawson, S. M. 2016). Thus, the identification of areas of high abundance and suitable habitats is fundamental for the development of appropriate spatial conservation planning for marine top predators (Hooker, S. K. et al. 2011a).

In South Australia (SA), increasing coastal zone development, coastal pollution, marine aquaculture, and fishery interactions, threaten the viability of coastal and offshore dolphin populations (Bilgmann, K. et al. 2008, Hamer, D. J. et al. 2008, Kemper, C. M. and Gibbs, S. E. 2001, Lavery, T. J. et al. 2008, Lavery, T. J. et al. 2009). Our understanding of the magnitude of these problems and ability to provide effective management solutions to them is hindered by the limited knowledge about the ecology of these populations. The effective protection and management of dolphins in SA requires spatially explicit data on their distribution and potential threats. Such information is required to prioritize areas for conservation, zoning design, impact assessment and resource management decisions. The need for this information has recently become more critical as zoning of all SA's marine parks is schedule for review in 2022, and there is strong commitment from wildlife agencies to ensure that the marine planning process includes the conservation needs of marine top predators such as dolphins.

The bottlenose dolphin (*Tursiops* sp.) is a cosmopolitan marine top predator, extensively distributed in temperate and tropical waters around the world. Currently there are two widely accepted species within the genus, the common bottlenose dolphin (*T. truncatus*) and the Indo-Pacific bottlenose dolphin (*T. aduncus*). Recently, a potential third species was described for coastal waters of southern Australia, the Burrunan dolphin (*Tursiops australis*) (Charlton-Robb, K. et al. 2011). The taxonomy of this putative new species is still contentious (Perrin, W. F. et al. 2013, Committee on Taxonomy 2016), therefore we refer to them here as southern Australian bottlenose dolphins (*Tursiops* cf. *australis*). Southern Australian bottlenose dolphins appear to form small, resident and genetically differentiated populations (Charlton-Robb, K. et al. 2015), and population structuring may be occurring at small spatial scales in relation to environmental factors (e.g., location of oceanographic front, Bilgmann, K. et al. 2007b). So far, six populations of southern Australian bottlenose dolphins have been identified spread over ~2500 km of coastline based on molecular markers: i) coastal waters from Esperance (Western Australia) to St. Francis Island (SA); ii) inshore waters of Coffin Bay (SA); iii) Gulf Saint Vincent (SA); iv) Spencer Gulf (SA); v) inshore waters of Port Phillip Bay (Victoria); and vi) inshore and coastal waters of Gippsland Lake, Victoria, and northern Tasmania (Bilgmann, K. et al. 2007a, Charlton-Robb, K. et al. 2011, Charlton-Robb, K. et al. 2015, Pratt, E. A. L. et al. under review). Throughout their distribution, southern Australian bottlenose dolphins are exposed to different environmental conditions and anthropogenic activities, but little is known about how these may influence their distribution patterns. Studies in Gulf Saint Vincent, SA, showed that the distribution patterns of southern Australian bottlenose dolphins are influenced by a variety of ecogeographic variables, likely linked to prey distribution and availability (Cribb, N. et al. 2013, Zanardo, N. et al. 2017). For example, the distribution of dolphins inhabiting the Port River estuary and Barker Inlet in Adelaide, SA's state capital, was mainly related to habitat type, with dolphins preferring mainly bare sand habitat (Cribb, N. et al. 2013). Along Adelaide's metropolitan coast, however, dolphin distribution varied seasonally and was influenced mainly by a combination of water depth, benthic habitat type and slope (Zanardo, N. et al. 2017). Both studies identified priority areas for dolphin conservation along this coast and highlighted the need for future studies to evaluate the influence of human activities (e.g., vessel traffic, fishing, and ports) on dolphin distribution.

The largest population of southern Australian bottlenose dolphins (n= 306, 95% CI: 291–323) studied to date inhabits the coastal waters of Coffin Bay, a small embayment (263 km^2) located within the Thorny Passage Marine Park, Eyre Peninsula, SA (Chapter 2). The high biological productivity of the bay and the apparent low predation risk likely explains the high density of dolphins in this area (Chapter 2, Chapter 3). Coffin Bay is an heterogeneous ecosystem with two distinctive areas, the outer area, which is exposed to the oceanographic conditions of the Southern Ocean, and the inner area, which is a shallow inverse estuary consisting of a variety of habitats across several interconnected embayments (DEH 2004, Kämpf, J. and Ellis, H. 2015). About 6% of Coffin Bay waters are currently classified as sanctuary zones (*i.e.* areas of high conservation value where only low-impact recreation activities are allowed, but motorized water sports and fishing are prohibited), while the rest of the bay is zoned as a multiple use marine park where several human activities are allowed (e.g., boating, oyster aquaculture, recreational fishing, DENR 2010, Saunders, B. 2009). Among the human activities with potential detrimental effects to the local dolphin population are aquaculture and vessel traffic. The inner area is home to SA's leading Pacific oyster aquaculture industry with several areas designated for farming (*i.e.* Point Longnose area, Port Douglas, Mount Dutton and Kellidie bays; Figure 4.1). Furthermore, the bay attracts substantial power boating activity, particularly during summer and Easter tourism seasons, including recreational fishing, fishing charters and cruises to experience the work in oyster farms and, to a small degree, for dolphin watching (DEWNR 2012). Despite the importance of Coffin Bay as a habitat for a sizeable population of southern Australian bottlenose dolphins, the current lack of information on the dolphins' distribution patterns in relation to environmental conditions and human activities hampers the identification of important habitats and potential threats. This spatial information is crucial for improving future decision-making regarding the zoning of MPAs in SA.

In this study we use an ensemble of SDMs (Thuiller, W. et al. 2009) to assess the spatio-temporal distribution of southern Australian bottlenose dolphins in relation to a variety of ecogeographical and anthropogenic variables in Coffin Bay, SA. The aim was to identify areas of high probability of dolphin occurrence, gain insights into the habitat requirements of the species and evaluate the relevance of the current sanctuary zones to the protection of dolphins within this MPA. The results improve our understanding of the spatial ecology of the species; illustrate the importance of considering environmental and anthropogenic factors in SDMs, and supports future spatial conservation planning in southern Australia.

4.2. Methodology

4.2.1. Study area

Coffin Bay is part of the Thorny Passage Marine Park, which is located in Eyre Peninsula, SA (Figure 4.1). Coffin Bay's benthic habitats are mainly seagrass beds, followed by unconsolidated bare substrate, invertebrate community, low profile reef, macroalgae, cobble and medium profile reef (Figure 4.1). The bay is divided by a spit of land into an inner (~123 km^2) and an outer area (~155 km^2), and water exchange between these two areas is restricted through a narrow (2 km) opening (Kämpf, J. and Ellis, H. 2015). The inner area is a shallow (mean depth ~2.5 m with tides of approx. 1.3 m) system that consists of several interconnected bays (e.g., Port Douglas, Mount Dutton and Kellidie, DEH 2004, Kämpf, J. and Ellis, H. 2015). This area is considered an inverse estuary because evaporation rates exceeds precipitation during the austral summer resulting in hypersaline waters; while in winter salinity is diluted because of freshwater inputs due to precipitation, temporal creeks draining surface water and several underground sources (Kämpf, J. and Ellis, H. 2015, Saunders, B. 2009). The outer area connects the waters from the inner area to the Great Australian Bight, and is influenced by oceanographic features of the Southern Ocean (DEH 2004), with cold waters flowing from the south-east and warm and relatively low-nutrient waters coming from the west (Middleton, J. F. and Bye, J. A. T. 2007). Water depth increases from the shoreline to more than 25 m depth in the centre and most exposed section of the bay. In the outer area productivity is low during winter; however, in the western tip of Eyre Peninsula, close to the northern limit of Coffin Bay, a summer-autumn (February and March) upwelling brings cold, nutrient-rich water to the surface (Kämpf, J. et al. 2004, Petrusevics, P. 1993).

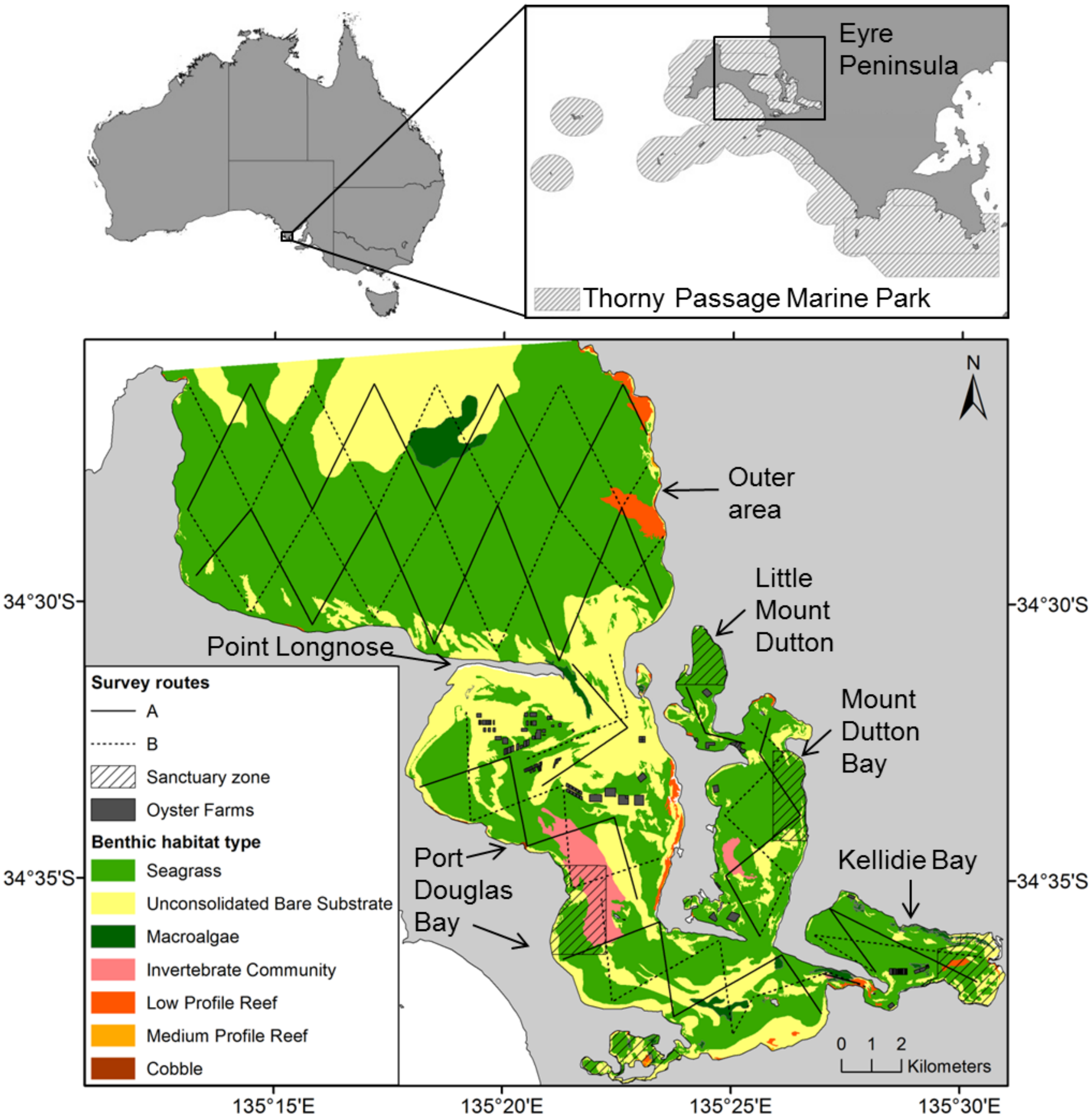

Figure 4.1. Location of Coffin Bay within the Thorny Passage Marine Park, Eyre Peninsula, South Australia. Study area showing the zig-zag transect layout (Survey routes A and B) used to cover the outer and the inner areas of Coffin Bay, oyster farms and sanctuary zones. Colours as indicated in the legend represent the different types of benthic habitats (Database provided by the Department of Environment, Water and Natural Resources, South Australian Government).

4.2.2. Survey design and data collection

Boat-based line-transect surveys were conducted between September 2013 and October 2015 to collect data on dolphins, vessels and environmental variables. Two different vessels were used for surveys, a 6.5 m semi-rigid inflatable with twin 80 hp outboard motors or a 7.2 m rigid aluminium vessel with twin 115 hp outboard motors. Surveys were conducted along two alternative ‘equal spaced zigzag’ transect routes covering areas with different environmental conditions (e.g., depth, distance to shore, temperature, salinity) and human activities (e.g., location of aquaculture farms, distribution of vessels). Each route consisted of ~130 km of total transect length and transects’ vertices were placed 4 km apart. Transects covered 85.5 km^2 in the inner area and 154.1 km^2 in the outer area. Surveys were done during daylight hours, at an average speed of 15 km/hr and under good weather conditions (*i.e.* Beaufort state ≤3, good-average visibility, no rain or fog, swell height <1 m). During surveys, an observer on each side of the boat searched continuously for dolphins and vessels from 90° degrees off the left and right beam to 5° beyond the bow using Fujinon 7 x 50 binoculars or the naked eye. A group of dolphins was defined as all animals seen within a radius of approx. 100 m (Wells, R. S. et al. 1980). Whenever a group of dolphins was sighted the position of the research vessel on the transect was recorded with a GPS, and search effort was suspended to approach the group within 10-20 m, and record their location using GPS and group size. Whenever an operating (*i.e.* navigating or fishing) power vessel, or group of vessels (defined as ≥2 vessels encountered within a radius of 100 m), was sighted on a transect the following data were gathered: GPS position on transect, number of vessels, horizontal sighting angle, and downward angle (in reticles) to vessel (or to the centre of the group of vessels), measured with the binoculars compass and reticles, respectively. This information was used to derive the position of vessels using formulae proposed by Lerczak, J. A. and Hobbs, R. C. (1998). Data on environmental variables (water depth, sea surface temperature, turbidity, salinity and pH) were collected *in situ* at the location of every group of dolphins encountered, every 2 km along the transect line, and at the beginning and end of each transect leg. A handheld multiparameter was used to record sea surface temperature (SST), salinity and pH; water visibility was measured using a Secchi disc; and depth was recorded using the boat’s depth sounder.

4.2.3. Data analysis

4.2.3.1. Response variable

A Geographic Information System (GIS) in ArcMap 10.3.1 (Esri) was used to create spatial layers of all response and explanatory variables at 500 x 500 m grid cell resolution. The location of dolphin groups and survey tracks were imported into ArcMap to create a binary presence-absence grid of dolphins while taking into account survey effort. A grid layer of survey effort (km^2) was generated by adding a 500 m buffer (average distance to which dolphins could be reliably observed from the boat) on either side of the transect surveyed. Survey coverage in each 500 x 500 m grid was quantified by calculating the total amount of area surveyed on-effort within each grid. To account for uneven effort between the inner and outer area of Coffin Bay, we determined the mean survey effort per grid for each area separately (data not shown).

Obtaining data on true absences in the case of mobile species is difficult (MacKenzie, D. I. and Royle, J. A.2005). Particularly in dolphin studies, false absences (*i.e.* consider that a species is absent from an area when in fact is present) can occur due to observer error (visibility bias), when animals are underwater and remain undetected (availability bias), or if survey effort is not high enough to ensure a reliable coverage of the study area (Barbet-Massin, M. et al. 2012, MacKenzie, D. I. and Royle, J. A. 2005, MacLeod, C. D. et al. 2007). Including false absences in models that require presence-absence data can produce inaccurate predictions of species distribution (Gu, W. and Swihart, R. K. 2004). To reduce false absences, we defined absence cells in this study based on areas with highest survey effort (Phillips, S. J. et al. 2009, Zanardo, N. et al. 2017). Every grid where a dolphin group was sighted was defined as a presence. Grids in the inner and outer areas with survey effort higher than the mean per area, and with no presence of dolphins, were considered true absences. We selected the same number of presence and absence grids in each area (inner and outer). Grids with lower survey effort than the mean were excluded from analysis.

4.2.3.2. Explanatory variables

Explanatory variables were selected based on the availability of data and published evidence suggesting that they could potentially affect the presence of dolphins or their prey as shown in other bottlenose dolphin studies (e.g., Bonizzoni, S. et al. 2014, Cañadas, A. and Hammond, P. S. 2008, Di Tullio, J. C. et al. 2015, Zanardo, N. et al. 2017). Explanatory variables (Table 4.1) were derived from data collected *in situ* or from available spatial data-layers. Layers on coastline, habitat type, and zoning of marine parks were obtained from the NatureMaps provided by the South Australian Government (Department of Environment, Water and Natural Resources, available at https://data.environment.sa.gov.au/NatureMaps/Pages/default.aspx). The location of aquaculture leasing zones (hereafter referred as oyster farms), were obtained from the Spatial Information Services of Primary Industries and Resources SA (PIRSA).

Each 500 × 500 m grid within the study area was characterised by each ecogeographical and anthropogenic explanatory variable considered in this study (Table 4.1). The distance to sanctuary zones, oyster farms, and to land was measured using the Euclidean distance (*i.e.* the shortest straight distance in m) function in ArcMap. Each grid cell was assigned a habitat type (i.*e.* seagrass beds, unconsolidated bare substrate, low profile reef, macroalgae, invertebrate community, cobble and medium profile coral reefs) according to the habitat covering the greatest proportion of each cell. To generate raster layers of the environmental data collected *in situ* (*i.e.* water depth, SST, salinity, water visibility and pH), the point data were interpolated in ArcMap using the Ordinary Kriging function and a spherical semivariogram model (500 m cell size) within the Spatial Analysis Tools. The vessel encounter rate for each grid cell was calculated in ArcMap as the number of vessels sighted divided by the survey effort (km^2) per cell.

Table 4.1. List of anthropogenic and ecogeographic variables considered for modelling the presence-absence of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay. For each variable we show its classification, the type (*i.e.* categorical or numeric) and range of values, and the data source. It is also indicated if a particular variable was used in overall and/or seasonal models.

Classification	Explanatory variables	Type: values	Data source	Included in models: Overall	Included in models: Seasonal
Anthropogenic	Distance to Sanctuary Zone	Numeric, continuous: 0 – 21,188 m	NatureMaps	*Yes*	*Yes*
	Distance to farms	Numeric, continuous: 0 – 15,558 m	PIRSA	*Yes*	*Yes*
	Distance to land	Numeric, continuous: 0 – 6,756 m	NatureMaps	*Yes*	*Yes*
	Vessels encounter rate[1]	Numeric, continuous: 0 – 700	*In situ*	*No*	*Yes*
Ecogeographic	Benthic habitat type	Categorical, categories: seagrass beds, unconsolidated bare substrate, low profile coral reefs, macroalgae, invertebrate community, cobble and medium profile coral reefs	NatureMaps	*Yes*	*Yes*
	Water depth	Numeric, continuous: 0 – 36 m	*In situ*	*Yes*	*Yes*
	Salinity (surface) [1]	Numeric, continuous:	*In situ*	*No*	*Yes*

	30 – 47 PSU			
Sea surface temperature[1]	Numeric, continuous: 11.5 – 25.9 °C	*In situ*	*No*	*Yes*
Water visibility[1]	Numeric, continuous: 0 – 16.5 m	*In situ*	*No*	*Yes*
pH[1]	Numeric, continuous: 7.7 – 9.0	*In situ*	*No*	*Yes*

[1] These variables vary temporally (see Results) and were pooled by austral season and used only in the seasonal SDMs.

4.2.3.3. *Ensemble species distribution modelling*

To model the presence-absence of dolphins in relation to explanatory variables, we used an ensemble modelling approach that combined results from five different algorithms implemented in 'Biomod2' package in R v.3.3.2 (Thuiller, W. et al. 2009): two regression methods, generalised additive models (GAMs, Guisan, A. et al. 2002) and generalised boosted models (GBMs, Friedman, J. et al. 2000); one classification technique, classification tree analysis (CTA, De'ath, G. and Fabricius, K. E. 2000); and two machine learning approaches, random forest (RF, Breiman, L. 2001) and maximum entropy (MaxEnt, Phillips, S. J. et al. 2006). Before running the SDMs, correlations between continuous explanatory variables were investigated using correlation coefficients (threshold = 0.7) and variance inflation factors (VIF, threshold = 3; Zuur, A. F. et al. 2010). The VIF is based on the square of the multiple correlation coefficients resulting from the regression of a predictor variable against all other predictor variables. Highly correlated variables were then excluded from the set of variables used for SDMs using the stepwise procedures 'vifcor' and 'vifstep' with the package 'usdm' in R (Naimi, B. 2015). The vifcor first finds a pair of variables which has the maximum linear correlation (greater than the threshold), then excludes one of them which has greater VIF; these steps are repeated until there is no variable remaining with a correlation coefficient greater than the threshold. Similarly, vifstep first calculates VIF for all variables, then excludes the variable with highest VIF (if this is greater than threshold), and these steps are repeated until no variables with VIF greater than threshold remains (Naimi, B. 2015).

SDMs were built for the entire study period and for the whole study area to determine general distribution patterns. The explanatory variables benthic habitat type (Figure 4.1), water depth, and distance to sanctuary zones, oyster farms, and to land (Results S1-Figure S1, Supplementary material, Appendix III) were included in all SDMs. Encounter rate of vessels and ecogeographic variables such as SST, salinity, water visibility and pH varied in space and time (Results S1-Figure S2, Supplementary material, Appendix III). Considering that these variables could influence the distribution of dolphins or their prey, we used them to model seasonal patterns of dolphin distribution. Previous results indicated that dolphins in the inner area of Coffin Bay have low emigration rates (Chapter 2), strong site fidelity, and most are year-round residents to the area (Chapter 3). Furthermore, the response curves of the most important variable of the models for the whole study area indicated that a plateau of high probabilities of dolphins occurred at values within ranges that are only characteristic of the inner area (see Results 4.3.1.). Based on this information we used data collected in the inner area to built SDMs for this area in particular, and identify the most important variables influencing the distribution of dolphins residing in the inner area. We also built SDMs for austral spring, summer, autumn and winter in the inner area to explore seasonal changes in distribution patterns.

SDMs were built using a binomial error distribution with logit as the link function. The five SDMs were built using a random training sample (75% of the records); and the remaining sample (25%) was used for evaluating the models' predictive performance (Thuiller, W. et al. 2009). This procedure was repeated 10 times (*i.e.* 10-fold cross-validation) for each SDM method, resulting in 50 different statistical models calibrated for each dataset. The importance of the explanatory variables was assessed using a randomisation procedure in Biomod2 based on 10 permutations (Thuiller, W. et al. 2009). This procedure calculates the correlation between the standard predictions (*i.e.* fitted values) and predictions where one variable has been randomly permutated, thus allowing direct comparison between models regardless of the modelling method. When the correlation between the two predictions is low it indicates that the variable is important in the model, and when the correlation is high the variable is not important. According to the mean correlation coefficient, explanatory variables are ranked from zero to one. Variables with zero ranking have no influence in the model, while variables ranked high (closest to one) are considered as the most influential in the model (Thuiller, W. et al. 2009).

The use of presence-absence data in SDMs can result in models predicting species occurrence in areas where the species does not occur (false positives), or in models failing to predict species presence where the species does occur (false negatives) (Franklin, J. 2010, Guisan, A. and Thuiller, W. 2005). To determine the predictive performance of single SDMs, and compare them, models were evaluated using the area under the curve (AUC) metric of the receiver operating characteristics plot (Fielding, A. H. and Bell, J. F. 1997) calculated in Biomod2. AUC measures the ratio between the observed presence-absence values and the model predictions, and its values range from zero to one, with values above 0.5 indicating that the predictions of the model perform better than what would be expected by chance (Fielding, A. H. and Bell, J. F. 1997).

Finally, the five modelling methods were combined to obtain an ensemble prediction of dolphin presence (Thuiller, W. et al. 2009). To generate the ensemble models, only SDMs with AUC values above 0.5 were considered and the contribution of selected SDMs to the ensemble model was weighted based on their predictive accuracy (*i.e.* models with higher evaluation scores were given more weight) (Marmion, M. et al. 2009). Maps of probability of dolphin occurrence were created based on the ensemble models, where values closer to zero indicate low probabilities, and values closer to one indicate higher probability of presence. When using distribution models to predict occurrence probability of a species to other areas, the values of explanatory variables in the original study area have to be within the ranges of values in the new areas to avoid overestimating the suitability of new areas (Franklin, J. 2010, Phillips, S. J. et al. 2006). Since the inner and outer areas of Coffin Bay differ in the ranges of explanatory variables (Results S1-Figure S1, Supplementary material, Appendix III), the ensemble predictions of dolphin distribution were done only for the areas corresponding to each dataset (*i.e.* either the whole Coffin Bay or the inner area only). These included cells where data on explanatory variables was available but there were no presence-absence records because of low or null survey effort. Lastly, we used AUC values to compare the performance of the ensemble models with the performance of single SDMs (Marmion, M. et al. 2009).

4.3. Results

We encountered 620 groups of dolphins (587 and 33 in the inner and outer areas, respectively) over 144 days of surveys (covering 39 and 11.5 times the transects of the inner and outer areas, respectively) between September 2013 and October 2015. Survey effort and number of dolphin groups sighted varied between seasons, and between the inner and the outer areas of Coffin Bay (Table 4.2, Figure 4.2). Overall the highest survey effort and number of dolphin sightings occurred within the inner area (Table 4.2, Figure 2).

Table 4.2. Summary of boat survey effort conducted in Coffin Bay per season between September 2013 and October 2015 including number of transects surveyed in the inner and outer areas, respectively, number of southern Australian bottlenose dolphin (*Tursiops* cf. a*ustralis*) groups encountered, and number of cells with presences (*i.e.* cells with survey effort above the mean effort and presence of dolphins) used to model the presence-absence of dolphins.

Study Area		Overall	Spring	Summer	Autumn	Winter
Total	Number of dolphin groups sighted on effort	620	197	96	168	159
	Number of cells with presences	246	108	67	104	109
Inner	Number of transects surveyed	39	13.5	7.5	11	7
	Number of dolphin groups sighted on effort	587	190	89	155	153
	Number of cells with presences	222	102	64	96	104
Outer	Number of transects surveyed	11.5	3	1.5	5	2
	Number of dolphin groups sighted on effort	33	7	7	13	6
	Number of cells with presences	24	6	3	8	5

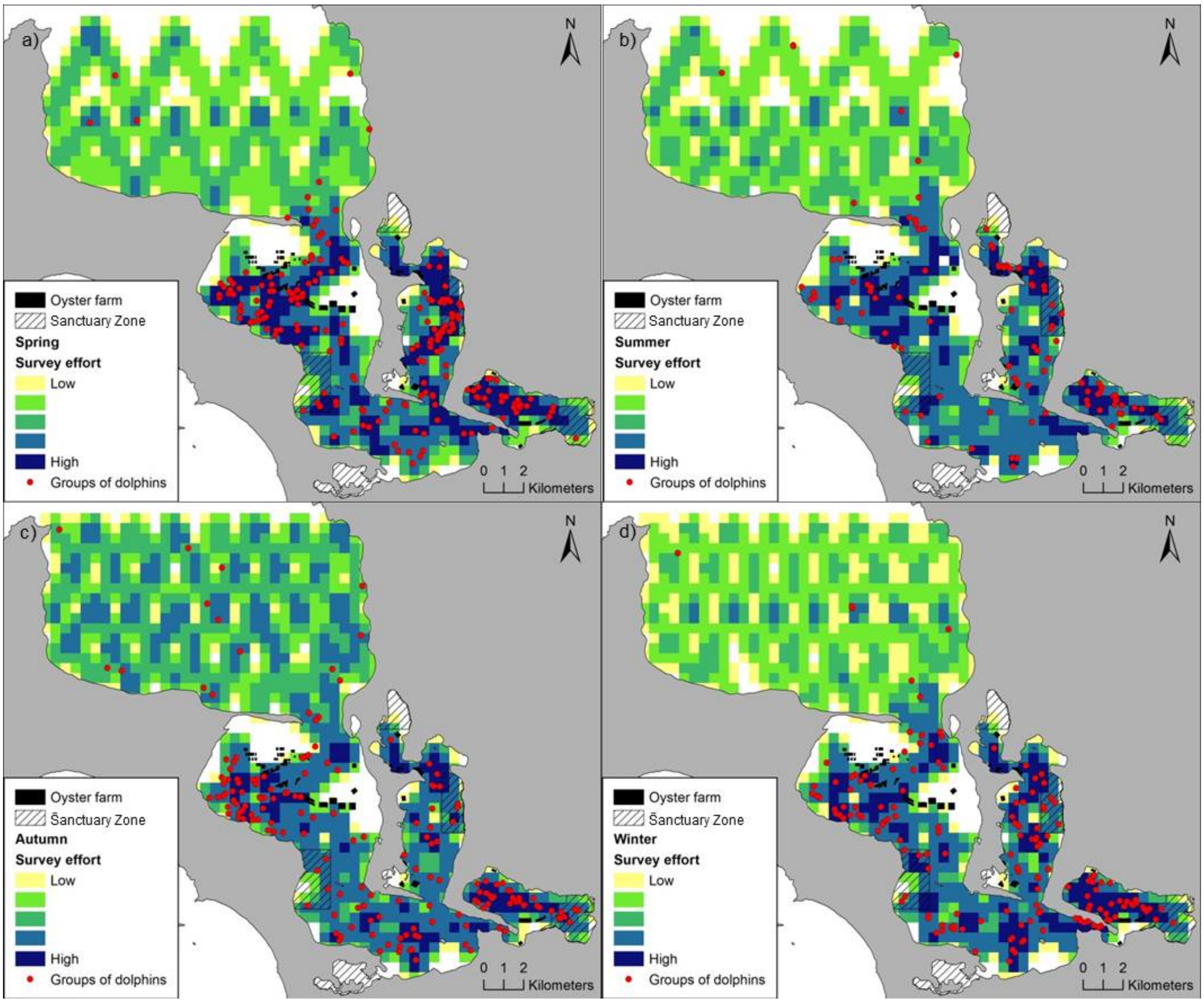

Figure 4.2. Map of survey area showing survey effort and groups of southern Australian bottlenose dolphins (*Tursiops* cf. a*ustralis*) encountered during a) spring; b) summer; c) autumn; and d) winter in Coffin Bay between September 2013 and October 2015. Cells with values of survey effort above the mean effort per season are indicated with light blue and blue colours; these cells were used to define presence and absences of dolphins to be included in the species distribution models.

4.3.1. Dolphin occurrence across Coffin Bay

When considering the entire study area over all the study period, collinearity was detected between distance to farm and distance to sanctuary zone (r = 0.84). After running 'vifstep', distance to farm was discarded from the models. Thus, the explanatory variables included in SDMs for the whole study area were habitat type, distance to land, distance to sanctuary zones, and water depth (Table 4.3). Single SDMs for the whole study area performed better than random models (AUC median = 0.88; range: 0.82 – 0.93), and ensemble models (AUC =

0.908) had better performance than most single SDMs (Figure 4.3). For the whole study area, the most important variable in all single SDMs was distance to sanctuary zone; followed by water depth, distance to land and habitat type (Table 4.3). The response curve of most SDMs showed that the probability of dolphin occurrence was higher in areas between 500 and 5,000 m from sanctuary zones, and where water depth was shallower than 15 m, with peaks in dolphin occurrence at water depths of 2 – 4 m and 7 – 10 m (Results S2-Figure S3, Supplementary material, Appendix III). These ranges of distance to sanctuary zones and water depth are characteristic of the inner area only (Results S1-Figure S1, Supplementary material, Appendix III). Accordingly, the ensemble model of the whole study area predicted high dolphin presence mainly within the inner area of Coffin Bay (Figure 4.4). Similarly, seasonal models of the whole study area selected distance to sanctuary zone as the most important variable (or distance to oyster farm, depending on which of these correlated variables was included in the models), and also show that the highest dolphin presence occurs in the inner area (Results S4, Supplementary material, Appendix III).

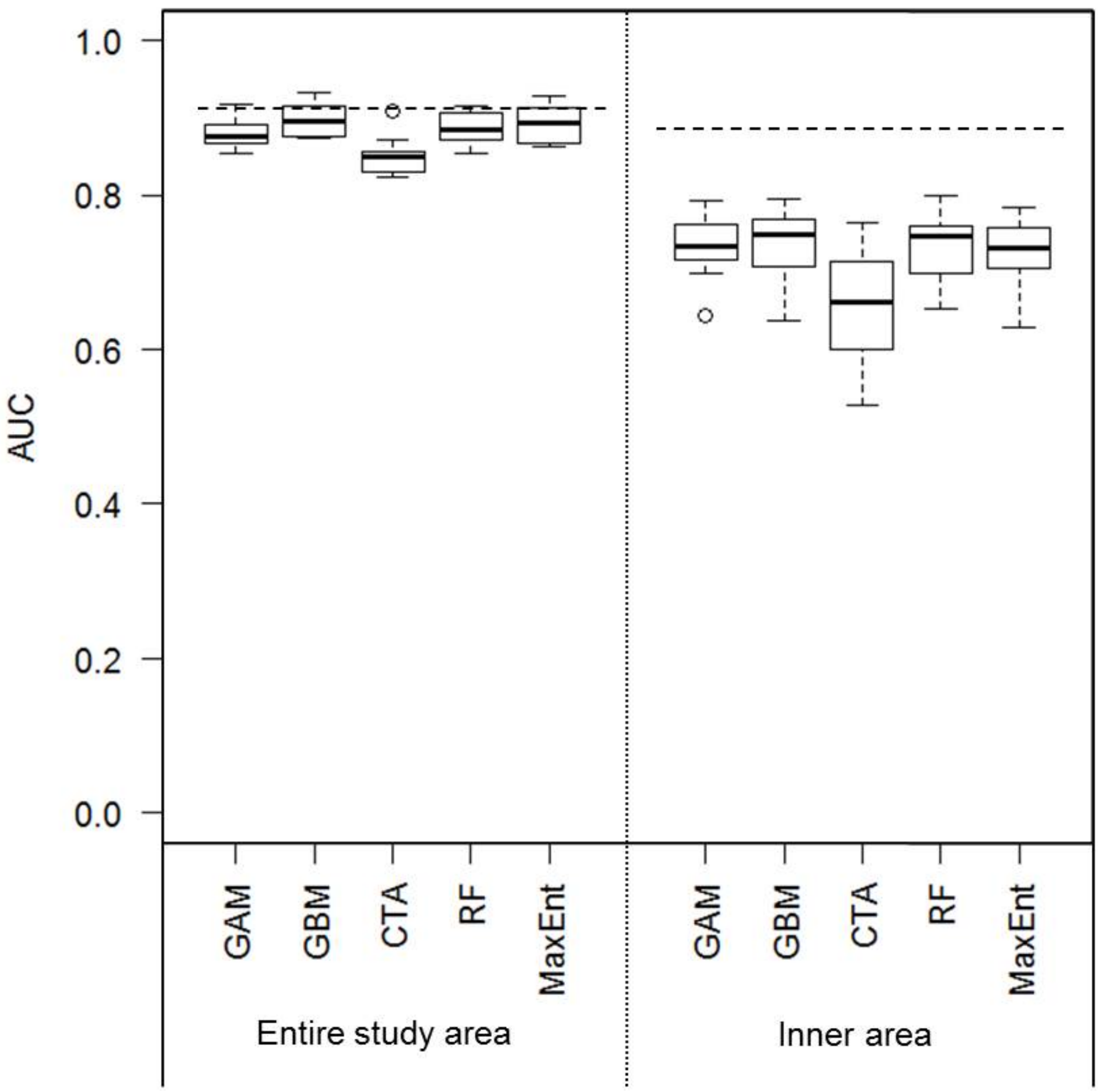

Figure 4.3. Performance of species distribution models built with datasets of the entire study area (left) and the inner area (right) of Coffin Bay. Box-plots for the model accuracy (AUC: area under the curve of the receiver operating characteristics plot) of the 10 cross-validation runs of each modelling algorithm (GAM: generalised additive model; GBM: generalised boosted model; CTA: classification tree analysis; RF: random forest; and MaxEnt: maximum entropy), and dashed line indicating the predictive performance (AUC) of ensemble models for each dataset. Values of AUC higher than 0.5 indicate that the model predictions perform better than random.

Table 4.3. Importance of ecogeographical and anthropogenic variables used in SDMs of southern Australian bottlenose dolphins (*Tursiops* cf. a*ustralis*) for the whole study area and for the inner area of Coffin Bay. Variable importance is presented as the mean percentage over 10 cross-validation runs of each single modelling algorithm and as the mean of means amongst them. Ecogeographical variables of greatest influence are highlighted in bold. GAM = generalised additive model; GBM = generalised boosted model; CTA = classification tree analysis; RF = random forest; and MaxEnt = maximum entropy.

Study area	Models	Habitat type	Distance to land	Distance to oyster farm[1]	Distance to sanctuary zone	Water depth
Whole	GAM	2.9	11.9	--	**54.7**	30.5
	GBM	0.4	4.8	--	**65.6**	29.2
	CTA	0.1	2.7	--	**68.8**	28.4
	RF	1.4	12.2	--	**55.8**	30.7
	MaxEnt	3.8	11.0	--	**50.0**	35.2
	Mean of means	1.7	8.5	--	**59.0**	30.8
Inner	GAM	5.9	13.3	13.4	6.1	**61.3**
	GBM	0.7	11.2	8.8	4.8	**74.5**
	CTA	0.8	3.0	3.2	1.3	**91.7**
	RF	1.5	18.7	12.6	9.6	**57.6**
	MaxEnt	5.9	19.5	14.2	10.1	**50.4**
	Mean of means	2.9	13.1	10.4	6.4	**67.1**

[1] Distance to oyster farm was excluded from the modelling procedure for the whole study area as it showed collinearity with distance to land.

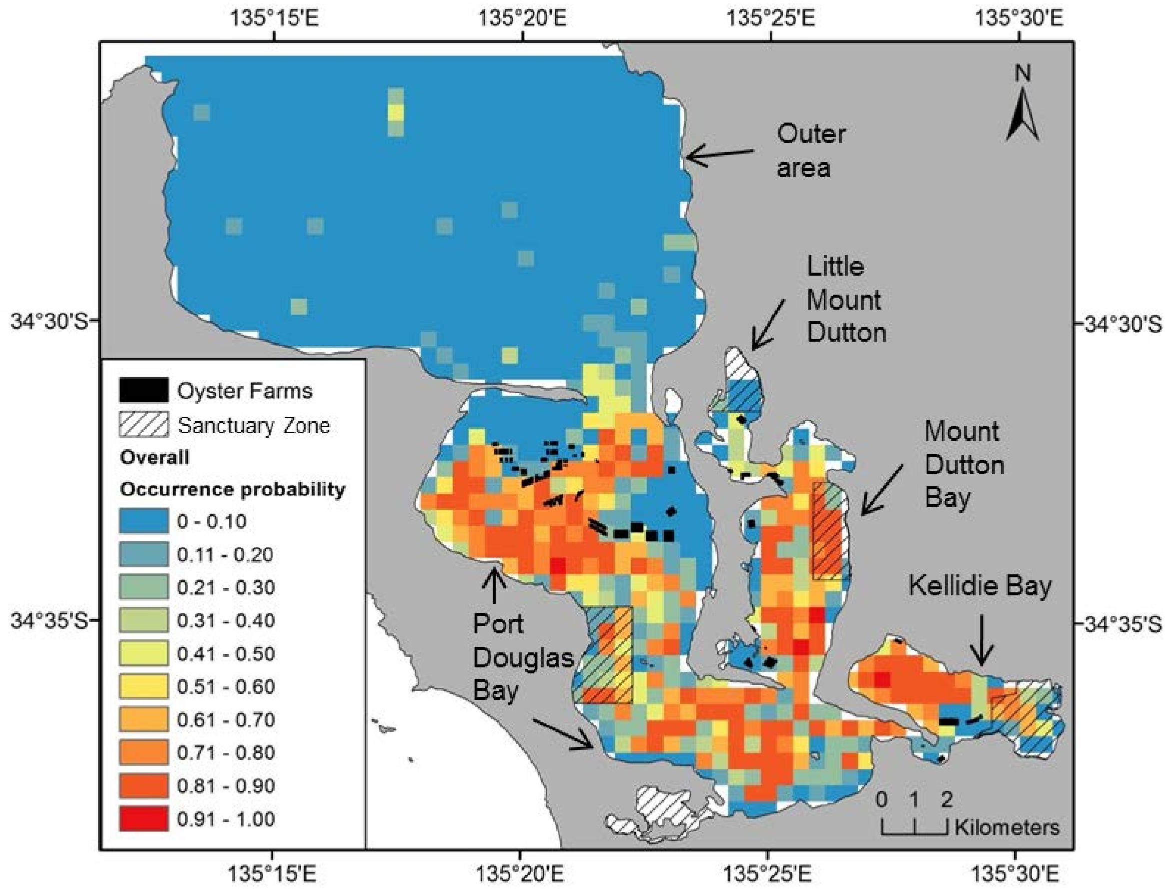

Figure 4.4. Ensemble model of southern Australian bottlenose dolphins (*Tursiops* cf. a*ustralis*) probability of occurrence in Coffin Bay for the overall study period (September 2013 – October 2015). The coloured shading, as detailed in the legend, represents probability of dolphin occurrence.

4.3.2. Dolphin occurrence in inner area

We found no collinearity between the explanatory variables considered for SDMs of the inner area throughout the entire study period (r < 0.26 and VIF < 1.3 for all combinations of variables), thus all variables were retained for analysis. Single SDMs of the inner area performed better than random models (AUC median = 0.72; range: 0.53 – 0.80), and ensemble models outperformed all single SDMs (AUC = 0.88; Figure 4.3). The most important variable affecting the distribution of dolphins in the inner area over the entire study period was water depth, followed by distance to land and oyster farms. The importance of distance to sanctuary zones and habitat type was considerably lower (Table 4.3). The probability of dolphin occurrence was higher in areas deeper than 2 m, within a distance of 1,000 m from land, and within 2,500 m from oyster farms (Results S2-Figure S4, Supplementary material, Appendix III). The ensemble model of the inner area predicted high dolphin presence mainly in the north-west part of Port Douglas, in some parts of Mount Dutton Bay, and the western part of Kellidie Bay (Figure 4.5a).

4.3.3. Seasonal dolphin occurrence in inner area

No collinearity was found amongst most explanatory variables of the inner area by season. Only in autumn salinity showed high collinearity (VIF = 3.4) and was discarded from modelling after running vifstep (Table 4.4). Most single SDMs of the inner area performed better than random models (AUC > 0.5) for all seasons, except for some CTAs (Figure 4.6). The ensemble models outperformed all single SDMs in every season; AUC of ensemble models for spring, summer and winter was 0.84, and for autumn was 0.80 (Figure 4.6). In general, most seasonal SDMs identified water depth as the most important variable, followed by distance to land (Table 4.4); which is concordant with results of overall models for the inner area (Table 4.3). Exceptions to these general patterns included one algorithm for spring and three for autumn that had distance to land as the most important variable, and two algorithms for summer that identified pH as an important variable (Table 4.4). Response curves of SDMs showed variability among SDMs (see examples in Results S3-Figure S5, Supplementary material, Appendix III). Ensemble predictions showed that, among all seasons, summer exhibited the lowest probability of dolphin presence (Figure 4.5b-e). The highest probabilities of dolphin occurrence during summer were in the central part of Kellidie Bay, and the northern part of Mount Dutton Bay that connects to Little Mount Dutton (Figure 4.5c). In the remaining seasons, the highest probability of dolphins were in areas where water depth exceeds 2 m including the western sector of Kellidie Bay, the central part of Mount Dutton Bay and around the farms of Port Douglas Bay (Figure 4.5b,d,e). The seasonal predictions for dolphins of the inner area are concordant with seasonal predictions obtained when using data from the entire study area (see Results S4, Supplementary material, Appendix III).

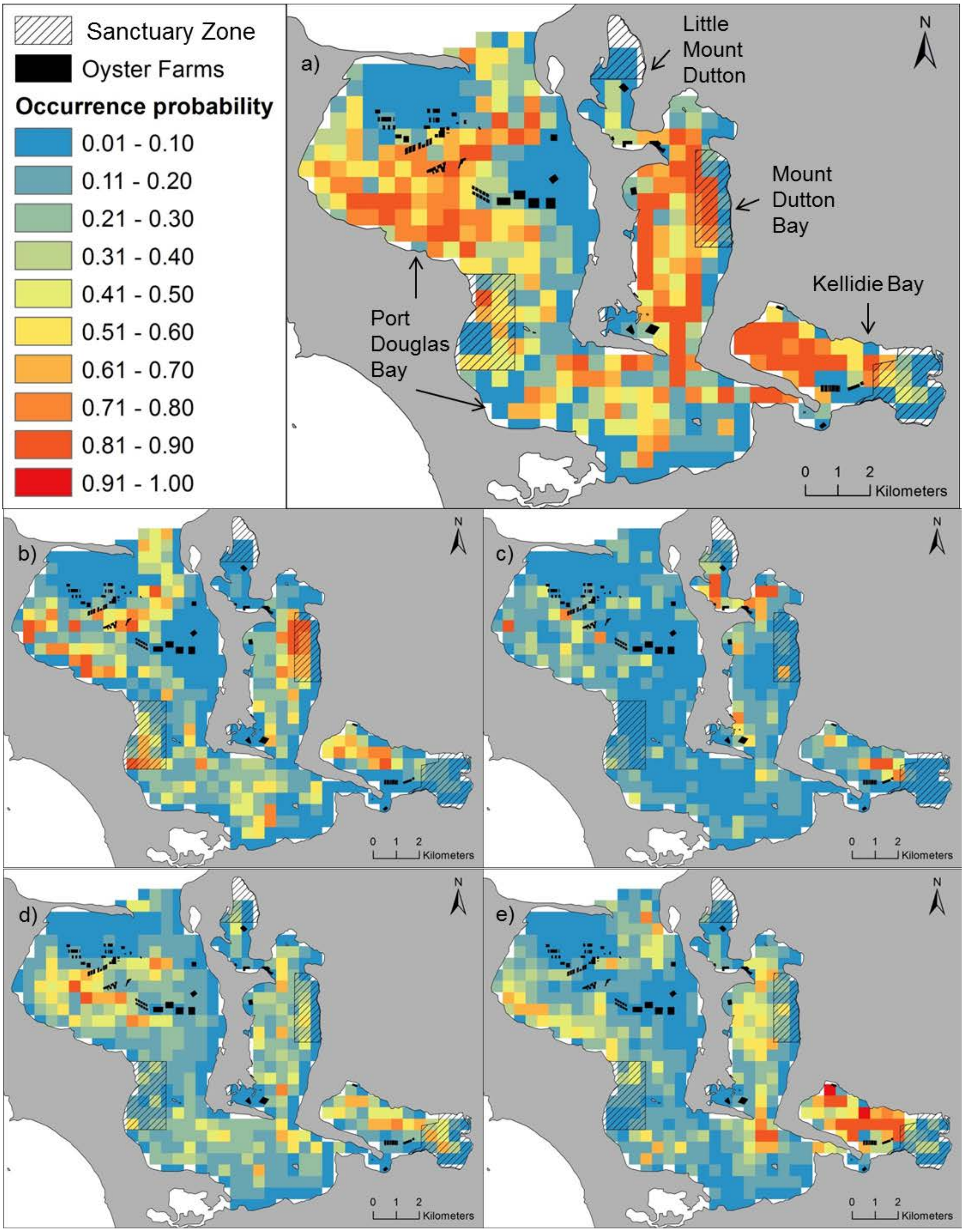

Figure 4.5. Ensemble models of southern Australian bottlenose dolphin (*Tursiops* cf. a*ustralis*) probability of occurrence in the inner area of Coffin Bay for: a) over the entire study period; b) spring; c) summer; d) autumn; and d) winter. Colours as shown in the legend indicate the probability of occurrence of dolphins.

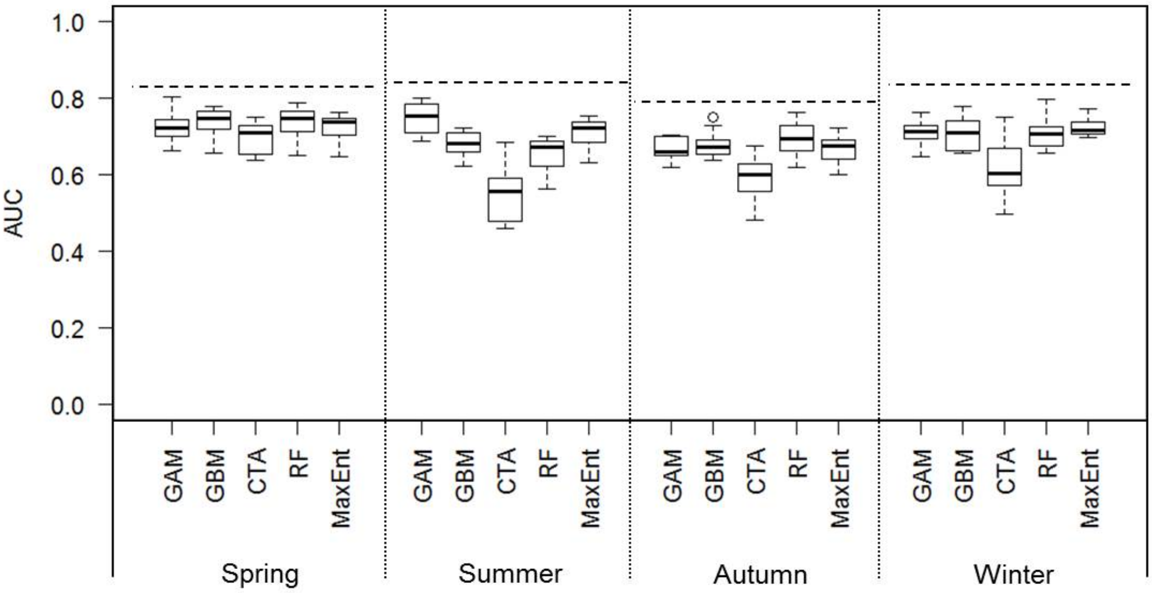

Figure 4.6. Performance of species distribution models built with seasonal (*i.e.* spring, summer, autumn, winter) datasets of the inner area of Coffin Bay. Box-plots for the model accuracy (AUC: area under the curve of the receiver operating characteristics plot) of the 10 cross-validation runs of each modelling algorithm (GAM: generalised additive model; GBM: generalised boosted model; CTA: classification tree analysis; RF: random forest; and MaxEnt: maximum entropy), and dashed line indicating the predictive performance (AUC) of ensemble models for each dataset. Values of AUC higher than 0.5 indicate that the model predictions perform better than random.

Table 4.4. Importance of ecogeographical and anthropogenic variables for southern Australian bottlenose dolphins (*Tursiops* cf. a*ustralis*) in the inner area of Coffin Bay by season, using five types of models: generalised additive model (GAM), generalised boosted model (GBM), classification tree analysis (CTA), random forest (RF) and maximum entropy (MaxEnt). Ecogeographical variables of greatest influence are in bold. (NOTE: Values are presented only for those non-correlated variables included in each model.)

Season	Model	Habitat	Distance to land	Distance to oyster farm	Water depth	Distance to sanctuary zone	Vessel encounter rate	Salinity[1]	Sea surface temperature	pH
Spring	GAM	6.5	**25.4**	1.6	24.2	8.2	3.7	7.4	7.8	15.1
	GBM	0.8	27.2	3.9	**41.9**	6.8	2.4	2.3	5.2	9.4
	CTA	2.3	23.2	4.8	**31.2**	13.6	3.7	2.3	8.1	10.7
	RF	0.9	26.1	5.2	**36.7**	9.1	3.7	2.6	6.8	9.0
	MaxEnt	2.4	27.8	4.1	**28.7**	10.8	1.4	9.7	6.3	8.7
Summer	GAM	9.3	17.9	12.4	**26.2**	2.0	2.8	3.2	10.4	15.8
	GBM	3.3	12.9	19.2	18.6	4.2	3.3	0.2	11.3	**26.9**
	CTA	8.4	16.7	15.6	14.6	9.2	0.0	0.0	10.2	**25.2**
	RF	4.9	13.1	18.1	**21.2**	7.6	3.6	1.3	13.3	17.0
	MaxEnt	7.9	13.2	17.1	**21.8**	5.2	10.4	5.7	9.4	9.2
Autumn	GAM	18.7	**31.1**	3.6	23.7	6.3	9.9	--	1.1	5.5
	GBM	5.0	24.2	8.6	**32.6**	12.8	9.4	--	1.8	5.5

	CTA	3.0	19.8	12.2	**32.3**	11.8	11.0	--	3.2	6.7
	RF	5.5	**23.9**	10.5	23.6	13.6	10.0	--	5.5	7.3
	MaxEnt	10.0	**28.2**	5.9	26.3	4.4	14.1	--	4.0	7.3
Winter	GAM	10.3	21.8	7.5	**27.1**	8.9	5.2	11.1	2.0	6.1
	GBM	0.8	14.7	5.1	**39.5**	4.5	3.0	18.3	1.1	13.2
	CTA	0.0	7.9	3.7	**37.4**	0.0	4.0	18.0	5.7	23.3
	RF	1.9	17.7	7.8	**33.2**	7.3	4.0	13.4	3.1	11.6
	MaxEnt	8.9	23.1	5.9	**29.5**	10.0	2.6	11.6	2.6	5.8

[1] Salinity was excluded from the modelling procedure for autumn as it showed collinearity with other variables.

Table 4.5. Probability of occurrence of southern Australian bottlenose dolphins (*Tursiops* cf. a*ustralis*) predicted by the inner area's ensemble models in sanctuary zones (SZ) of Coffin Bay. Overall and seasonal probability values (mean ± SD) of all the grids falling in each SZ (*i.e.* in Kellidie, Mount Dutton, Little Mount Dutton and Port Douglas) or outside them are shown.

Sanctuary zone	Area (km^2)	No. grids	Overall (mean ± SD)	Spring (mean ± SD)	Summer (mean ± SD)	Autumn (mean ± SD)	Winter (mean ± SD)
Kellidie	4.5	18	0.27 ± 0.27	0.25 ± 0.24	0.1 ± 0.09	0.12 ± 0.2	0.25 ± 0.26
Little Mount Dutton	3.1	5	0.07 ± 0.01	0.18 ± 0.12	0.05 ± 0.02	0.12 ± 0.07	0.11 ± 0.07
Mount Dutton	3.1	17	0.52 ± 0.35	0.22 ± 0.16	0.48 ± 0.36	0.11 ± 0.14	0.23 ± 0.17
Port Douglas	4.8	18	0.42 ± 0.23	0.22 ± 0.11	0.36 ± 0.26	0.11 ± 0.08	0.2 ± 0.16
Outside	107.5	437	0.39 ± 0.29	0.22 ± 0.18	0.22 ± 0.22	0.15 ± 0.16	0.23 ± 0.2

4.3.4. Dolphin occurrence and sanctuary zones

Probability of dolphin occurrence in sanctuary zones ranged from 0.04 – 0.89 (Figure 4.5). Amongst all sanctuaries, the one located in Mount Dutton Bay showed the highest probability (mean ± SD = 0.52 ± 0.35) of dolphin occurrence considering the overall study period (Figure 4.5; Table 4.5). The seasonal mean probabilities of dolphin occurrence were below 0.5 for all sanctuaries (Table 4.5).

4.4. Discussion

Effective management of wildlife populations requires sound knowledge of species distributions and associated threats. Here, using an ensemble modelling approach we determined the spatio-temporal distribution patterns of southern Australian bottlenose dolphins (*Tursiops* cf. *australis*) in Coffin Bay, a heterogeneous ecosystem located within a multiple use marine park in SA, and how both ecogeographical and anthropogenic factors influenced these patterns. Models of the whole Coffin Bay indicated that dolphins' probability of occurrence was influenced mainly by distance to sanctuary zones and water depth. High probability of dolphin occurrence was predicted almost exclusively for the inner area of Coffin Bay, which is consistent with the high density of dolphins recorded for this area (Chapter 2), and indicates that the inner area represents an important and productive habitat for southern Australian bottlenose dolphins. When looking at models of the inner area only, they showed that dolphins favoured waters greater than 2 m deep, within a distance of 1,000 m from land and 2,500 m from oyster farms. Despite the seasonality in environmental conditions and anthropogenic activities, little variation was observed in dolphin occurrence patterns and the most important explanatory variables across seasons. Overall, we found that areas with the highest probability of dolphin presence were located in three different embayments within the inner area. A sanctuary zone in Mount Dutton Bay covers areas of moderate to high probability of dolphin presence; however, in Kellidie and Port Douglas Bays the areas of highest dolphin probability fell outside sanctuaries. These findings are useful to better-inform spatial management measures in SA's marine parks and improve conservation of dolphins in southern Australia.

Dolphin distribution is known to be influenced by prey distribution and predation risk (Acevedo-Gutiérrez, A. and Parker, N. 2000, Heithaus, M. R. and Dill, L. M. 2006, McCluskey,

S. M. et al. 2016). Therefore, characteristics of the habitat such as water depth, distance to coast, salinity, sea surface temperature, among others, are usually used as proxies of prey availability because they are related to oceanographic processes that enhance local productivity (e.g., Di Tullio, J. C. et al. 2015, Parra, G. J. et al. 2006, Zanardo, N. et al. 2017). Coffin Bay dolphins favoured the waters of the inner area. Shallow, sheltered, inverse estuaries, such as the inner area of Coffin Bay, are usually highly productive systems (Kämpf, J. 2014) that can sustain high densities of fish and top predators like dolphins. The total nutrient loads in the inner area of Coffin Bay are higher than those of outer area (EPA 2014), and it is likely that this enhances the productivity in the former resulting in higher abundance of prey. Actually, several fish and cephalopod species that are known to constitute part of the diet of bottlenose dolphins in SA (Gibbs, S. E. et al. 2011), use Coffin Bay as a nursery and feeding area (DENR 2010). In addition, it is likely that differences in predation risk between the inner and outer area of Coffin Bay may also influence dolphin occurrence patterns in the study area. White sharks (*Carchharodon carcharias*), one of the predators of dolphins along SA's coast (Bruce, B. D. 1992), can be found close to shore in <5 m depth, but they seem to prefer continental shelf waters <100 m depth (Bruce, B. et al. 2006). The shallow waters of the inner area and the narrow connection with the outer area may restrict the use of the former by sharks, thus resulting in lower predation risk in the inner area. Future studies incorporating biotic variables such as the presence and abundance of prey and predators into SDMs are needed to explicitly test these hypotheses.

Both ecological and social factors can influence the spatial distribution of wildlife. The social structure of animal populations can strongly influence individual patterns of space use (Blondel, D. V. et al. 2009, Campbell, P. et al. 2006, Tanner, C. J. and Jackson, A. L. 2012). Social structure analysis of southern Australian bottlenose dolphins in Coffin Bay showed that two communities of similar size (each one with at least 70 individuals) occurred in the inner area, one in the Port Douglas area and another one in Mount Dutton and Kellidie Bays (Diaz-Aguirre, F. 2017). Furthermore, space use patterns of resident individuals of the inner area showed that they have small representative ranges (<33.5 km^2) and many dolphins restrict their movements to a single embayment (Chapter 3). Thus, the areas of high probability of dolphin occurrence identified here appear to reflect the strong site fidelity, restricted ranging patterns and the social clustering of dolphins to particular embayments within the inner area of Coffin Bay. Similar patterns have been observed in inshore bottlenose dolphins in Port Stephens, Australia (e.g. *T. aduncus*, Wiszniewski, J. et al. 2009, Möller, L. M. et al. 2007).

In temperate regions, dolphins can display seasonality in their distribution patterns as they follow changes in prey abundance and availability, which are driven by seasonal changes in water conditions (Sprogis, K. R. et al. 2016, Zanardo, N. et al. 2017). For example, likely in response to availability and movements of prey, southern Australian bottlenose dolphins along the Adelaide metropolitan coast favour shallower nearshore waters during summer and autumn, and move to deeper farther from shore waters in winter (Zanardo, N. et al. 2017). Even though Coffin Bay is exposed to pronounced spatial and temporal variability in environmental conditions (Figure S2, Supplementary material, Appendix III), the ensemble predictions of dolphin distribution showed no major seasonal patterns, at least not at the spatio-temporal resolution used in this study. This temporal stability in the distribution patterns of southern Australian dolphins in Coffin Bay suggest that the availability of prey in the inner area is enough to fulfil dolphins needs year round, contrary to what is observed along the Adelaide coast (Zanardo, N. et al. 2017). The Adelaide metropolitan coast is an open environment, likely less productive than Coffin Bay, where the abundance of southern Australian bottlenose dolphins varies throughout the year, and individuals show varying levels of site fidelity and residency (Zanardo, N. et al. 2016). In contrast, the inner area of Coffin Bay is a highly productive inverse estuary (see above), where the numbers of dolphins remain almost constant across the season (Chapter 2), and individuals display strong patterns of residency and site fidelity (Chapter 3), which further supports the idea that prey abundance in this area can sustain dolphins needs across seasons.

Anthropogenic activities such as aquaculture and vessel traffic are known to affect dolphin distribution patterns (e.g., Bearzi, G. et al. 2016, Bonizzoni, S. et al. 2014, Lusseau, D. and Bejder, L. 2007). Dolphin response to aquaculture presence is variable and complex. Some studies elsewhere showed that dolphins were attracted to areas with aquaculture (Kemper, C. M. et al. 2006, Markowitz, T. M. et al. 2004), while others showed that dolphins were less likely to go into areas where aquaculture was occurring, even though farms were located in habitats with characteristics favored by dolphins (Watson-Capps and Mann 2005). In Coffin Bay, oyster farms are located in shallow areas less than 2 m deep, while dolphins seem to prefer waters greater than 2 m deep. Whether dolphins have been displaced from areas now occupied by oyster farms, since the farms were established, is unknown. In general, shellfish aquaculture is known to increase nitrogen levels into the ecosystem altering local ecology, especially in areas where tidal and other flushing is minimal (Würsig, B. and Gailey, G. 2002). The inner area of Coffin Bay has slow flushing (Kämpf, J. and Ellis, H. 2015) and high nutrient loads (EPA 2014). Thus, dolphins favouring areas within 500 to 2,500 m from oyster farms is likely in response to higher nutrients and a potential increase in prey abundance in the proximity of farms. Further studies on dolphin diet and prey distribution within the study area are needed to test this hypothesis.

Studies on the impacts of boats on dolphins have found that dolphins alter their behaviour in the short-term when density of vessels increases, and that this can also lead to changes in their distribution patterns in the longer term (Lusseau, D. and Bejder, L. 2007). Although the influence of encounter rate of vessels was not as strong as other variables in explaining the distribution of dolphins at the spatio-temporal scale considered in this study, response curves showed that the probability of dolphin presence decreased as vessel encounter rates increased (Figure S5, Supplementary material, Appendix III) suggesting that dolphins in Coffin Bay tend to occur in areas with little vessel traffic. Future behavioural research and long-term monitoring of this population would help elucidate whether dolphins' short-term behaviour is affected by the presence of oyster farms or vessels, and if management measures are required to prevent potential long-term consequences.

4.4.1. Implications for conservation

Wildlife-habitat modelling approaches are fundamental for the design of comprehensive and effective marine protected areas for marine top predators (Hooker, S. K. et al. 2011b). Similarly to Zanardo, N. et al. (2017), the ensemble model approach used in this study performed better than single SDMs. Thus ensemble modelling provides a robust approach for identifying important areas for marine top predators, evaluate importance of variables influencing distribution patterns, and for guiding decision making in spatial conservation planning. In this study, the ensemble predictions showed the importance of the inner area of Coffin Bay for southern Australian bottlenose dolphins. Our findings highlight areas with high probability of dolphins (>0.6) located in three different embayments (*i.e.* parts of

Kellidie, Mount Dutton and Port Douglas Bays, see Figure 4.5a) within the inner area. These areas were identified here as important at the population level; however, evidence indicates that each of these embayments is an important area for different social communities (Diaz-Aguirre, F. 2017).

The sanctuary zones of Thorny Passage Marine Park cover areas with low (<0.3) to moderate (0.31 – 0.6) probability of dolphin presence in Kellidie and Port Douglas Bays, while Mount Dutton Bay sanctuary covers areas with relatively high probability of presence. However, in general, areas with the highest probability of dolphin presence are outside the sanctuary zones, where dolphins are exposed to multiple anthropogenic threats associated with vessel traffic, recreational fishing and oyster farming. Dolphins living close to farms can be under risk of entanglement with aquaculture gear, which may cause injuries or dolphin death (Kemper, C. M. et al. 2005, Kemper, C. M. et al. 2006, Watson-Capps, J. J. and Mann, J. 2005). The farming system used in Coffin Bay uses structures that result in debris washing up on beaches (DEH 2004), including poles, baskets, rubber bands and plastic clips. During this study, four calves were observed swimming with rubber bands entangled around their necks, while two of them were still alive at the end of the study, the remaining two were presumed dead (unpublished data). Also, a dolphin was entangled in fishing lines, which restricted his swimming, and the marine park authorities took action to release it (unpublished data). The expansion of current, or the establishment of new oyster farms in Coffin Bay should take into account the areas of high dolphin presence identified here to minimize interactions with aquaculture equipment and potential displacement of dolphins from important habitats.

Marine mammals are considered as 'species of ecological value' in the management plan of the Thorny Passage Marine Park (Bryars, S. et al. 2016). However, this marine park, as many others in SA, was established with little information on the distribution and abundance of southern Australian bottlenose dolphins. Recent findings showing that Coffin Bay constitutes the area with highest density of southern Australian bottlenose dolphin (Chapter 2), and the findings presented here should encourage the integration of the species into the monitoring program and zoning arrangements of this park. To reassure the protection of the population inhabiting Coffin Bay, we suggest that three dolphin conservation zones should be established in accordance with the distribution patterns presented here. We recommend locating these zones in the north-west part of Port Douglas, in part of Mount Dutton Bay and in the western part of Kellidie Bay.

4.5. Supplementary material

Results S1. Spatial and temporal patterns of explanatory variables.

Results S2. Response curves of species distribution models for the overall study period.

Results S3. Response curves of the seasonal species distribution models for the inner area of Coffin Bay.

Results S4. Seasonal probability of dolphin occurrence in the entire study area.

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CHAPTER 5: GENERAL DISCUSSION

Information on demographics and spatial ecology is essential for conservation and to inform management strategies of wildlife populations. The southern Australian bottlenose dolphin (*Tursiops* cf. *australis*) is endemic to southern Australia and appears to live in small resident populations in coastal areas. Across their distribution, southern Australian bottlenose dolphins are exposed to multiple threats from human activities associated with coastal areas, including in marine protected areas (MPAs) which allow for multiple human uses (Chapter 1). The paucity of knowledge about the species ecology across most of its known distribution has hampered conservation and management efforts. This is particularly the case across the 19 multiple use marine parks recently established (2012) in South Australia (SA), which aim to effectively conserve and manage protected species such as dolphins (DEWNR 2012). Thus, in these parks information on the demography and spatial ecology of the species is urgently needed to guide spatial conservation planning.

This PhD thesis aimed to fill in some of the knowledge gaps around the demographics and spatial ecology of southern Australian bottlenose dolphins by investigating a population inhabiting Coffin Bay, a productive embayment located within the Thorny Passage Marine Park (TPMP), SA. I used boat-based surveys, photo-identification techniques, biopsy sampling, mark-recapture modelling, clustering and spatial analysis to investigate their abundance and sex-specific demographic parameters (Chapter 2), individual site fidelity and ranging patterns (Chapter 3), and spatial distribution patterns in relation to ecogeographic and anthropogenic variables (Chapter 4). In this chapter, I highlight the main findings of my thesis (Chapters 2 – 4), expand on the ecological implications of a high density of resident dolphins and how they thrive in such a small area, and discuss why Coffin Bay is an important area for southern Australian bottlenose dolphins. I review potential threats to dolphins inhabiting Coffin Bay and provide some recommendations for management of this dolphin population. Finally, I outline future research needed to further our understanding of the ecology and impacts of human activities on southern Australian bottlenose dolphins.

5.1. Coffin Bay: an important area for southern Australian bottlenose dolphins

Demographic analysis showed that Coffin Bay, particularly the small inner area (123 km^2), is home to the largest population of southern Australian bottlenose dolphins reported to date (Chapter 2). In the inner area the population size remained relatively stable across seasons showing an extremely low emigration rate (Chapter 2), with most individuals showing high levels of site fidelity and restricted ranging patterns (Chapter 3). Furthermore, species distribution modelling showed that dolphins particularly favour the shallow waters of the inner area of Coffin Bay (Chapter 4). These findings suggest that Coffin Bay, and particularly the inner area, constitutes an important habitat with high conservation value for southern Australian bottlenose dolphins. The demography and spatial ecology patterns of southern Australian bottlenose dolphins inhabiting Coffin Bay is likely a result of the high productivity and predictability of food resources in this area, as well as low predation risks for the dolphins.

5.1.1. Ecological relevance of a highly productive area to sustain a high density of dolphins

An interplay of bottom-up and top-down effects regulates the functioning of marine ecosystems and the abundance of upper-trophic-level populations (Hunt and McKinnell 2006) such as dolphins. In Coffin Bay, an upwelling occurring during summer-autumn months off the adjacent continental shelf bring nutrient rich waters into nearshore waters of the bay (Kämpf et al. 2004; Kämpf and Ellis 2015). Local sources of nutrients (e.g., agricultural runoff, urban runoff and overflow of septic systems from small towns) also likely add to the high nutrient levels of Coffin Bay (EPA 2014). The inner area of Coffin Bay in particular, is an inverse estuary with slow flushing and high levels of nutrients loads; systems with such characteristics are usually highly productive and support high abundance of fish. The highly productive waters of Coffin Bay, especially in the inner area, likely sustain high prey abundance and may constitute one of the main drivers influencing the dolphins demographic and distribution patterns described here. Furthermore, the shallow waters of the inner area and its narrow connection with the more exposed waters of the outer area, is possibly restricting the use of the area by large predatory sharks which can prey upon dolphins, leading to low predation risks in the area compared to the open coast.

In highly productive habitats, where food resources are predictable (e.g., estuarine areas in marine ecosystems), dolphins tend to develop high site fidelity and range over relatively small areas that provide the resources they need (Chapter 3). In temperate regions, however, seasonal variability in environmental conditions can lead to changes in the distribution patterns of prey and ultimately result in dolphins exhibiting seasonal movements. Seasonal changes in the distribution and abundance of southern Australian bottlenose dolphins has been recorded in the less productive coastal waters of Adelaide, SA, where individuals exhibit different degrees of site fidelity, and show a shallow to deep water change in distribution from warmer to colder months (Zanardo et al. 2016; Zanardo et al. 2017). Despite the spatio-temporal variability of environmental conditions (sea surface temperature and salinity) in Coffin Bay, dolphins preference for the shallow waters of the inner area remained relatively consistent across seasons (Chapter 4). The temporal stability of the distribution patterns of Coffin Bay's dolphins was also reflected in the sex-specific demographics of the population, with male and female abundance remaining relatively constant across seasons and showing negligible emigration rates from the inner area (Chapter 2). These findings, suggest that prey resources are available year-round in the inner area, and are likely sufficient to sustain the abundant resident population of dolphins inhabiting this area (Chapters 2 – 4). High prey availability year round is likely promoted by the high productivity and diversity of habitats found within the inner area of Coffin Bay (Miller et al. 2009). This area is considered a regionally important nursery and feeding area for several fish species (DENR 2010) which are known to be prey items of bottlenose dolphins elsewhere in SA (Gibbs et al. 2011).

The negligible difference in demographic parameters (Chapter 2) and space use patterns (Chapter 3) among male and female dolphins inhabiting the inner area of Coffin Bay indicates that both sexes are able to fulfil their resource needs, not only for food but also for mating and calving. Contrary to the absence of sex-bias in ranging patterns of dolphins in Coffin Bay, in other areas adult males use larger ranges than adult females possibly because males have to cover larger areas to search for mating partners while females tend to be more philopatric (Möller and Beheregaray 2004; Urian et al. 2009; Möller 2012; Sprogis et al. 2016; Wells et al. 2017). The idea that dolphin space use patterns in Coffin Bay are not driven by their sex is further supported by evidence indicating that, in general, both sexes of southern Australian bottlenose dolphins seem to show relatively equal probabilities of dispersal (Pratt et al. under review). Furthermore, the low emigration rate of dolphins from the inner area (Chapter 2) and the restricted ranging patterns of residents (Chapter 3) are supported by the genetic data (Pratt et al. under review). Particularly, the inner area population has restricted gene flow and a significant genetic differentiation to other southern Australian bottlenose dolphin populations, albeit moderate gene flow was estimated between dolphins of the outer area to dolphins of Esperance/St. Francis Island (Pratt et al. under review).

5.1.2. Fine-scale spatial structure: potential causes and consequences

When individuals have high site fidelity to an area, such as the dolphins in Coffin Bay (Chapter 3), they become familiar with local ecological conditions and may adapt to maximise the use of available resources (Switzer 1993; Switzer 1997). Strong competition for food resources, however, can occur in areas highly populated by conspecifics, and to avoid competition individuals may exhibit small ranging patterns and show spatial segregation (Gowans et al. 2008). The population of southern Australian bottlenose dolphins inhabiting the inner area of Coffin Bay seems to be an example of these ecological pressures at play in this system. The inner area supports a high density (*i.e.* seasonal range: 1.57 – 1.70 individuals/km^2) of dolphins (Chapter 2) with individual animals showing fine-scale space use patterns (*i.e.* representative ranges <35.5 km^2). As a result there are moderate levels of spatial segregation among individuals inhabiting different bays within the inner area of Coffin Bay (Chapter 3).

The individuals' fine-scale spatial structure is associated to the population's social structure (Diaz-Aguirre 2017). The dolphin population inhabiting the inner area consists of two social communities of similar size (each one with at least 70 individuals) that are somewhat spatially segregated (Diaz-Aguirre 2017). The core areas (50% kernel) of these communities are discrete and do not overlap, but their representative ranges (95% kernel) overlap in an area where mixed community groups were observed. One of these communities mainly uses the Port Douglas area, while the other tends to inhabit the area including Mount Dutton and Kellidie Bays (Diaz-Aguirre 2017). Moreover, results presented here at the individual level indicate that within the community of Mount Dutton-Kellidie Bays, some dolphins seem to remain in only one of these bays (Chapter 3). Diaz-Aguirre (2017) proposed that the fine-scale social structure in Coffin Bay is delineated and maintained by differences in environmental conditions between embayments, individual adaptations to local ecological conditions, and genetic relatedness and kinship relationships. The different embayments (*i.e.* Port Douglas south and north, Mount Dutton and Kellidie) of Coffin Bay exhibit different prey assemblages (Whitmarsh, unpublished data), so it is possible that individuals/communities have adapted to exploit different food resources as a mean of reducing competition in a highly populated area (Chapter 3, Diaz-Aguirre 2017).

Although overall the inner area of Coffin Bay is an important area for southern Australian bottlenose dolphins, some areas showed higher probability of dolphin occurrence than others (Chapter 4). The areas of high dolphin probability of occurrence included the north-west part of Port Douglas, most of Mount Dutton Bay and the western part of Kellidie Bay (Chapter 4). The spatial variability of dolphin occurrence, environmental conditions and anthropogenic activities across Coffin Bay (Chapter 4), has important implications for the spatial conservation of these animals. Southern Australian bottlenose dolphins inhabiting different embayments of the inner area may be facing different potential threats.

5.2. Potential impacts of human activities on southern Australian bottlenose dolphins in Coffin Bay

Southern Australian bottlenose dolphins are under threat from multiple human activities that overlap with their coastal distribution (Chapter 1). Even though Coffin Bay is located within the TPMP, most of these waters are classified as areas of multiple use. In these areas human activities such as boating, fishing, and aquaculture, among others, are allowed and can potentially be detrimental to dolphins' health. Here, I discuss the potential impacts of human activities to the dolphins inhabiting Coffin Bay based on the demography and spatial ecology of this population.

5.2.1. Interaction with vessels

Anthropogenic activities in Coffin Bay waters involve vessel traffic. They are used by locals and tourists for recreational fishing, sailing, scenic cruises and water sports, and by oyster farmers, who usually navigate daily (multiple times per day, pers. obs.) to work on the aquaculture leases. It is well known that dolphins can modify their distribution patterns to avoid areas of high vessel usage and disturbance (Bejder et al. 2006b; Lusseau and Bejder 2007). Although the encounter rate of vessels was not amongst the most important variables explaining the seasonal distribution of dolphins in Coffin Bay, areas of high dolphin presence were located in areas of low vessel traffic, suggesting that dolphins may avoid areas with high vessel traffic (Chapter 4). If in Coffin Bay vessel traffic were to increase and extend to areas of high dolphins occurrence, then dolphins may be at risk from displacement of their current high used areas as seen in the Bay of Islands (Hartel et al. 2014). Future studies at finer temporal scale (e.g., daily or weekly instead of seasonally) will be needed to investigate behavioural responses of dolphins in relation to vessel activity.

5.2.2. Recreational fishing and aquaculture: a risk of dolphin entanglements

Marine debris such as fishing lines and discarded or lost aquaculture gear put dolphins under risk of entanglements (Kemper et al. 2005; Baulch and Perry 2014). In Coffin Bay, recreational fishers, either from vessels or from shore, use lines, hooks and weights that can get hooked on the rocky bottom and lost. Meanwhile, oyster farm gear such as rubber bands used to attach baskets, can be loosened and washed to the bottom (pers. obs.). During the two years of surveys, five dolphins were observed entangled in marine debris. These included four calves entangled with rubber bands (used in oyster farms) around their necks, and one adult with a recreational fishing line entangled between the dorsal fin and the tail (Chapter 4). Although the calves with rubber bands appeared to be swimming without difficulties, the bands seemed to be constricting their neck (pers. obs.), a condition that may become worse as they grow bigger. Two of these calves were seen multiple times until the end of the study; however, the other two were presumed dead because they were not seen again and their potential mothers were sighted several times swimming without the calf (pers. obs.). These entanglements were reported to the TPMP's managers, and actions were put in place to prevent future entanglements. Clean-ups of marine debris were organized, particularly involving the farming industry to collect debris (e.g., rubber bands, poles and baskets) which washed up from the farms, and alternative methods were proposed for securing the baskets instead of the rubber bands. The other dolphin, which was entangled in a fishing line, had restricted movement, and managers of the marine park successfully approached the animal to cut the lines. In surveys done after the disentanglement, this dolphin was observed alive; though still swimming with difficulty and in poor body condition (pers. obs.). Due to dolphin life history traits, even if these kind of entanglements cause the death of a few individuals, the survival rates of the population could be affected and potentially result in a population decline (Chapter 1). Although the purpose of this study was not to monitor or assess the impact of entanglements, these opportunistic records highlighted how multiple use MPAs can still pose risks to a local dolphin population. In this case, the role of managers and the engagement of stakeholders were essential to diminish the impacts and find ways to minimise threats to the wildlife.

5.2.3. Habitat degradation and harmful algal blooms

Coffin Bay is a productive area. The lack of historical data, however, prevents determining whether human activities in Coffin Bay had produced changes on nutrients levels and habitats over time, or if the current conditions are consistent with the historical normal state (EPA 2014). As in other systems, the presence of oyster farms may be contributing to the high nutrient loads in the inner area of Coffin Bay, which may be enhanced by the low flushing of the system. The habitats in the inner area of Coffin Bay are considered under stress from nutrient enrichment, and evidence shows that this has affected the species composition at lower trophic levels (e.g., dense epiphytes on seagrass meadows, dense jellyfish and ascidians) in several parts of the system (EPA 2014). Nutrient enrichment can result in the eutrophication of aquatic ecosystems and trigger harmful algal blooms (Anderson et al. 2002). Currently, Kellidie and Mount Dutton Bays are particularly vulnerable to harmful algal blooms due to their nutrient levels, shallow waters and slow flushing (EPA 2014). Harmful algal blooms have caused mass mortalities of dolphin prey, and algal toxins have been associated with marine mammal morbidity and mortality events across different areas of the world (reviewed by Van Dolah 2005). Since Kellidie and Mount Dutton Bays are highly important areas for about half of the inner area dolphins (Chapter 2, Chapter 4, Diaz-Aguirre 2017), and considering that many individuals showed high levels of site fidelity to these embayments (Chapter 3), the potential occurrence of harmful algal blooms here could have a catastrophic effect to the local dolphin population.

5.3. Conservation and management recommendations

In TPMP, where Coffin Bay is located, interactions between marine mammals and vessels, as well as tourism operations, are regulated through the ‘National Parks and Wildlife

(Protected Animals – Marine Mammals) Regulations 2010'. This includes restrictions on the distance and speed of vessels approaching dolphins, and restrictions on swimmers and food provisioning. Apart from these regulations and although marine mammals are considered a 'group of species of ecological value' in the management plan of TPMP, there are no specific conservation and management measures directed at monitoring or protecting southern Australian bottlenose dolphins. In the next section, I use findings from this thesis and recent information on the species to provide recommendations to improve the monitoring and management of the species within South Australia's marine parks.

5.3.1. Suggested amendments to TPMP management plan

A monitoring, evaluation and reporting program (MER) is used to measure the effectiveness of the management plan of TPMP in protecting their ecological values, including marine mammals. The MER establishes regular population counts of a few marine mammal species (*i.e.* Australian sea lion *Neophoca cinerea*, long-nosed fur seal *Arctocephalus forsteri*, Australian fur seal *Arctocephalus pusillus*, and southern right whale *Eubalaena australis*) as indicators (Bryars et al. 2016). The lack of baseline information for southern Australian bottlenose dolphins prevented their inclusion in the current monitoring program. The findings presented here on the demographics and spatial ecology of the population (Chapters 2 – 4), as well as the information on their social structure (Diaz-Aguirre 2017) and population genetics (Pratt et al. under review), should encourage managers to include southern Australian bottlenose dolphins in the TPMP's MER program. This will allow the use of the park's management framework to ensure the long term monitoring of the dolphin population, detection of trends and impact assessment of potential threats, which will contribute to the conservation of this species. Furthermore, I recommend marine park managers to establish cooperation agreements with local researchers to facilitate future monitoring of the dolphin population.

5.3.1.1. Long-term monitoring of southern Australian bottlenose dolphins in Coffin Bay

Findings presented here suggest that Coffin Bay, and particularly the inner area, is an important habitat for the largest population of southern Australian bottlenose dolphins reported to date (see above 5.1.). A systematic long-term photo-identification monitoring program should be established to track population trends in abundance, detect changes in space use patterns and evaluate potential impacts of local threats. The methodology used here and findings of this study provide a platform for the development of a long-term monitoring program of dolphins in Coffin Bay. Considering the consistency across seasons on dolphins' abundance and their low emigration rate from the inner area (Chapter 2), as well as individuals' high site fidelity (Chapter 3), it is possible that yearly photo-identification surveys, instead of seasonal, would suffice to keep track of the population size. However, to facilitate the design of a cost-effective long-term monitoring program capable of detecting population trends (e.g., Taylor et al. 2007; Brown et al. 2016), multiple scenarios of sampling effort should be assessed using Gerrodette (1987) inequality model and the available data on dolphins' demographic parameters provided here for Coffin Bay (Chapter 2). The monitoring of space use patterns and potential impacts of local threats require further survey effort (see below).

5.3.1.2. Suggested modifications to current zoning arrangements

The zoning arrangement of the park currently prohibits fishing and motorised water sports (e.g., jet skiing and water skiing) in sanctuary zones, which reduce disturbance to dolphins in these areas (Bryars et al. 2016). These zones were established with the aim to protect habitats, and not dolphins in particular (DEWNR 2012). Though, the predicted improvement on habitat quality and changes in fish and invertebrate populations inside sanctuaries (Bryars et al. 2016) could potentially have a positive effect on the dolphins. However, sanctuary zones currently occupy less than 10% of TPMP and areas with the highest probability of dolphin occurrence were outside sanctuaries zones where multiple human activities are allowed (Chapter 4). Habitats outside sanctuary zones are exposed to human activities which could potentially degrade dolphin habitat (Bryars et al. 2016) and lead to decreases in dolphin numbers. Declaring the entire inner area as a sanctuary zone would result in major conflicts with other users of the bay. For these reasons, and considering the fine-scale spatial and social structure of the population (see Section 5.1.2.), we suggest that at least three small sanctuary zones should be established to cover the areas of highest probability of dolphin occurrence within the inner area (Chapter 4). These sanctuaries should be located in the north-west part of Port Douglas, in part of Mount Dutton Bay and in the western part of Kellidie Bay (Chapter 4). The creation of new sanctuaries should follow public consultation to diminish conflicts with users of the area and to ensure better compliance of management measures.

5.3.1.3. Monitor and enforce compliance of current regulations

The current regulations of the 'National Parks and Wildlife (Protected Animals – Marine Mammals) Regulations 2010' establish restrictions on the distance and speed of vessels approaching dolphins, and restrictions on swimmers and food provisioning. This measures aim to reduce disturbance of dolphins, however, the first step for them to be an effective tool for protecting dolphins is compliance (Scarpaci et al. 2003; Howes et al. 2012; Guerra and Dawson 2016). Water patrols undertaken by South Australia Marine Park managers and by fisheries officers from Primary Industries and Regions SA (PIRSA), are essential to ensure compliance. These patrols should be particularly intensive during tourism holidays (e.g., Christmas-New year and Easter) when vessel traffic is considerably higher than in the rest of the year (pers. obs.).

5.3.1.4. Systematic clean-ups of marine debris in Coffin Bay

To reduce the chances of dolphins entanglement in marine debris, as well as to reduce the impact of human activities in the entire ecosystem, clean-ups should be conducted systematically across TPMP. The clean-ups should not be limited to collect marine debris that washed up to shores, but should also involve cleaning the seabed. Major efforts to clean seabed and shallow areas should be done in the inner area Coffin Bay, where a high density of dolphins (Chapters 2 – 4) cohabitates with one of the most important Pacific oyster industries in SA. TPMP's managers should continue to involve the aquaculture industry and the local community, to ensure ongoing clean-ups and their effectiveness as a management measure.

5.3.2. Public awareness and education about dolphins in Coffin Bay

Public awareness and education could aid conservation of southern Australian bottlenose dolphins in Coffin Bay. The local community and multiple users of TPMP, including tourists and the aquaculture industry, should be aware of: a) the importance of Coffin Bay for the resident population of dolphins; b) the regulations restricting distance and speed of vessels approaching dolphins, and the importance of compliance; c) the limits of different zoning arrangements within the marine park and restrictions of anthropogenic activities (e.g., location of sanctuary zones where fishing and motorized water sports are prohibited); d) the potential impacts of marine debris (e.g., fishing and aquaculture gear) on dolphins, and the importance to minimize their impact. Moreover, since dolphins are considered an excellent umbrella species, using them to inform the public about their ecology and threats can result in increased public awareness on the importance of protecting not only the species but also their habitat (Notarbartolo di Sciara et al. 2016). Strategies to generate awareness on these issues can be implemented by handouts of brochures at local businesses and regional information centres, signage placed at boat ramps, public and school talks, through media outlets, and during water patrols, among others. Furthermore, water patrols by TPMP's managers and fisheries officers from PIRSA could be used as mean to generate awareness on the importance of protecting southern Australian bottlenose dolphins and their ecosystem.

5.4. Recommendations for future research

This thesis provides baseline knowledge on the demographics and spatial ecology of southern Australian bottlenose dolphins inhabiting Coffin Bay, SA; however, it is limited in its temporal and spatial scale. Future research is needed to better understand the population dynamics and spatial ecology of southern Australian bottlenose dolphins over the long-term in Coffin Bay, as well as to determine the impacts of threats, and to test several hypotheses formulated throughout this thesis. The long-term monitoring of the population (see 5.3.1.1.) and the integration of multidisciplinary information will enhance our understanding on the species ecology, their role within the ecosystem, and impacts of threats, which is fundamental to inform conservation in the TPMP. Here I outline some recommendations for future research.

5.4.1. Assess the population viability of southern Australian bottlenose dolphins in Coffin Bay

Population viability analyses (PVA) are important tools used to determine effective management strategies and facilitate species conservation (Boyce 1992; Reed et al. 2002; Manlik et al. 2016). PVAs are used to assess the long-term persistency of a population under different threat scenarios, either current or predicted (Boyce 1992; Reed et al. 2002; Manlik et al. 2016). Even though southern Australian bottlenose dolphins inhabiting Coffin Bay are within a marine protected area, they are under potential threats from the multiple anthropogenic activities allowed in this park (see 5.2.). The impact of these threats on the viability of the dolphin population is unknown. The obtained population parameters from this study could be used together with life history data to conduct a PVA and determine the viability of the population in Coffin Bay under different scenarios (e.g., Burkhart and Slooten 2003; Vermeulen and Bräger 2015).

5.4.2. Investigate the impact of vessel interactions on dolphins' behaviour and distribution

The presence of vessels can affect the short-term behaviour and distribution of dolphins (Lusseau 2003; Bejder et al. 2006a; Lusseau 2006; Lusseau and Bejder 2007; Pirotta et al. 2015); however, this has not been investigated so far in Coffin Bay (see 5.2.1.). Future studies using focal follow methods and Markov Chains to model anthropogenic impacts (e.g., Lusseau 2003; Peters et al. 2012), should investigate how the presence and density of vessels may affect the behaviour, group structure and movements of southern Australian bottlenose dolphins. This research should compare dolphin behaviour between areas and periods of different vessel density within Coffin Bay.

5.4.3. Evaluate the impact of entanglements on dolphin's health

Opportunistic observations during this thesis indicated that marine debris (*i.e.* ghost fishing lines and rubber bands from oyster farms) can result in dolphin entanglements, constituting a risk of injury and mortality (see 5.2.2.). A proper quantification of entanglements and assessment of their impacts on dolphins is needed. Entanglement can result in immediate mortality through drowning or injury, or progressive debilitation over time (Laist 1997). To quantify immediate mortality (or part thereof as dead individuals can sink to the seabed) we encourage the recovery of dolphin carcasses, which can be conducted by South Australia Marine Park managers either through patrolling of Coffin Bay waters and beaches or in response to reports of carcasses by park's users. These mechanisms, together with surveys directed to monitor dolphins, should be used to detect live entanglements. In these cases, frequent surveys including behavioural observations and photographic records should be done to keep track of individuals' conditions (e.g., type and place of entanglement, injuries, swimming ability, body condition) until -whether viable- attempts to disentangle dolphins are organized by South Australia Marine Park managers. Finally, to determine the impact of marine debris on the dolphin population, estimates of the proportion of death caused by marine debris in relation to other causes of death should be done, though this is usually difficult to achieve due to multiple reasons (see review by Baulch and Perry 2014).

5.4.4. Investigate productivity, prey availability and the feeding ecology of southern Australian bottlenose dolphins in Coffin Bay

In this thesis, I hypothesized that the distribution patterns of dolphins (Chapter 4) and the individuals' fine scale spatial structure (Chapter 3) are driven by different productivity between the inner and the outer areas and by differences in prey availability between embayments, respectively. Studies on dolphin feeding habits integrated with information on prey availability are necessary to test this hypothesis. Although there is some evidence on the productivity of the system and differences in the fish assemblages in the different embayments (Chapter 3, Chapter 4), the gap in knowledge about dolphin feeding habits prevents hypothesis testing. Future research aimed at determining dolphin diet and their trophic level will help understand their ecological role within this ecosystem. The skin and blubber samples of dolphins collected during this study can be used for analysis of stable isotope ratios and fatty acid signatures to assess dolphins feeding ecology (Browning et al. 2014). Furthermore, the trophic overlap between the individuals of different communities found in Coffin Bay should be determined to test if differences in feeding habits are linked to factors driving the spatial patterns (Chapters 3 and 4) and social structure (Diaz-Aguirre 2017) of this population. Moreover, incorporating data on prey availability and social structure into species distribution modelling could help elucidate if different communities show differences in habitat preferences.

5.4.5. Investigate the population dynamics of southern Australian bottlenose dolphins in the TPMP

This thesis focused on the dolphins of Coffin Bay, and particularly the inner area, which constitutes only a small portion of the TPMP. Dolphins within the study area favour the inner area (Chapter 4), which is home to a genetically differentiated population (Pratt et al. under review). Despite the high site fidelity and restricted ranging patterns of resident dolphins of the inner area, some individuals move into the outer area (Chapter 3) and possibly beyond. Limited survey effort of the outer area prevented the evaluation of movements and space use patterns of individuals in this area. Future research should include higher survey effort in the outer area, and ideally use two vessels to survey simultaneously the inner and outer areas to better understand these patterns and assess population dynamics (Chapter 2). Furthermore, research on southern Australian bottlenose dolphins from other areas of TPMP and beyond the park should be integrated with data from Coffin Bay. The photo-ID catalogue of Coffin Bay should be matched with catalogues generated for other areas, including the catalogues already available from SA coast (e.g., Zanardo et al. 2016).

5.4.6. Identify areas for future research on southern Australian bottlenose dolphins

The distribution of species can be accurately predicted in ecosystems where data are limited when using a combination of habitat models built with data from multiple ecosystems (Redfern et al. 2017). To predict the distribution of southern Australian bottlenose dolphins in data-poor areas of TPMP and other coastal and estuarine areas of southern Australia, the ensemble models generated for the estuarine waters of Coffin Bay (Chapter 4) should be combined with those from Adelaide’s metropolitan coast (e.g., Zanardo et al. 2017). This approach will allow identifying potential areas where dolphin research efforts should be focused and will contribute to spatial conservation planning and the protection of this species.

5.5. Conclusions

Conservation and spatial management of wildlife populations require sound information on demographics and spatial ecology. This thesis presents baseline information on population size, migration patterns, site fidelity, representative ranges and distribution patterns of southern Australian bottlenose dolphins in Coffin Bay, South Australia. I found a high year-round density of dolphins with individuals displaying high levels of site fidelity, restricted ranging patterns and high probability of occurrence in the inner area of Coffin Bay. I suggest that these patterns are driven and maintained by the high productivity of this system coupled with low predation risks. Overall, these results highlight the importance of the inner area of Coffin Bay for southern Australian bottlenose dolphins and the conservation value of this site within southern Australia. The dolphin population inhabiting Coffin Bay is a good target for area-based conservation. The potential threats that these dolphins face within the multiple use marine park could be monitored and effectively managed by incorporating the species into TPMP's management plan. The knowledge generated in this study constitute the basis for designing the long-term monitoring of the population and as a way forward to assess trends, impacts of threats and population viability. Future studies should continue to improve our understanding on the dolphin population’s ecology and to facilitate information for their long-term management. This will improve spatial conservation planning of the species within South Australia’s marine parks.

5.6. References

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APPENDIX I: Supporting information – Chapter 2

Table S1. Criteria used for evaluating a) photographic quality and associated scale scores, and b) distinctiveness of dorsal fins. Quality score for each criterion were summed and photographs classified into three grades of overall quality (Q): “Q1”= “excellent” photos with a total value of 6 or 7; “Q2”= “good” photos with a total value ranging from 8 to 11; and “Q3”= “poor” for photos with total score higher than 11 (derived from Urian *et al.*, 1999, Urian *et al.*, 2015).

a) Photographic quality				
QUALITY CRITERIA	DESCRIPTION	SCALE SCORES		
Focus/Clarity	Sharpness of the image. Lack of clarity may be caused by poor focus, excessive enlargement, poor developing or motion blur; for digital images, poor resolution resulting in large pixels.	2 = excellent focus	4 = moderate focus	9 = poor focus, very blurry
Contrast	Range of tones in the image. Images may display too much contrast or too little. Photographs with too much contrast lose detail as small features wash out to white. Images with too little contrast ‘lose’ the fin into the background and features lack definition.	1 = ideal contrast	3 = either excessive contrast or minimal contrast	-------
Angle	Angle of the fin to the camera.	1 = perpendicular to camera	2 = slight angle	8 = oblique angle
Partial	A partial rating is given if little of the fin is visible as to	1 = the fin is fully	-------	8 = the fin is

	the likelihood of re-identifying the dolphin is compromised on that basis alone. Fins obscured by waves, or other dolphins, were evaluated using this rating.	visible, leading & trailing edge		partially obscured
Proportion of the frame filled by the fin	An estimate of the percentage area that the fin occupies relative to the total area of the frame	1 = greater than 5%; subtle features are visible	-------	5 = less than 1%; fin is very distant

b) Distinctiveness of dorsal fins

DISTINCTIVENESS SCORE		DESCRIPTION
D1	Very distinctive	Highly distinctive features (singular or multiple) in dorsal fins that are evident even in distant or poor quality photograph: one or several large features (e.g., missing tops, extended tips, large notches) or multiple small features (e.g., 5 or more small notches).
D2	Average distinctiveness	Average amount of information content, with moderately distinctive features visible on the fin: 1 major feature (e.g., notch) or at least 2 or multiple smaller features (e.g., nicks).
D3	Not distinctive	Very little information content in pattern, markings or leading and trailing edge features: fins basically ‘clean’ except for minor scarring or very small nicks.

Methods S1: Models assumptions, validation and goodness of fit.

Several assumptions have to be met under the POPAN and PCRD models to obtain precise estimates of population parameters; if the assumptions are violated the estimates can be biased downwards or upwards (Table S2). To validate assumptions of homogeneous capture and survival we used Test 2 and Test 3, respectively, of the program U-CARE (Choquet *et al.*, 2005). Test 2.CT was used to test for heterogeneity in capture probabilities, including testing for trap response. Test 3.SR was used to test for a transience effect (*i.e.* dolphins sighted only once during the study period more often than expected), and Test 3.SM to examine potential differences in the expected time of first recapture between the 'new' and 'old' individuals captured at any occasion and then seen again at least once (Choquet *et al.*, 2005). The results of these tests are included in Table S2.

The violation of some assumptions may not bias the parameters estimates, but could cause extra binomial variation (Williams *et al.*, 2002). The variance inflation factor ($\hat{c}$) was determined to examine if there was extra binomial variation in the data. Values of $\hat{c}$ indicate whether the data has good fit to the general model ($\hat{c} \approx 1$), if there is extra binomial variation due to data under-dispersed ($\hat{c} < 1$) or over-dispersed ($1 < \hat{c} < 3$), or if there is a structural problem with the general model ($\hat{c} > 3$) (Lebreton *et al.*, 1992). In case of a good fit or under-dispersion (*i.e.* $\hat{c}$ <1), no adjustments to $\hat{c}$ were done, models were compared using $\hat{c} = 1$ output and model selection was based on values of Akaike Information Criteria corrected for small sample size (AICc) (Cooch and White, 2014). While in case of over-dispersion (*i.e.* $\hat{c}$ >1), the value of $\hat{c}$ was used to adjust the output, and model selection was based on values of quasi Akaike Information Criteria corrected for small sample size (QAICc) instead of AICc (Cooch and White, 2014). The *goodness-of-fit* (GOF) of POPAN models was tested with program U-CARE (Choquet *et al.*, 2005). The χ^2 value obtained from the sum of Test 2 and Test 3 was divided by the total degrees of freedom to calculate $\hat{c}$. As there is no appropriate method available in MARK to test GOF of PCRD models (White and Burnham, 1999), the overall model fit could not be evaluated. However, we evaluated if the open part of the PCRD model fitted the data well. The data of the 39 S-periods considered in the PRCD were collapsed into the corresponding P-periods and the resulting encounter histories with six sampling occasions (P-periods) were used to fit Cormack–Jolly–Seber (CJS) models (Cormack, 1964; Jolly, 1965; Seber, 1965; Lebreton *et al.*, 1992). The GOF of the CJS model was determined using the ‘median $\hat{c}$’ approach implemented in program MARK (Cooch and White, 2014). We used three as the upper bound, three intermediate points between the upper and lower bounds, and 1,000 replicates at each design point. Finally, closure assumption for each P-period was explored with CloseTest software (Stanley and Richards, 2005, 2011), particularly using the Otis *et al.* (1978) closure test for capture-recapture data.

Table S2. Assumptions of models, indicating whether they apply to POPAN and/or PCRD, consequence on abundance estimate if the assumption is violated, and validation(s) followed.

Models' assumptions	Consequence	Validations	References
Assumptions applicable for both POPAN and PCRD models			
1. Marks are unique, recognizable, identified properly when recaptured, and retained throughout the study period.	Bias upwards	1.1. Marks used are unique to each individual dolphin, they are naturally acquired marks in the edges of their dorsal fins (nicks, cuts and deformities), and the tissue does not regenerate (Würsig and Würsig, 1977). 1.2. Used only excellent-good photographs (Q1 and Q2) of distinctive dorsal fins (D1 and D2) (Urian *et al.*, 1999, 2015). 1.3. Regular sampling over a two year period and at 2-3 months intervals allowed us to track changes in dorsal fin marks. 1.4. Only two experienced researchers entered photographs into the catalogue, then they were double-checked by them or by a third researcher ensuring that individuals were identified properly when first added to the catalogue and when recaptured.	Pollock *et al.*, 1990, Williams *et al.*, 2002
2. All (marked and unmarked) individuals have the same (homogeneous) probability of being captured within a sampling period.	Bias downwards	2.1. Only included in the analysis the dolphins encountered on effort along the pre-established transects, which were designed to cover evenly the study area. 2.2. Every time a school of dolphin was encountered we aimed to take photos of all the individuals present regardless of the distinctiveness of their dorsal fins. 2.3. Validation 1.2. applies. 2.4. For POPAN models the the GOF test with U-CARE (Global TEST, number of groups =3; $\chi2= 28.249$, $p = 0.7027$, d.f. = 33) suggested that the assumptions of homogeneous capture (2) and survival (3) probabilities were met. 2.5. For PCRD models the GOF test (of CJS models fit to the data pooled per P-period) showed that the assumption of equal capture (TEST 2) was not	Pollock *et al.*, 1990, Williams *et al.*, 2002

Models' assumptions	Consequence	Validations	References
Assumptions applicable for both POPAN and PCRD models			
		violated (χ2 = 7.011, df = 9; p = 0.635).	
3. All individuals have the same probability of survival.	Bias downwards	3.1. Dolphins' survival probabilities can vary by sex and age class (e.g., Silva *et al.*, 2009, Stanton and Mann, 2012, Fruet *et al.*, 2015). In our analysis we grouped individuals by sex to explore and account for potential variations in survival of males and females. As both adults and independent juveniles were included in the dataset the homogenous survival probability assumption may be violated. However, the age class effect should be minimized as the non-distinctive individuals (which are often juveniles) and dependent calves were excluded (Brown *et al.*, 2016). 3.2. Validation 2.4. applies to POPAN models. 3.3. For the open part of PCRD models the GOF test showed that the overall TEST 3 was not met (χ^2 = 42.303, df = 14; p = 0.0001), indicating some degree of violation to equal survival assumption. However, the groups components indicate that the overall TEST was met for females (χ^2 = 3.5174, df = 5; p = 0.6208) but not for the other groups. For males none of the components of the test were met (TEST 3.SR: χ^2 = 11.3110, df = 1, p = 0.0008; and TEST 3.Sm: χ^2 = 9.0199, df = 2, p = 0.0110). For unknown-sex individuals TEST 3.SR was	Pollock *et al.*, 1990, Williams *et al.*, 2002

Models' assumptions	Consequence	Validations	References
Assumptions applicable for both POPAN and PCRD models			
		not met (χ^2 = 11.6814, df = 3, p =0.0086), while TEST 3.Sm was met (χ^2 = 6.7740, df = 3, p = 0.0795). This indicates that both males and unknown-sex groups showed evidence of a transience effect.	
4. The capture of an individual did not affect its subsequent recapture probability (*i.e.* trap-happy or trap-shy) during the sampling period.	Trap-happy = bias downwards. Trap-shy = bias upwards	4.1. Photo-identification is an instantaneous non-invasive technique where an individual is considered 'captured' in the first survey that is photo-identified and 'recaptured' whenever photo-identified in consecutive surveys. Therefore, the capture of an individual should not affect its subsequent recapture probability (see Parra *et al.*, 2006).	Pollock *et al.*, 1990
5. The probability of capture is independent between individuals.	Underestimation of precision	5.1. Dolphin populations are socially driven, so if we capture an individual the probability of capturing its close associates might be higher than the probability of capturing a non-associate (Connor *et al.*, 2000), thus it is likely that this assumption is violated. 5.2. As the violation of this assumption may cause extra binomial variation, the variance inflation factor ($\hat{c}$) was determined: 5.2.1. $\hat{c}$ = 0.86 for POPAN models, indicating that the fully time dependent	Pollock *et al.*, 1990, Williams *et al.*, 2002

Models' assumptions	Consequence	Validations	References
Assumptions applicable for both POPAN and PCRD models			
		model fitted the data well; 5.2.2. $\hat{c}$ = 1.35 for PCRD models, indicating some overdispersion in the data; this $\hat{c}$ was used to adjust in the output of the models.	
6. Sampling is instantaneous.	Bias upwards	6.1. The assumption of instantaneous sampling (*i.e.* that sampling periods are short and birth, death, immigration and emigration do not occur during the recapture process) was likely satisfied as the sampling periods were completed within a short period of time (up to 20 days) in comparison with the dolphins lifespan (decades).	Pollock *et al.*, 1990, Williams *et al.*, 2002
7. The study area is constant over time.	----	7.1 The study area did not change during the study period and was covered evenly in each sampling occasion following the same pre-established transects.	Pollock *et al.*, 1990, Williams *et al.*, 2002
Assumptions applicable only for PCRD models			
8. The population remains closed across all S-periods within a P-period (*i.e.* with no births, deaths, permanent immigration or emigration).	Bias depends on the nature of gains and loses	8.1. The duration of P-periods was short (less than 3 months) in relation to the life-span of dolphins (decades), so is unlikely for births or deaths to occur. 8.2. Although we aimed to complete sampling periods within the shortest time possible given the requirement for survey conditions, this assumption may not be completely satisfied as some dolphins of inner area population may temporally emigrate within P-periods; in fact 48 dolphins were seen in both inner and outer areas (see results and discussion). 8.3. Results from Otis *et al.* (1978) CloseTest indicated that the population could be considered closed for most P-periods (*p*-values > 0.112), with no evidence of births, immigration, deaths or emigration, except for the second P-period (*p*-value = 0.034).	Pollock *et al.*, 1990, Kendall *et al.*, 1999

Table S3. POPAN models fitted to the dataset of southern Australian bottlenose dolphins encountered within the entire Coffin Bay study area (inner and outer). Models were built considering sex-specific groups (*i.e.* females, males and individuals of unknown sex) to estimate super-population size. Model building followed a stepwise forward procedure where models with different configurations of capture probability (p) were compared first (Models #: 1, 2, 3, 4, 5 and 6), then models with different apparent survival (Φ) (Models #: 4, 4.1, 4.2 and 4.3), and finally models with different probability of entry from the super-population to the sampled population (p_{ent}) (Model #: 4.2 and 4.2.1). In each step the Akaike Information Criterion corrected for small sample size (AICc) was used for model selection, the model with lowest AICc was considered the most parsimonious, and was thus selected as the basic model for the following step. Models are presented according to their AICc values in ascending order. To obtain final parameter estimates, the estimates of the models were averaged according to their AICc weights.

#	Model	AICc	ΔAICc	AICc Weights	Cumulative AICc weight (%)	Num. Par
4.2.1	$\{\Phi_{(group*.)}\ p_{(t)}\ p_{ent(t)}\}$	1249.08	0.00	0.99	98.7	14
4.2	$\{\Phi_{(group*.)}\ p_{(t)}\ p_{ent(group*t)}\}$	1259.06	9.98	0.01	99.3	20
4	$\{\Phi_{(group*t)}\ p_{(t)}\ p_{ent(group*t)}\}$	1260.63	11.55	0.00	99.6	33
6	$\{\Phi_{(group*t)}\ p_{(effort)}\ p_{ent(group*t)}\}$	1260.87	11.79	0.00	99.9	27
5	$\{\Phi_{(group*t)}\ p_{(group*effort)}\ p_{ent(group*t)}\}$	1263.34	14.26	0.00	100.0	34
1	$\{\Phi_{(group*t)}\ p_{(group*t)}\ p_{ent(group*t)}\}$	1269.04	19.96	0.00	100.0	43
4.1	$\{\Phi_{(t)}\ p_{(t)}\ p_{ent(group*t)}\}$	1274.15	25.08	0.00	100.0	23
4.3	$\{\Phi_{(.)}\ p_{(t)}\ p_{ent(group*t)}\}$	1280.78	31.70	0.00	100.0	19
3	$\{\Phi_{(group*t)}\ p_{(.)}\ p_{ent(group*t)}\}$	1282.68	33.60	0.00	100.0	25
2	$\{\Phi_{(group*t)}\ p_{(group*.)}\ p_{ent(group*t)}\}$	1282.68	33.60	0.00	100.0	26

[*] Subscripts indicate how parameters estimates were allowed to vary: $_{(group*t)}$, group and time dependent; $_{(group*.)}$, group dependant but constant in time; $_{(t)}$, time dependent with no group effect; and $_{(.)}$, constant with no group effect. An extra variation was allowed for capture probability: $_{(effort)}$, indicates that p is conditional to the number of sampling occasions (S-periods) within each P-period.

Table S4. Pollock's Closed Robust Design models fitted to the dataset of southern Australian bottlenose dolphins encountered in the inner area of Coffin Bay. Models were built considering sex-specific groups (*i.e.* females, males and individuals of unknown sex) to estimate population parameters. Model building followed a step-forward process were in the first step models with different configurations of capture (p) and recapture probability (c) were compared, while temporary emigration ($\gamma' = \gamma'' = 0$) was ignored and apparent survival let to vary in time by group (*group*t*) (Models No.: 1, 2, 3, 4 and 5 for models with p=c). In the second step, models with different survival probability (Φ) were compared considering time and group effects (Models #: 2, 2.1, 2.2 and 2.3). Finally models with different effects of temporary emigration were compared, including random ($\gamma' = \gamma''$) and Markovian ($\gamma' \neq \gamma''$) models, with or without time, and group effect on γ (Models #: 2.1, 2.1.1, 2.1.2, 2.1.3, 2.1.4 and 2.1.5). In each step the Quasi Akaike Information Criterion corrected for small sample size (QAICc) was used for model selection, as models output were adjusted with a $\hat{c}$=1.35. The model with lowest QAICc was considered the most parsimonious, and was thus selected as the basic model for the following step. Models are presented according to their QAICc values in ascending order.

No.	Model[1]	QAICc	Delta QAICc	QAICc Weights	Cumulative AICc weight (%)	Num. Par
2.1.1	$\{\Phi_{(group*.)}\ \gamma'_{(.)} \neq \gamma''_{(.)}\ p_{(s*t)}=c\}$	5481.23	0.00	0.75	75.3	44
2.1	$\{\Phi_{(group*.)}\ \gamma' = \gamma'' = 0\ p_{(s*t)}=c\}$	5483.49	2.26	0.24	99.6	42
2	$\{\Phi_{(group*t)}\ \gamma' = \gamma'' = 0\ p_{(s*t)}=c\}$	5491.91	10.68	0.00	100.0	54
2.3	$\{\Phi_{(t)}\ \gamma' = \gamma'' = 0\ p_{(s*t)}=c\}$	5498.45	17.22	0.00	100.0	44
2.1.3	$\{\Phi_{(group*.)}\ \gamma'_{(group*.)} = \gamma''\ p_{(s*t)}=c\}$	5553.27	72.04	0.00	100.0	123
2.1.2	$\{\Phi_{(group*.)}\ \gamma'_{(group*.)} \neq \gamma''_{(group*.)}\ p_{(s*t)}=c\}$	5558.31	77.08	0.00	100.0	126
5	$\{\Phi_{(group*t)}\ \gamma' = \gamma'' = 0\ p_{(group*s*t)}=c\}$	5560.55	79.32	0.00	100.0	132
2.1.4	$\{\Phi_{(group*.)}\ \gamma'_{(group*t)} = \gamma''\ p_{(s*t)}=c\}$	5574.30	93.07	0.00	100.0	135
2.1.5	$\{\Phi_{(group*.)}\ \gamma'_{(group*t)} \neq \gamma''_{(group*t)}\ p_{(s*t)}=c\}$	5582.16	100.93	0.00	100.0	147
3	$\{\Phi_{(group*t)}\ \gamma' = \gamma'' = 0\ p_{(group*s*.)}=c\}$	5663.67	182.44	0.00	100.0	33
1	$\{\Phi_{(group*t)}\ \gamma' = \gamma'' = 0\ p_{(s*.)}=c\}$	5668.71	187.48	0.00	100.0	21
4	$\{\Phi_{(group*t)}\ \gamma' = \gamma'' = 0\ p_{(.)}=c\}$	5710.62	229.39	0.00	100.0	16
2.2	$\{\Phi_{(.)}\ \gamma' = \gamma'' = 0\ p_{(s*t)}=c\}$	42894.63	37413.40	0.00	100.0	40

Φ, survival probability; p, capture probability; c, recapture probability; γ', probability of staying away from the study area given that the animal has left the area; γ'', probability of emigration from the study area.

[1] Subscripts indicate how parameters estimates were allowed to vary. Survival probability and emigration parameters were let to be: $_{(group*t)}$, group and time dependent varying between P-periods; $_{(group*.)}$, group dependent but constant between P-periods; $_{(t)}$, time dependent but equal for all groups; and $_{(.)}$, constant between fieldwork seasons but equal for all groups. Capture and recapture probabilities were allowed to be: $_{(group*s*t)}$, group and time dependent varying between all S-periods; $_{(group*s*.)}$, group dependent and constant within each P-period; $_{(s*t)}$, time dependent varying between all S-periods with no group effect; $_{(s*.)}$, constant within each P-period with no group effect; and $_{(.)}$, constant across all S-periods with no group effect.

$\gamma' = \gamma'' = 0$: no emigration model

$\gamma' = \gamma''$: random emigration model

$\gamma' \neq \gamma''$: Markovian emigration model

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APPENDIX II: Supplementary material – Chapter 3

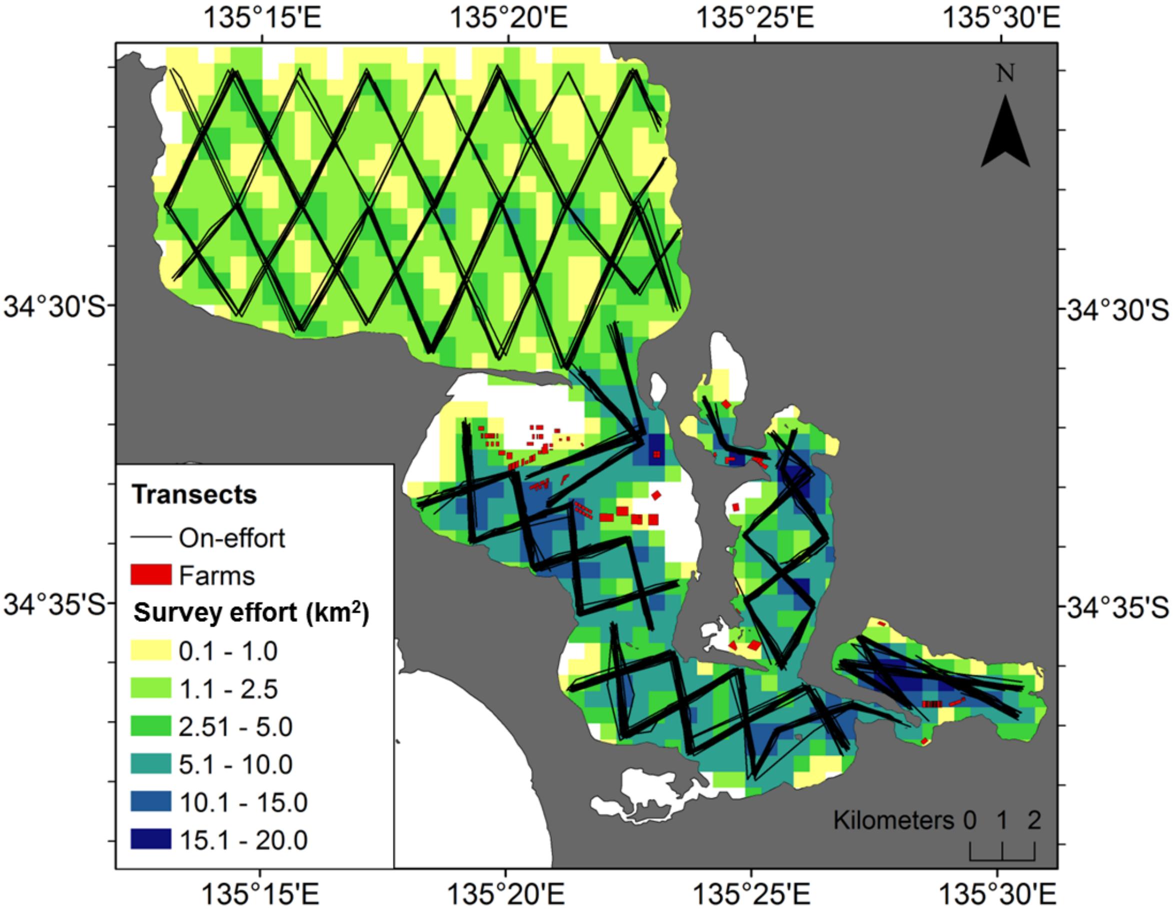

Figure S1. Survey effort done in Coffin Bay between September 2013 and October 2015. The layout of the transects surveyed on effort (lines) is shown. The coloured 500 x 500 m grid cells represent the survey effort in km^2 determined considering an area buffer of 500 m to the sides of each transect surveyed.

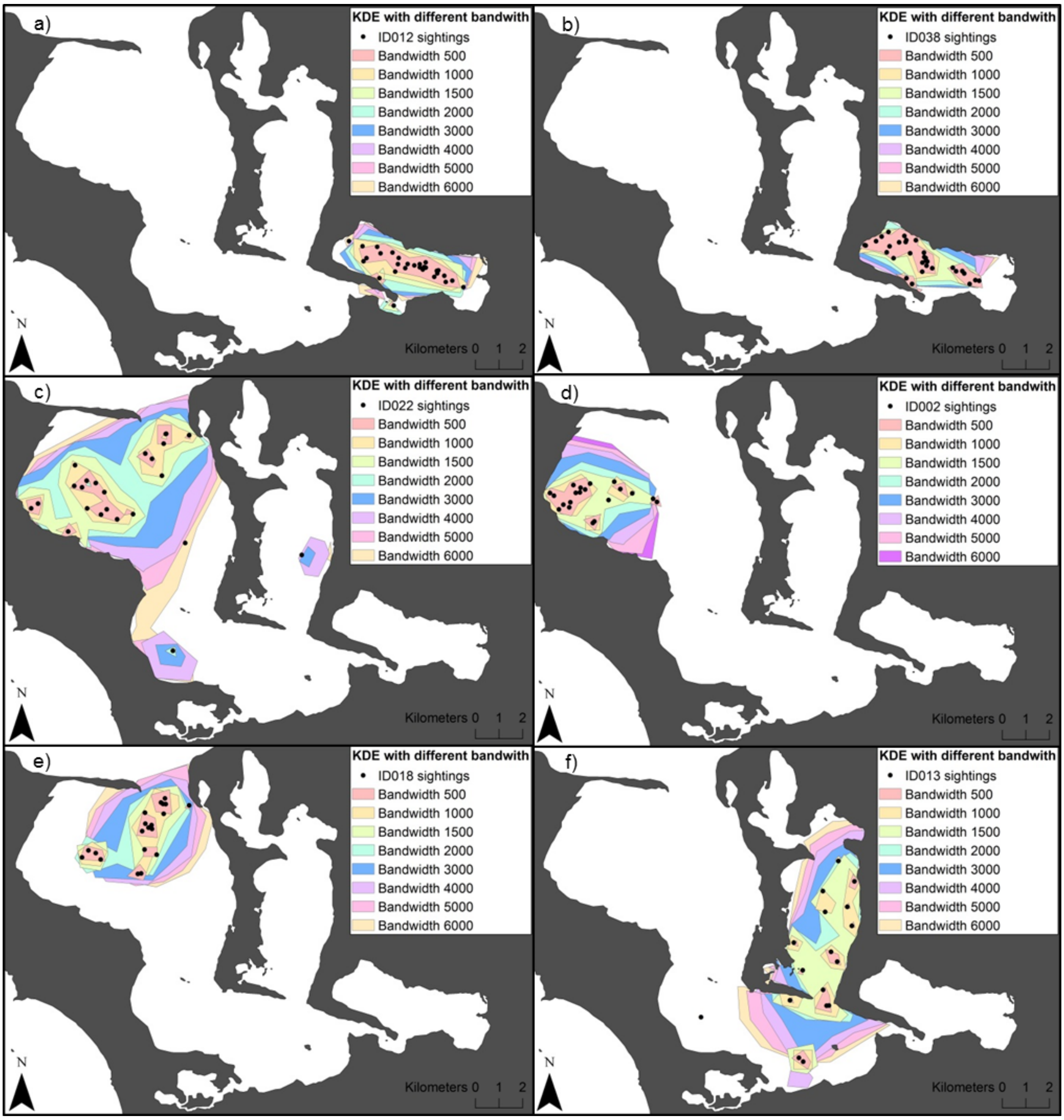

Figure S2. Examples of Kernel density estimates for six individual dolphins that represented the ranges that were observed of the individuals in the field (a) male ID012; b) male ID038; c) female ID022; d) female ID002; e) female ID018; and f) male ID013) using consistent settings of grid cell size (*i.e.* 200 x 200 m), kernel function (*i.e.* first order polynomial), and ridge parameter (*i.e.* 50), while using different trials of bandwidth value at: 500; 1,000; 1,500; 2,000; 3,000; 4,000; 5,000; and 6,000 m. After visual inspection of the different trials, the bandwidth selected for the analysis was fixed at 3,000 m because the UDs obtained with this value were not fragmented and not overly smooth.

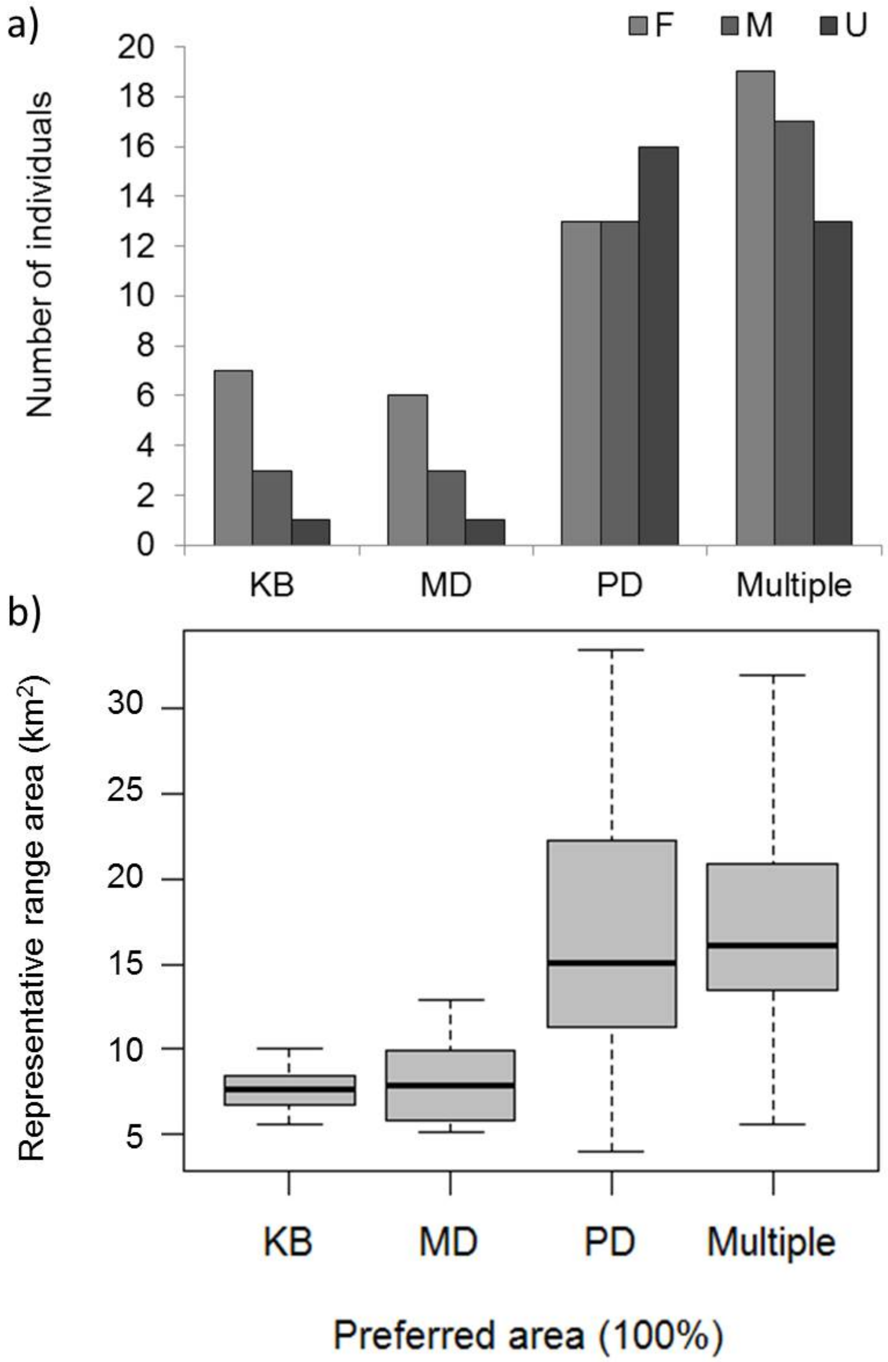

Figure S3. Southern Australian bottlenose dolphins photo-identified between September 2013 and October 2015 in just one of the bays of the inner area of Coffin Bay (KB, Kellidie Bay; MD, Mount Dutton Bay; and PD, Port Douglas Bay) and in 'Multiple' bays. a) Distribution of frequency of individuals (F, females; M, males; and U, unknown sex) per bay. b) Boxplot of the size of representative ranges for individuals of each bay. In boxplots, the bold line indicates the median value, the rectangle spans from the first quartile to the third quartile, and the whiskers above and below the box show the locations of the minimum and maximum values, respectively.

Table S1. Representative range (95% kernel range) sizes for different delphinid populations and species. The species, study area, size of individuals' representative range (mean ± SD), methodology and references for each study are shown. For comparative purposes, only examples using kernel methods to estimate representative ranges are presented here. Ranging patterns are shown for all individuals studied and separated by sex if available.

Species	Study area	Habitat type	Study period (duration)	Age class	Size of individuals' representative range (km^2) (Mean ± SD)	Methods	Reference
Tursiops cf. *australis*	Inner area of Coffin Bay, South Australia, Australia	Inshore waters/ inverse estuary	2013 – 2015 (2 years)	Non-calves (i.e. adults + juveniles)	15.2 ± 6.8 (Females = 14.7 ± 7.0) (Males = 15.6 ± 6.6)	Photo-identification. Kernel (95% UD) interpolation with barriers	*This study*
Tursiops truncatus	North Inlet-Winyah Bay estuarine system, South Carolina, USA	Inshore waters/ estuary	2011 – 2012 (1 year)	Not specified	139.2	Photo-identification. Kernel (95% UD), removing landmass after calculations	(Brusa, Young, & Swanson, 2016)
Tursiops truncatus	Calibogue Sound, South Carolina, USA	Inshore waters/ estuary	1994 – 1998 (4 years)	Not specified	51.3 ± 19.1 (Females = 63.4 ± 28.7) (Males = 51.1 ± 5.9)	Photo-identification. Adaptive Kernel (95% UD)	(Gubbins, 2002)
Tursiops truncatus	Sarasota, Florida, USA	Inshore waters	1993 – 2000 (7 years)	Adults	(Paired males = 162.6 ± 24.21) (Unpaired males = 72.11 ± 24.37)	Photo-identification. Kernel (95% UD), removing landmass after calculations	(Owen, Wells, & Hofmann, 2002)
Tursiops truncatus	Sarasota, Florida, USA	Inshore waters	2005 – 2008 (3 years)	Juveniles	64.7 ± 52.6	Photo-identification. Kernel (95% UD), removing landmass after calculations	(McHugh, Allen, Barleycorn, & Wells, 2011)
Tursiops truncatus	Indian River Lagoon, Florida, USA	Inshore waters/ estuary	1997 – 2007 (10 years)	Adults	(Female with calves = 76.50 ± 10.20) (Females without calves = 97.00 ± 11.50)	Photo-identification. Kernel (95% UD)	(Gibson, Howells, Lambert, Mazzoil, & Richmond, 2013)

Tursiops truncatus	Barataria Bay, Louisiana, USA	Inshore waters	2011 – 2014 (3 years)	Not specified (adults + subadults)	Females = 43.2 ± 27.55 * Males = 69.4 ± 30.79 *	Satellite tagging. Kernel (95% UD) interpolation with barriers, removing landmass after calculations	(Wells et al., 2017)
Tursiops aduncus	Bunbury, Western Australia, Australia	Inshore waters/ estuary and coastal waters	2007 – 2013 (6 years)	Adults	Females = 65.6 ± 30.9 * Males = 94.8 ± 48.15 *	Photo-identification. Kernel (95% UD) interpolation with barriers	(Sprogis, Raudino, Rankin, MacLeod, & Bejder, 2016)
Sotalia guianensis	Cananéia estuary, São Paulo, Brazil	Inshore waters/ estuary	2000 – 2010 (10 years)	Not specified (calves to adults)	13.5 ± 13.8	Photo-identification. Kernel (95% UD), removing landmass after calculations	(de Faria Oshima & de Oliveira Santos, 2016)
Sotalia flluviatilis	Baía Norte, Santa Catarina, Brazil	Inshore waters	1996 – 2002 (6 years)	Adults + calves/juveniles	15.22 ± 0.66 (Females = 15.91 ± 1.2) (Males = 14.09 ± 1.1)	Photo-identification. Kernel (95% UD), removing landmass after calculations	(Flores & Bazzalo, 2004)

*Indicates statistically significant sex-specific differences in the size of representative ranges.

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APPENDIX III: Supplementary material – Chapter 4

Results S1: Spatial and temporal patterns of explanatory variables

The explanatory variables benthic habitat type (Figure 4.1), depth, and distance to sanctuary zones, oyste farms, and to land (Figure S1) were considered fixed in time. In the entire study area, distance to land varied from 0 to 6,756m; and in the inner area this did not exceeded the 3,000 m (Figure S1a). Water depth varied from zero to 36 m; with the inner area waters only reaching up to 11 m depth (Figure S1b). The maximum distance to oyster farms in the outer area of Coffin Bay was 15,558 m, while in the inner area the maximum distance was 5,000 m approx. (Figure S1c). The maximum distance to sanctuary zones was 21,188 m the in outer area and in the inner area was less than 5,000 m (Figure S1).

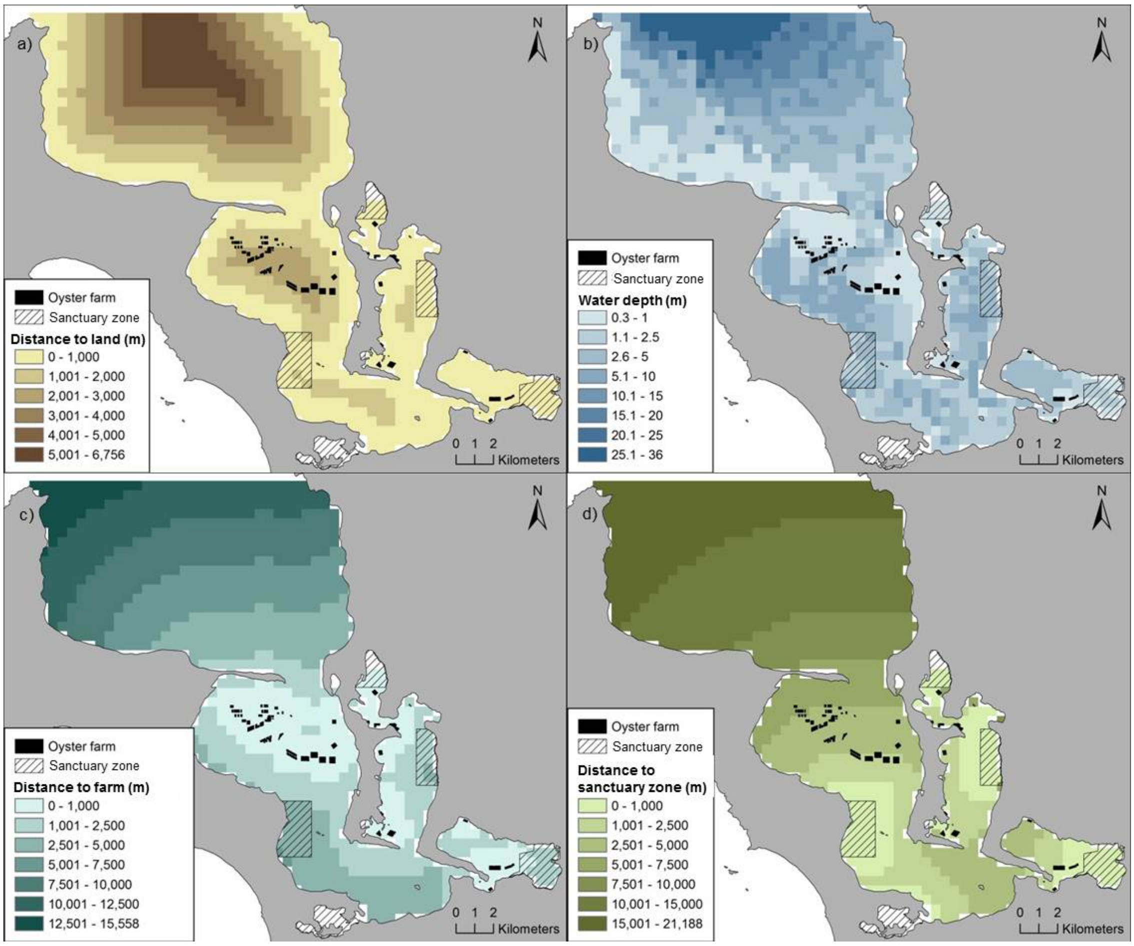


Figure S1. Fixed ecogeographical and anthropogenic variables considered in the modelling of southern Australian bottlenose dolphins (*Tursiops* cf. a*ustralis*) presence in Coffin Bay: a) distance to land; b) depth; c) distance to oyster farms; and d) distance to sanctuary zone.

Spatial and temporal variations were observed in the encounter rate of vessels and ecogeographic variables such as SST, salinity, water visibility and pH (Figure S2). Vessel encounter rates were higher in spring and autumn, and spread over most of the study area (Figure S2). In winter, SST was lower and relatively homogeneous (12.6 – 14.7 °C) across the study area; in the remaining seasons SST increased from the outer area towards the innermost parts of Coffin Bay, with the highest SST gradient (14.5 – 24.5 °C) recorded during summer and lesser gradients in autumn (15.5 – 19.1 °C) and spring (14.7 – 17.8°C; Figure S2). Salinity decreased from outer area towards inner area in winter (37.2 – 33.7 PSU), with lowest values recorded in Kellidie Bay; while the salinity gradient was inverted in the remaining seasons (35.7 – 37.3, 35.6 – 43.4, and 35.2 – 45.1 in spring, summer and autumn, respectively), with the highest values recorded in Kellidie and Mount Dutton Bays (Figure S2). Spatial patterns of water visibility accompanied the depth profile (Figures S1, S2). The pH tended to increase towards the inner parts of Coffin Bay. Both water visibility and pH were relatively consistent across seasons (Figure S2).

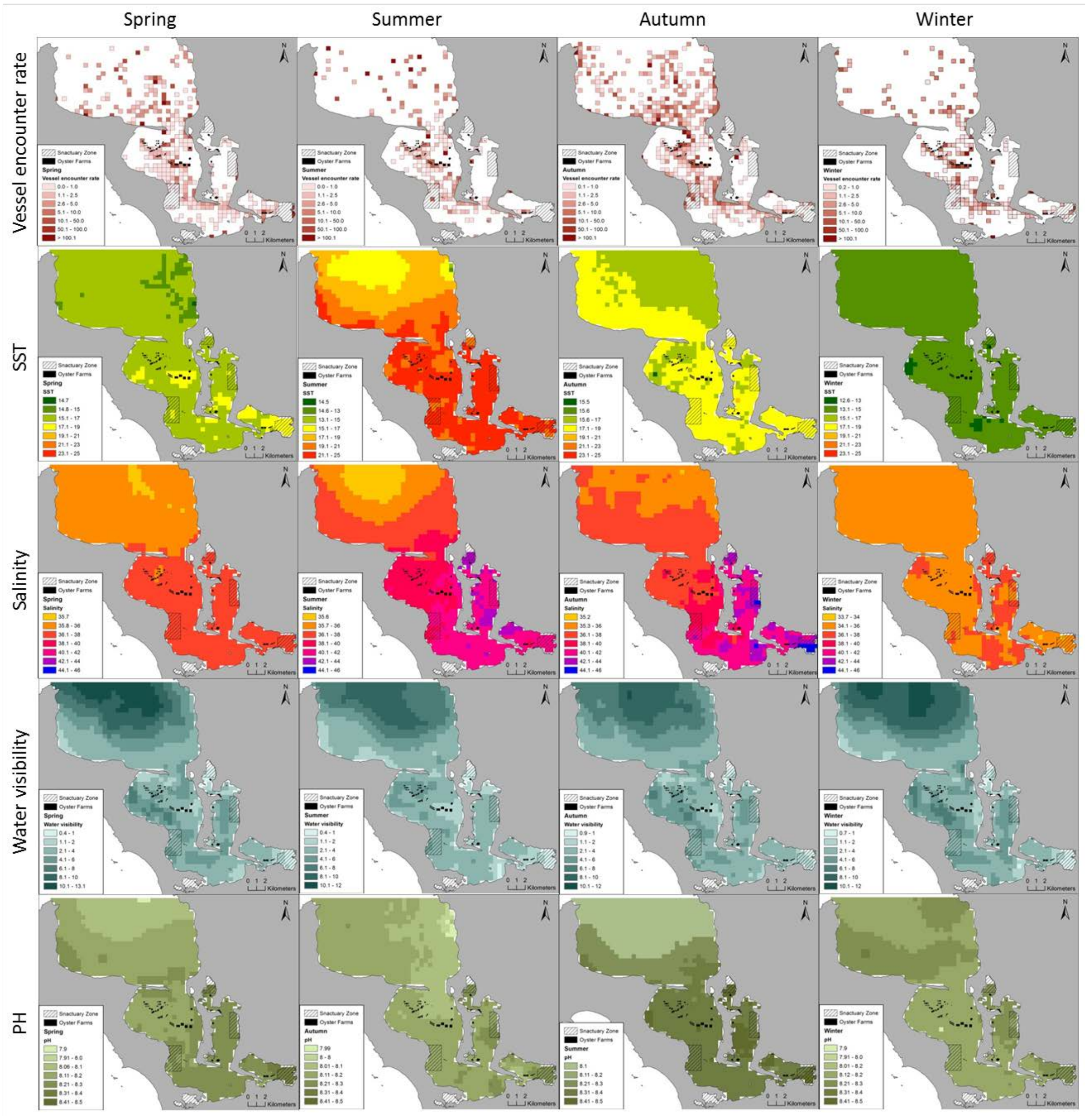


Figure S2. Ecogeographical and anthropogenic variables considered in the modelling of southern Australian bottlenose dolphins (*Tursiops* cf. a*ustralis*) presence in Coffin Bay by season. Columns from left to right correspond to: austral spring, summer, autumn, and winter. Each line corresponds to a variable, from top to bottom: encounter rate of vessels, sea surface temperature (SST), salinity, water visibility, and pH.

Results S2: Response curves of species distribution models for the overall study period

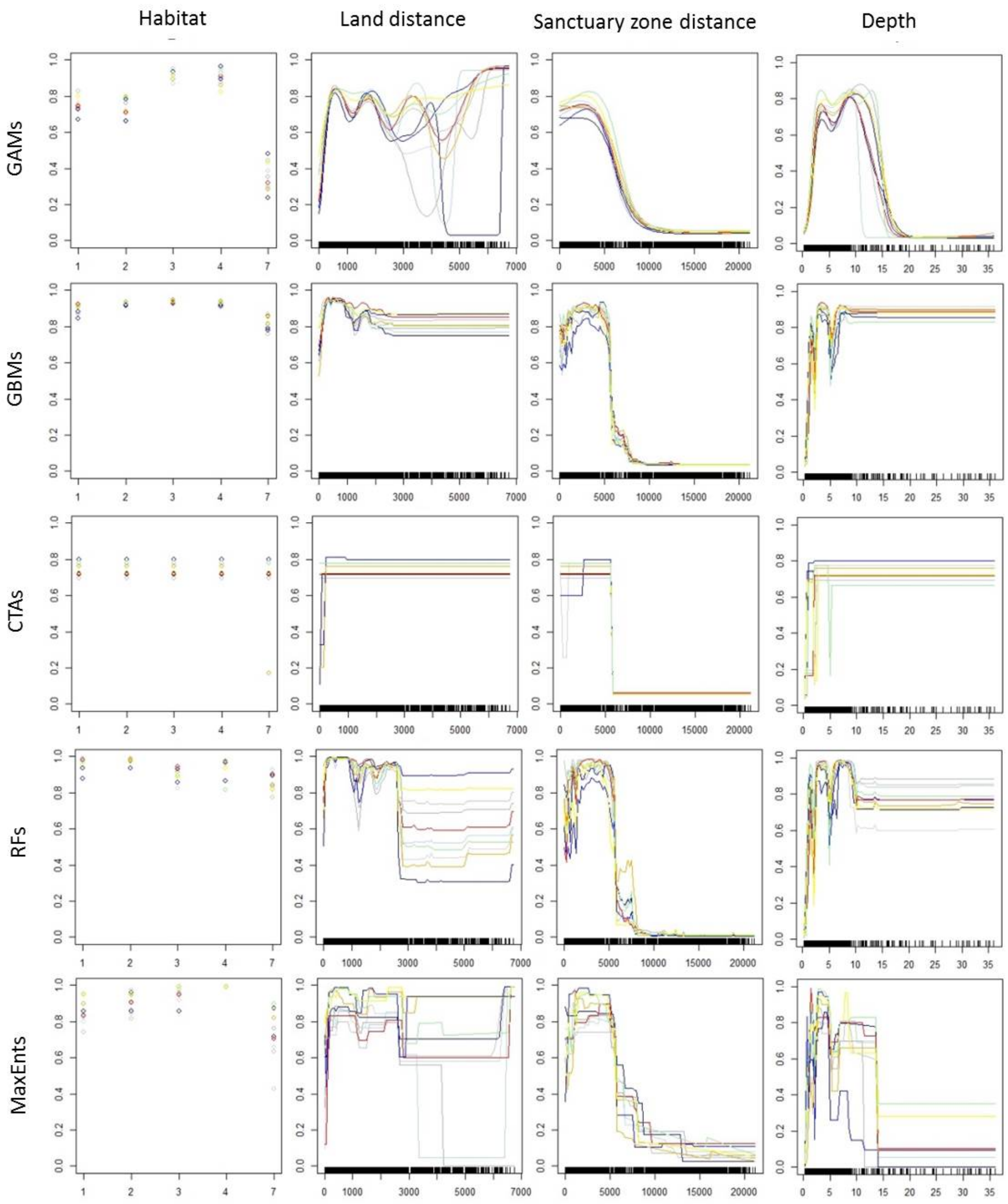


Figure S3. Response curves of presence of dolphins in relation to the explanatory variables obtained for species distribution models run for the entire study area over the entire study period (September 2013 – October 2015). Panes from top to bottom show the curves for each modelling algorithm (GAM, generalised additive model; GBM, generalised boosted model; CTA, classification tree analysis; RF, random forest; and MaxEnt, maximum entropy), and from left to right the explanatory variables (habitat, land distance, distance to sanctuary zone, and depth). Each coloured line represents one of the 10 cross-validation runs.

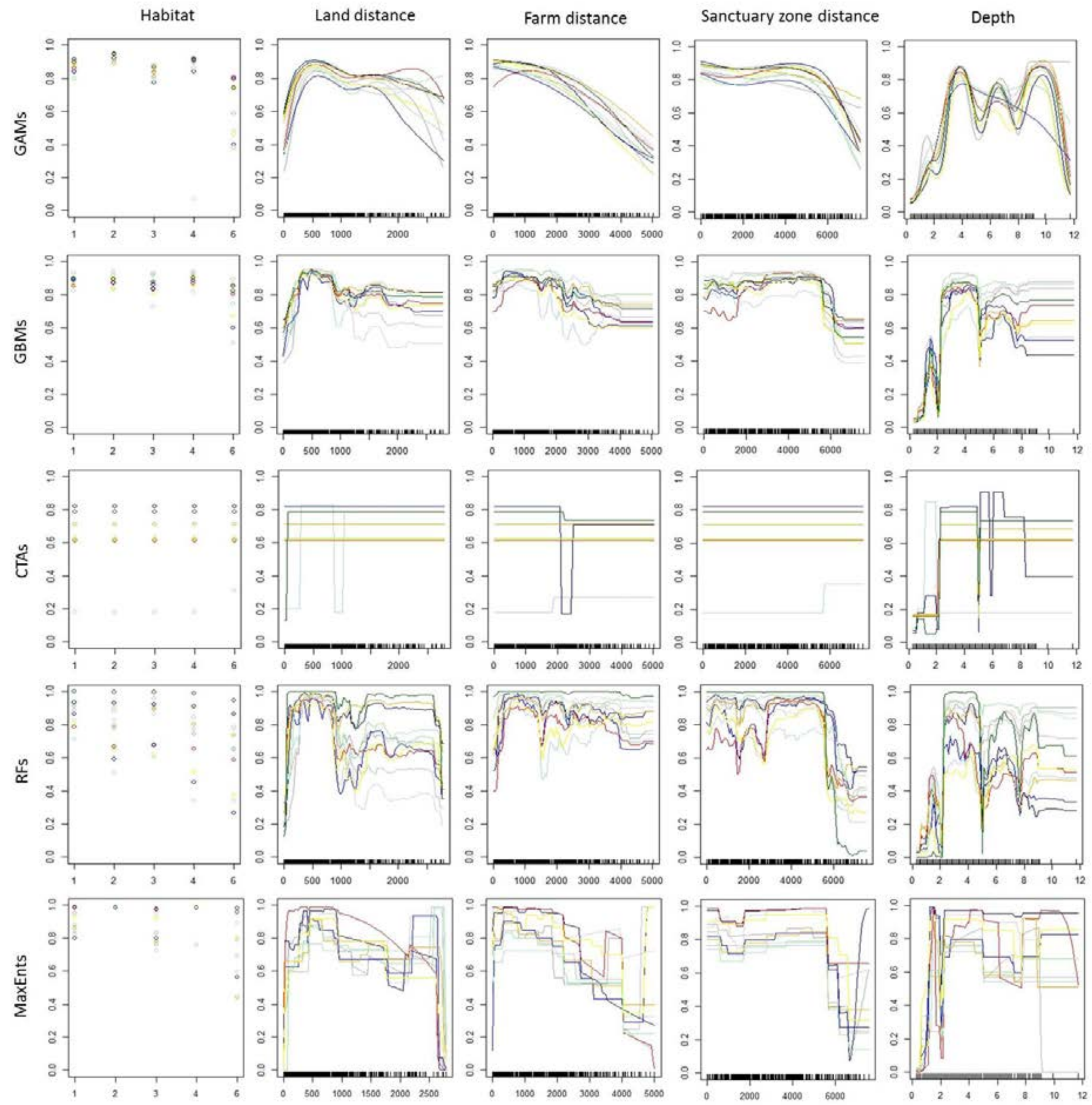


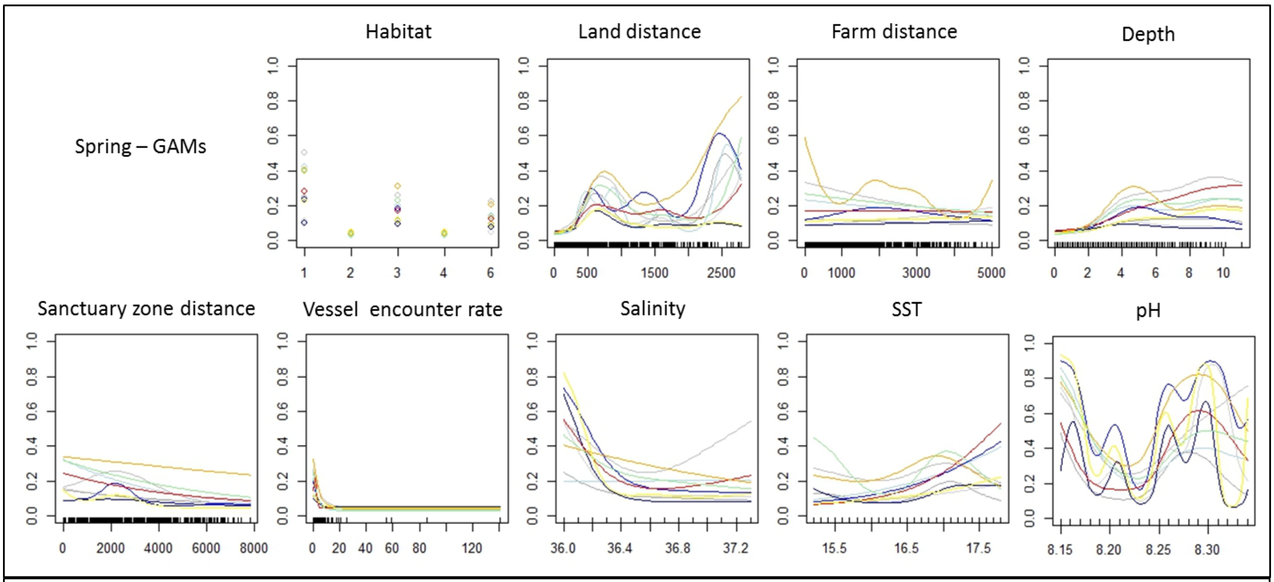
Figure S4. Response curves of presence of dolphins in relation to the explanatory variables obtained for species distribution models run for the inner area of Coffin Bay over the entire study period (September 2013 – October 2015). Panes from top to bottom show the curves for each modelling algorithm (GAM, generalised additive model; GBM, generalised boosted model; CTA, classification tree analysis; RF, random forest; and MaxEnt, maximum entropy), and from left to right the explanatory variables (habitat, land distance, distance to sanctuary zone, and depth). Each coloured line represents one of the 10 cross-validation runs.

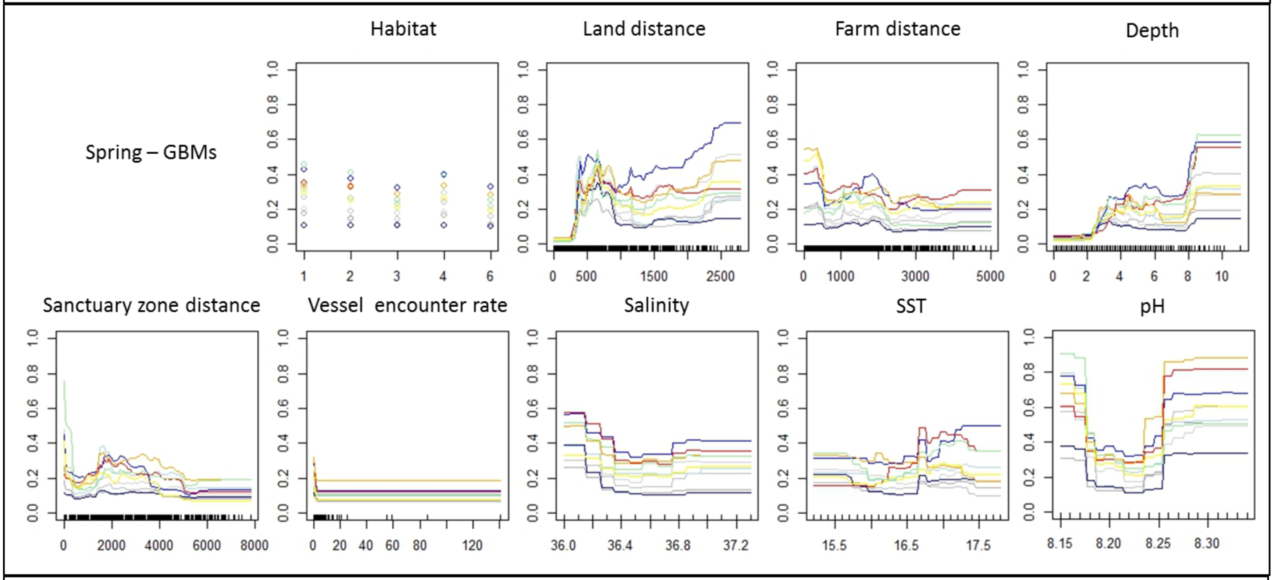
Results S3: Response curves of the seasonal species distribution models for the inner area of Coffin Bay

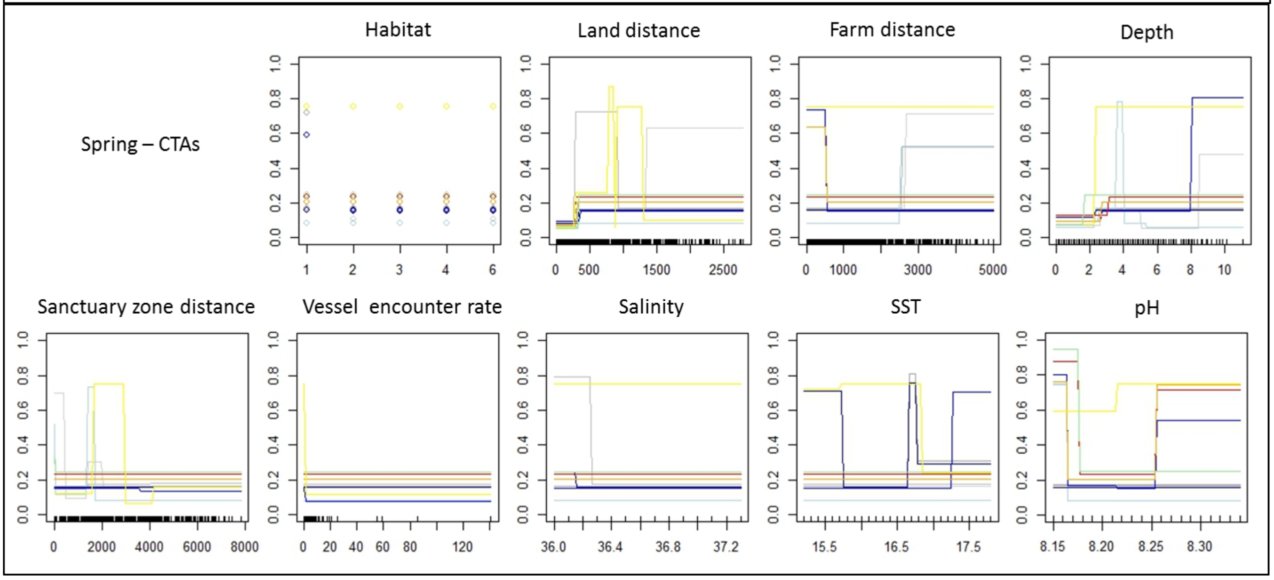
The response curves of presence of dolphins in relation to the explanatory variables obtained for seasonal species distribution models run for the inner area of Coffin Bay are presented in Figure S5.

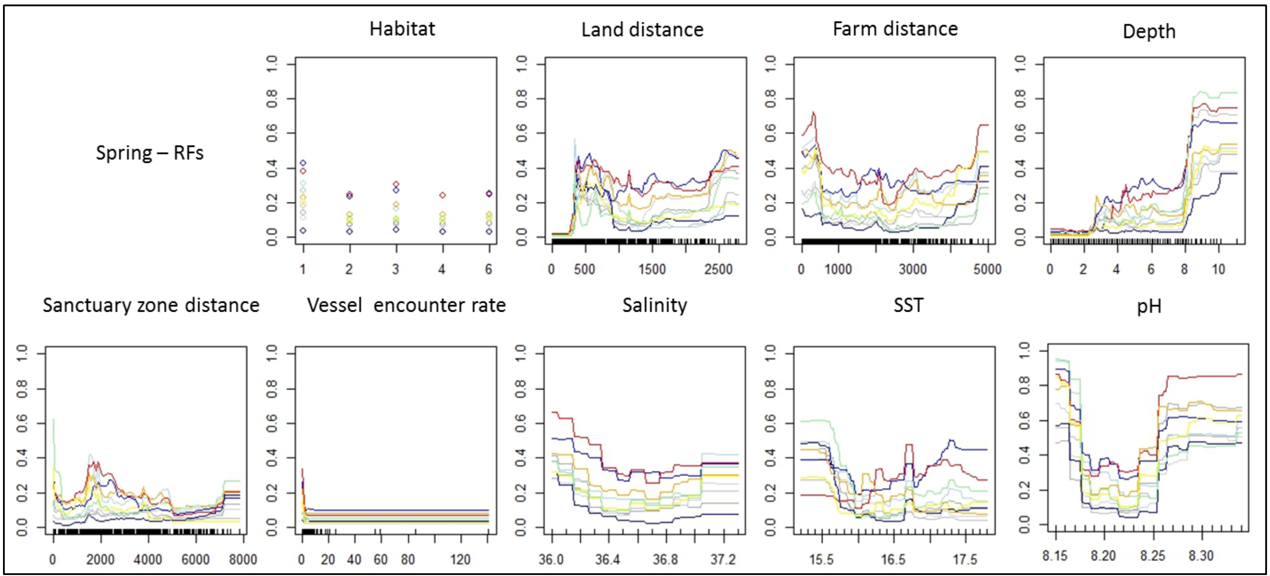
Figure S5. Response curves of presence of dolphins in relation to the explanatory variables obtained for seasonal species distribution models run for the inner area of Coffin Bay. Panes are presented ordered by austral season (Spring, Summer, Autumn, and Winter) are grouped per modelling algorithm (GAM, generalised additive model; GBM, generalised boosted model; CTA, classification tree analysis; RF, random forest; and MaxEnt, maximum entropy). Each coloured line represents one of the 10 cross-validation runs.

Spring SDMs’ response curves:








Spring – RFs
Habitat
Land distance
Farm distance
Depth
Sanctuary zone distance
Vessel encounter rate
Salinity
SST
pH
0.0
0.2
0.4
0.6
0.8
1.0
1
2
3
4
6
0
500
1500
2500
1000
3000
5000
8
10
2000
4000
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8000
20
40
60
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36.0
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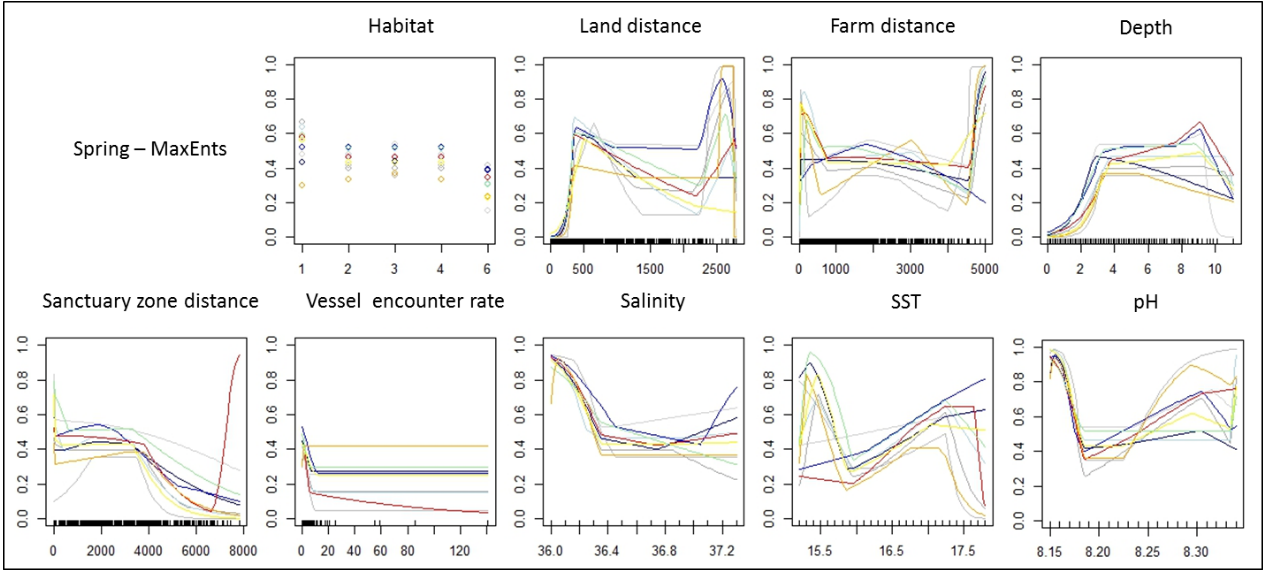
Spring – MaxEnts
Habitat
Land distance
Farm distance
Depth
Sanctuary zone distance
Vessel encounter rate
Salinity
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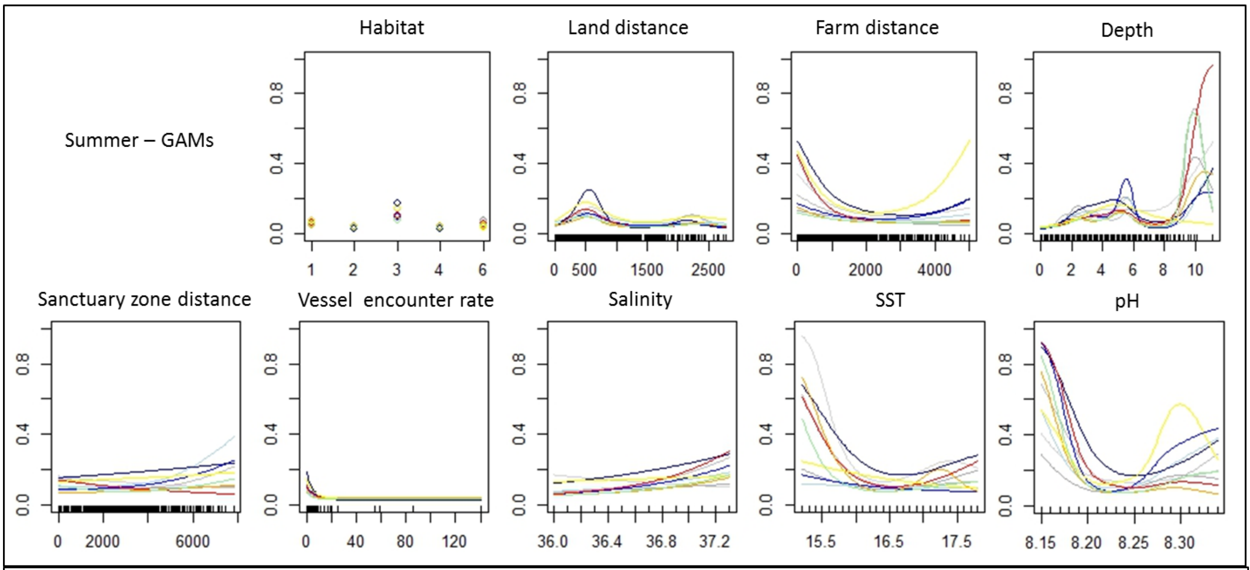
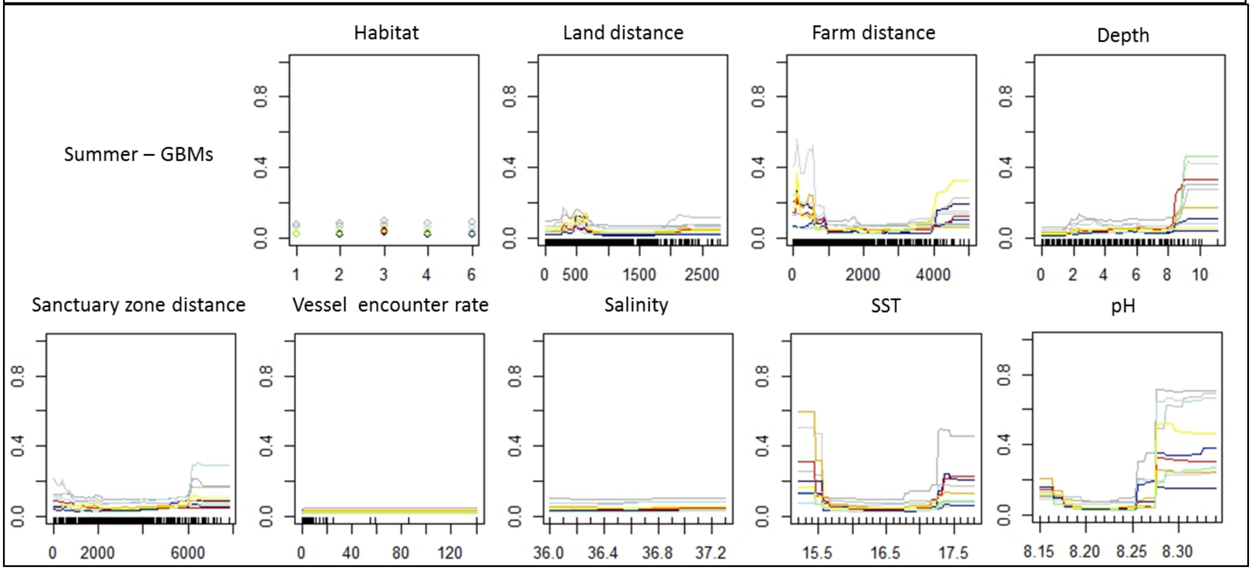
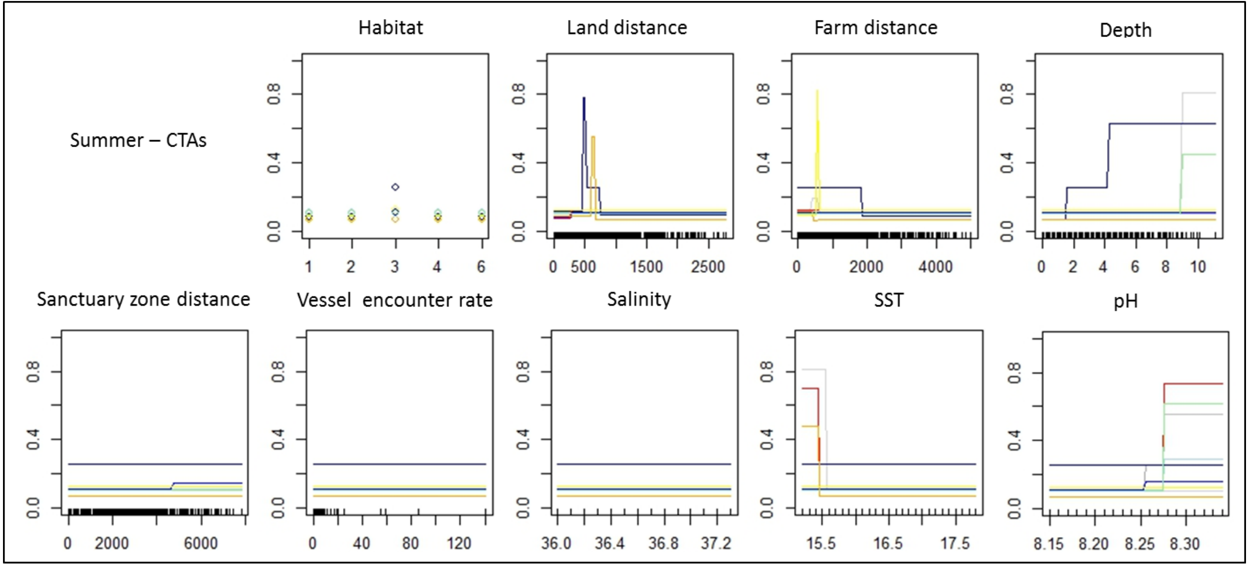
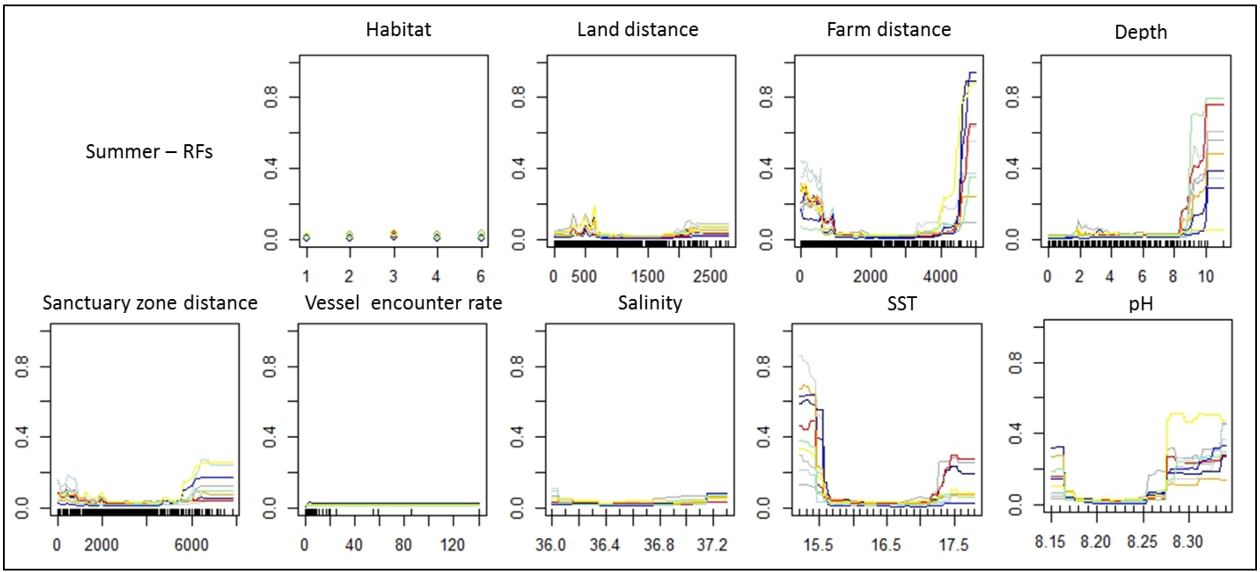
Summer SDMs' response curves:








Summer – RFs
Habitat
Land distance
Farm distance
Depth
Sanctuary zone distance
Vessel encounter rate
Salinity
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1 2 3 4 6
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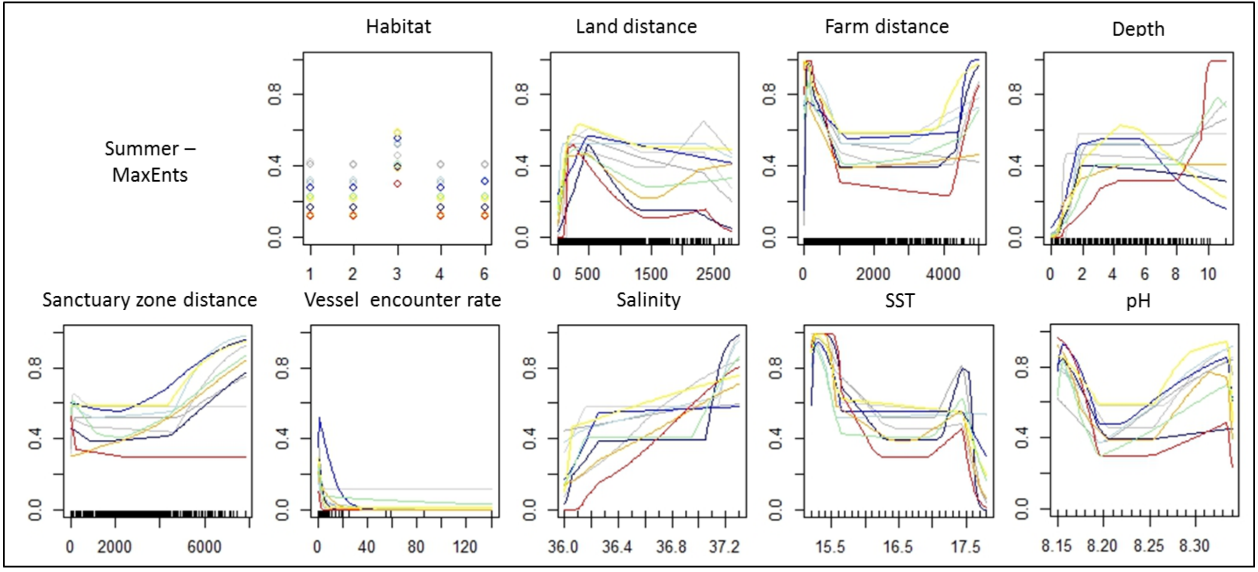
8.15 8.20 8.25 8.30


Summer – MaxEnts
Habitat
Land distance
Farm distance
Depth
Sanctuary zone distance
Vessel encounter rate
Salinity
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1 2 3 4 6
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0 2 4 6 8 10
0 2000 6000
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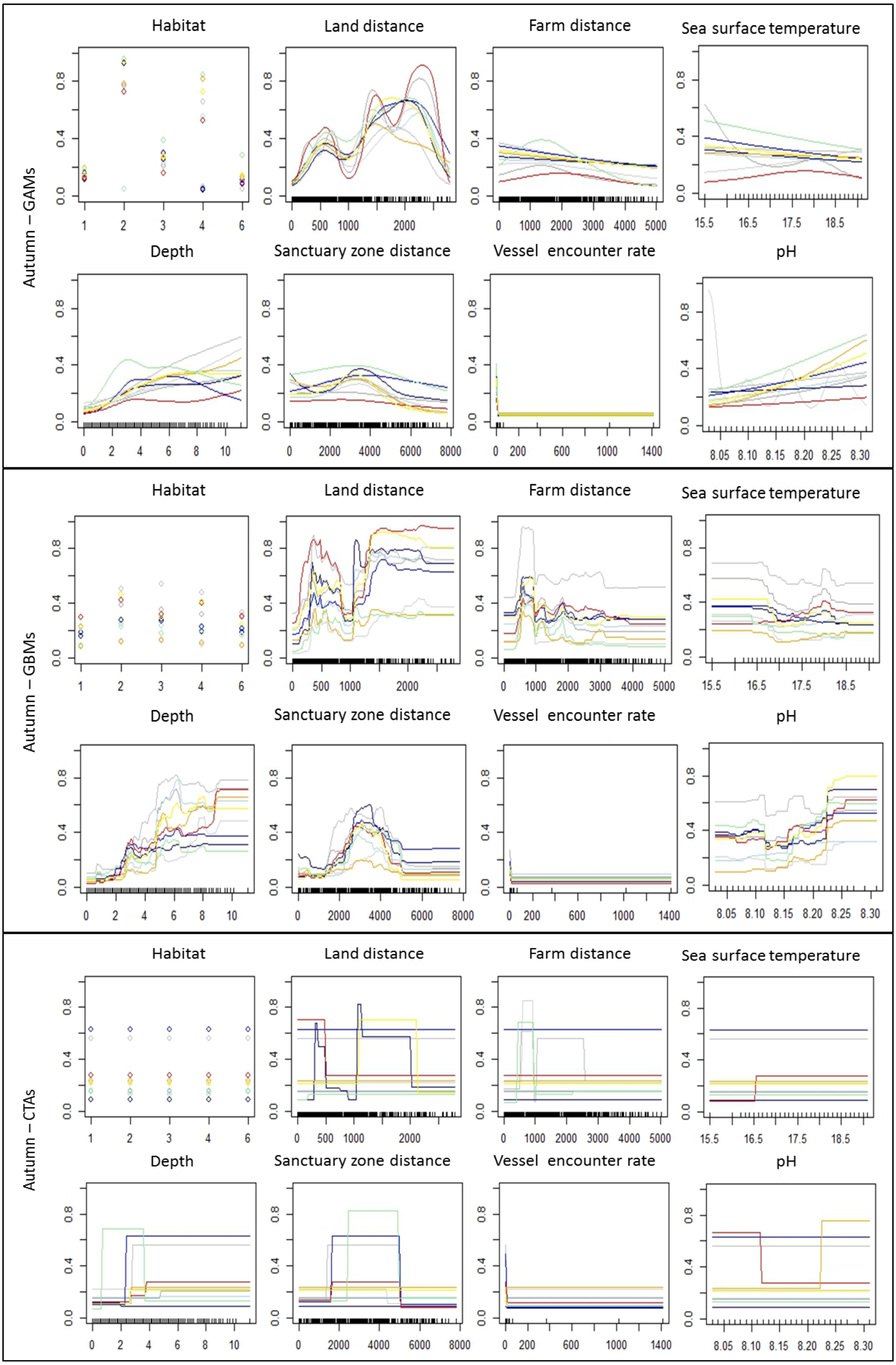
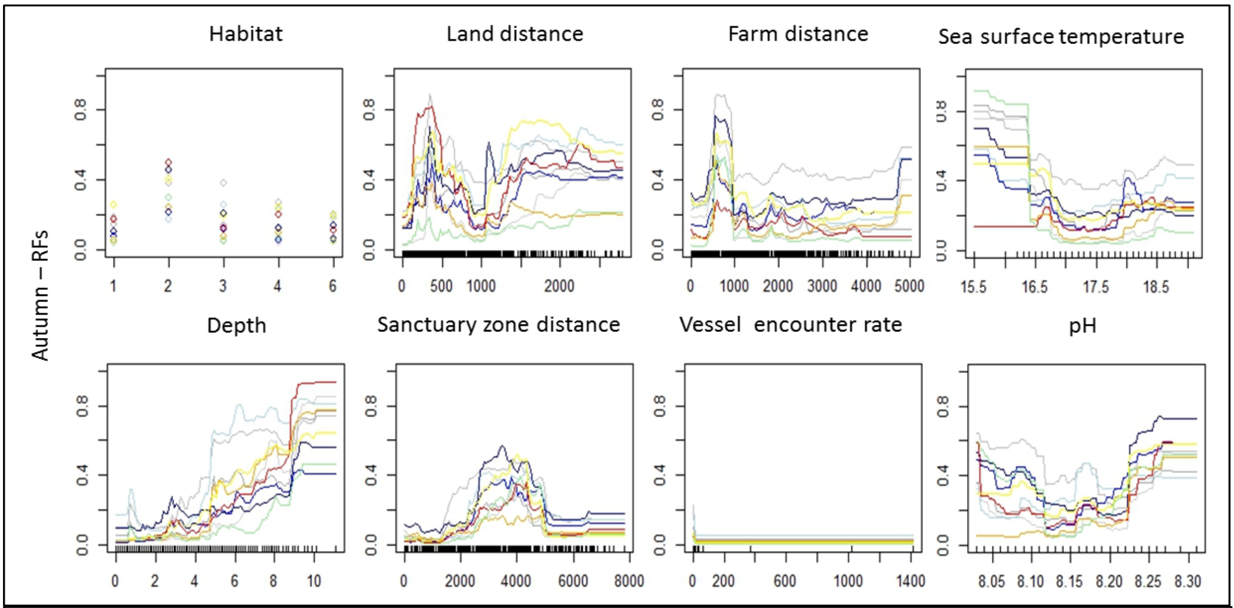
36.0 36.4 36.8 37.2
15.5 16.5 17.5
8.15 8.20 8.25 8.30

Autumn SDMs’ response curves:




Autumn – RFs
Habitat
Land distance
Farm distance
Sea surface temperature
Depth
Sanctuary zone distance
Vessel encounter rate
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17.5
18.5
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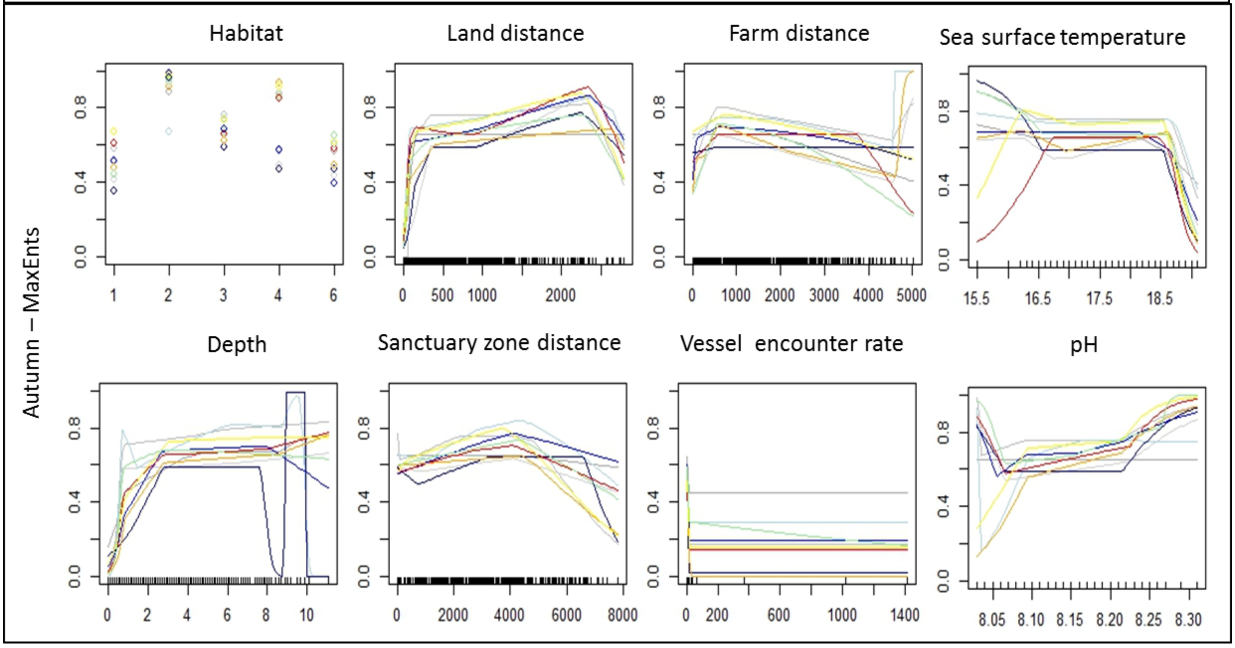
Autumn – MaxEnts
Habitat
Land distance
Farm distance
Sea surface temperature
Depth
Sanctuary zone distance
Vessel encounter rate
pH
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16.5
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2000
4000
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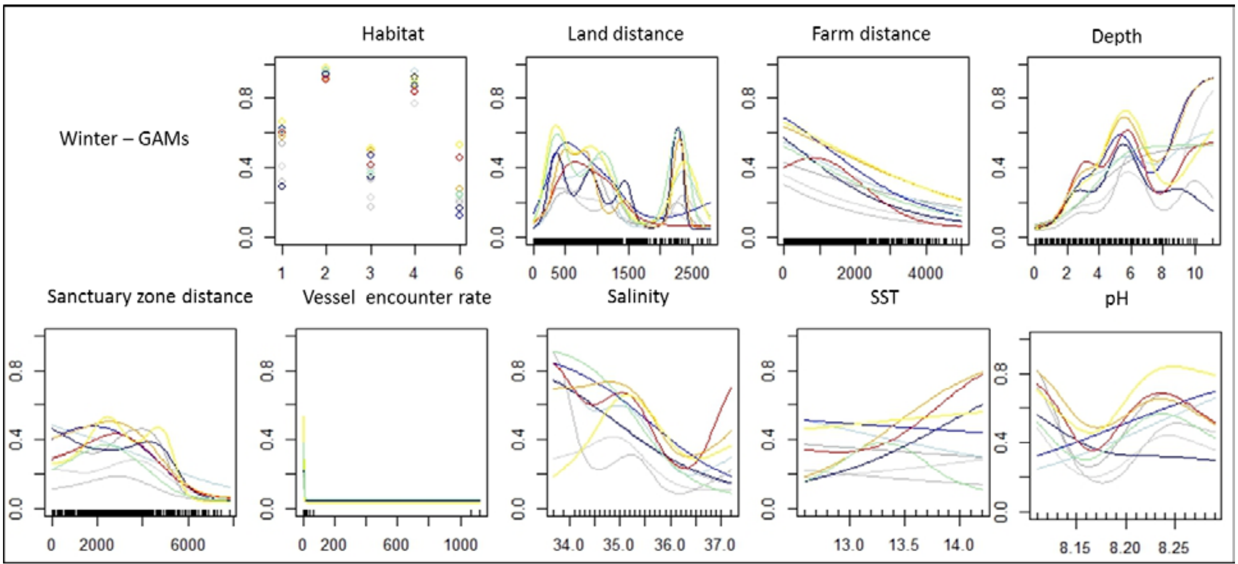
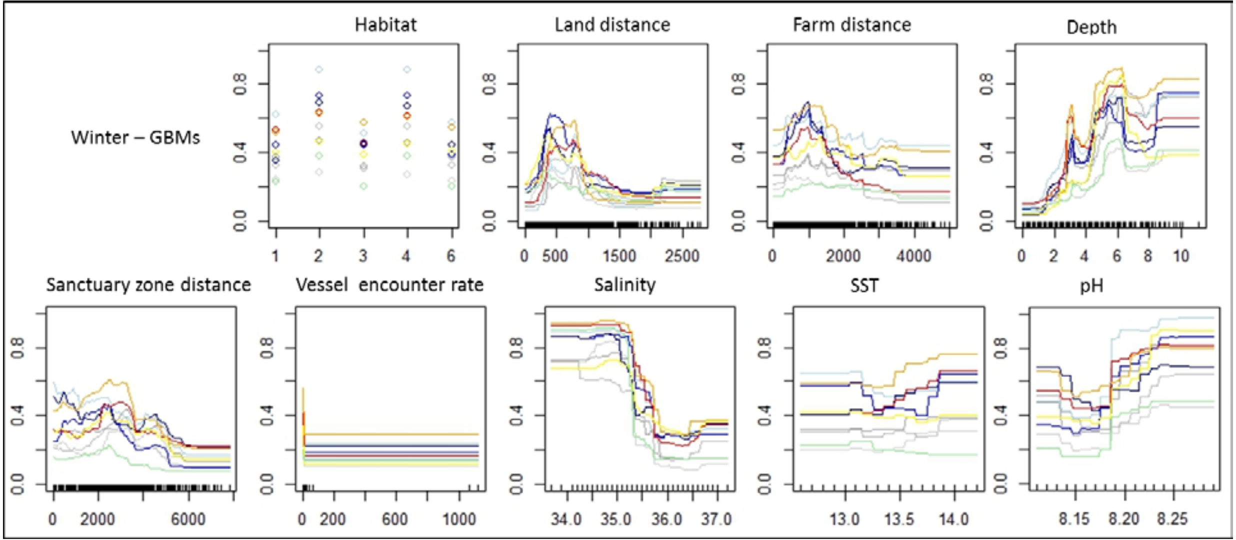
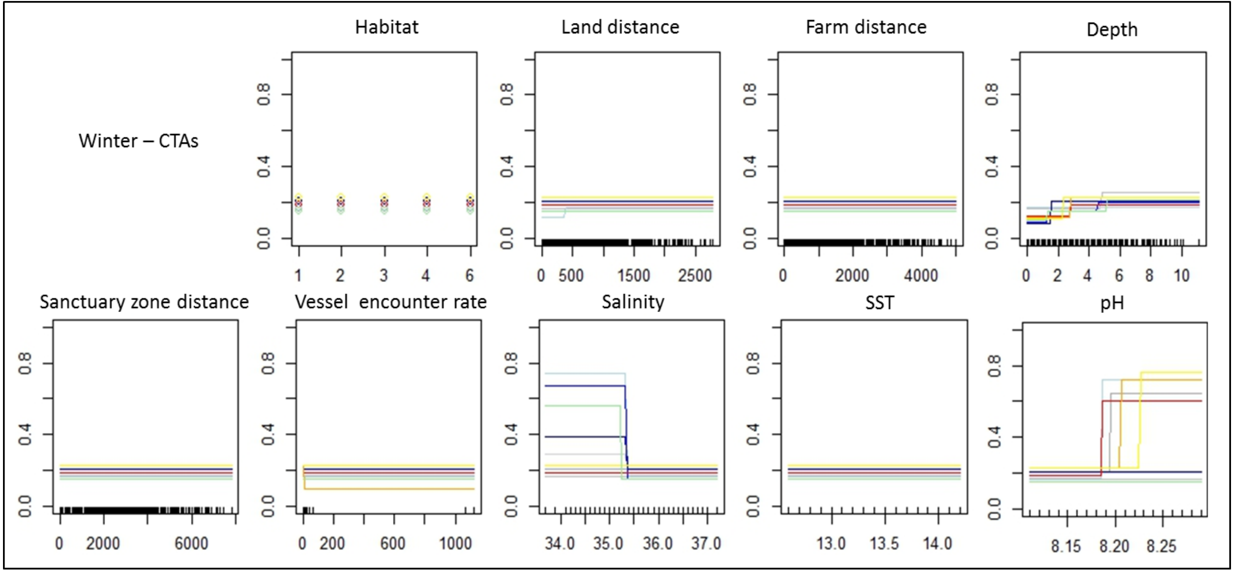
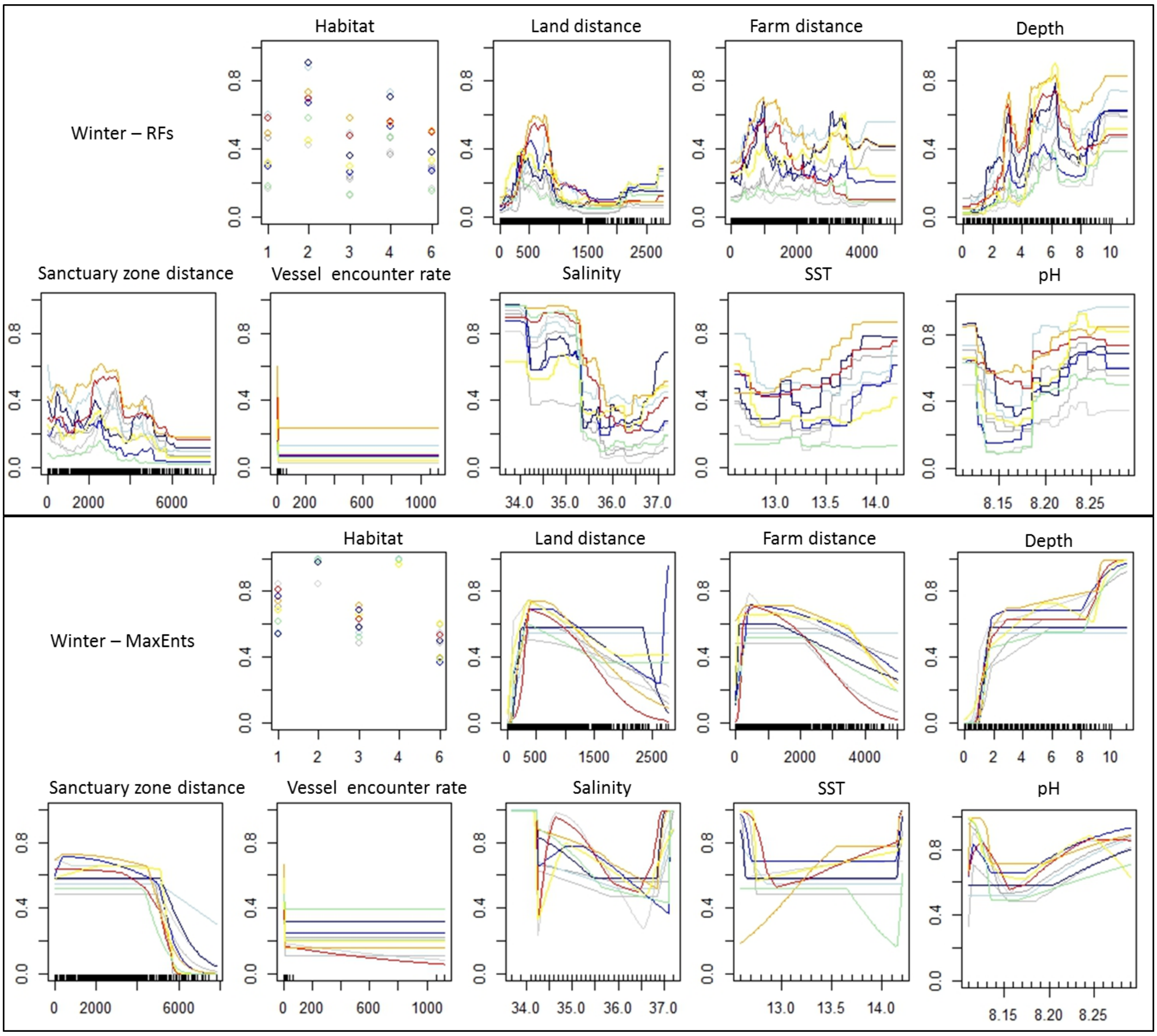
8.30

Winter SDMs' response curves:








Winter – RFs
Habitat
Land distance
Farm distance
Depth
Sanctuary zone distance
Vessel encounter rate
Salinity
SST
pH
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0.4
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3
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6
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500
1500
2500
2000
4000
8
10
6000
200
600
1000
34.0
35.0
36.0
37.0
13.0
13.5
14.0
8.15
8.20
8.25
Winter – MaxEnts

Results S4: Seasonal probability of dolphin occurrence in the entire study area

Collinearity was found between several explanatory variables and they were discarded from modelling after running VIF-step (threshold = 3) (see variables included in models in Table S1). For every season, single SDMs of the entire study area performed better than random models (AUC > 0.5; Figure S6). In summer and autumn the performance of ensemble models was slightly better than median performance of single modelling algorithms; while in spring and winter most single models outperformed the ensemble predictions (Figure S6). In general, the most important variables related with the presence of dolphins per season were either distance to oyster farms or distance to sanctuary zones instead of ecogeographic variables that change along the year such as vessels encounter rate, salinity or SST (Table S1). During spring, summer and autumn the most important variables for all SDMs was distance to farms followed by depth; except for GAMs and MaxEnt in spring, where depth was more important than distance to farms (Table S1). In general, the response curves of seasonal SDMs during these seasons indicated that the probability of dolphin occurrence is higher in cells closer to farms (less than 5000 m) and in shallower areas (less than 10 m). Differences in the shape of curves between seasons indicate that in spring dolphins occur mainly in areas within 3000 m from farms and at water depths ranging from 2 to 5 m; in summer dolphins prefer areas at less than 2000 m from oyster farms; and during autumn dolphins occur at 500 – 4000 m from farms (results not shown). In winter the first most important variables was distance to sanctuary zone and the second was water depth (Table S1). The response curves of SDMs in winter show that dolphins occurred at less than 4000 m from sanctuaries (results not shown).

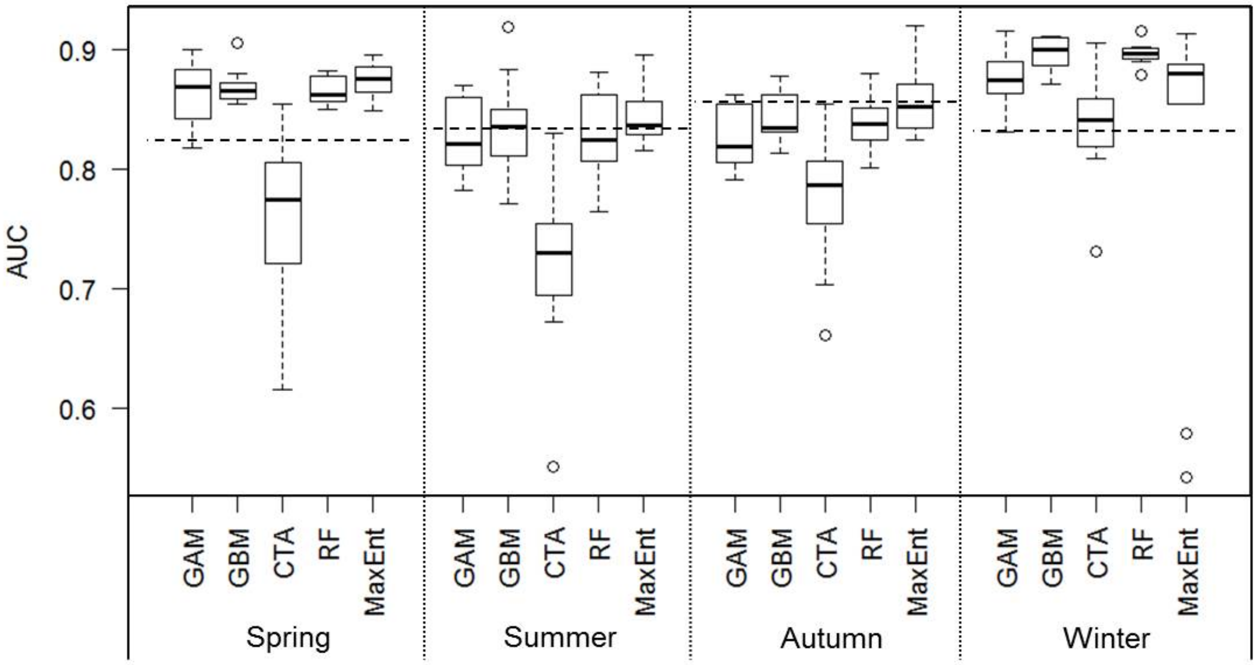

Figure S6. Box-plots for the model accuracy (AUC: area under the curve of the receiver operating characteristics plot) of the 10 cross-validation runs of each single species distribution model (GAM: generalised additive model; GBM: generalised boosted model; CTA: classification tree analysis; RF: random forest; and MaxEnt: maximum entropy), and dashed line indicating the predictive performance (AUC) of ensemble models for each season (spring, summer, autumn and winter). Values of AUC higher than 0.5 indicate that the model predictions perform better than random.

The ensemble models per season using data of the entire study area predicted higher probabilities of dolphins presence consistently in the inner area of Coffin Bay (Figure S7), where the distance to farms and oyster farms is less than 5000 m (Figure 4.3). Summer prediction showed the lowest probability of presence of dolphins compared with the rest of the seasons, the highest probability of dolphins in summer were in Kellidie bay and the northern part of Mount Dutton bay, including waters of Little Mount Dutton (Figure S7b). In the remaining seasons, the highest probability of dolphins presence were predicted in the western sector of Kellidie bay, where water is deeper than 2 m, in Mount Dutton bay and some parts of Port Douglas bay, particularly close to the oyster farms where water is deeper than 1 m (Figure S7a, c , d).

Table S1. Importance of ecogeographical and anthropogenic variables for bottlenose dolphins in the entire Coffin Bay per season, using five types of models: generalised additive model (GAM), generalised boosted model (GBM), classification tree analysis (CTA), random forest (RF) and maximum entropy (MaxEnt). Ecogeographical variables of greatest influence are in bold. (NOTE: Values are presented only for the variables included in models.)

Season	Models	Habitat	Land distance	Farm distance	Sanctuary zone distance	Depth	Vessel encounter rate	Sea surface temperature	pH	Salinity
Spring	GAM	6.52	11.79	28.53		**35.02**	2.21	15.96		
	GBM	1.3	7.83	**41.54**		34.73	3.07	11.53		
	CTA	0.46	11.51	**39.82**		30.8	4.47	12.97		
	RF	1.5	9.85	**38.99**		30.57	5.21	13.87		
	MaxEnt	2.89	6.11	35.25		**41.67**	1.01	13.06		
Summer	GAM	11.39	20.91	**41.51**		21.18	5			
	GBM	4.6	22.5	**51.16**		19.17	2.57			
	CTA	8.46	17.92	**51.32**		19.7	2.61			
	RF	5.27	23.65	**49.34**		19.14	2.59			
	MaxEnt	6.13	12.3	**62.12**		14.46	4.99			
Autumn	GAM	8.6	13.4	**41.6**		25.8	5.9	1.9	2.9	
	GBM	2.2	5.5	**50.3**		27.5	9.1	2.6	2.8	
	CTA	5.4	5.9	**38.5**		29.3	13.5	3.6	3.8	
	RF	1.9	9.9	**42.6**		21.9	9.3	7.6	6.8	
	MaxEnt	2.4	6.1	**58.3**		18.7	7.4	3.3	4.0	

	GAM	3.76	19.94		**38.06**	23.67	1.46			7.87	5.24
	GBM	0.36	9.95		**48**	29.1	2.17			5.03	5.4
Winter	CTA	0.25	8.76		**40.85**	33.05	4.92			8.22	3.98
	RF	1.08	12.25		**43.73**	25.27	3.42			6.66	7.6
	MaxEnt	2.15	10.21		**51.5**	18.47	2.1			9.11	6.49

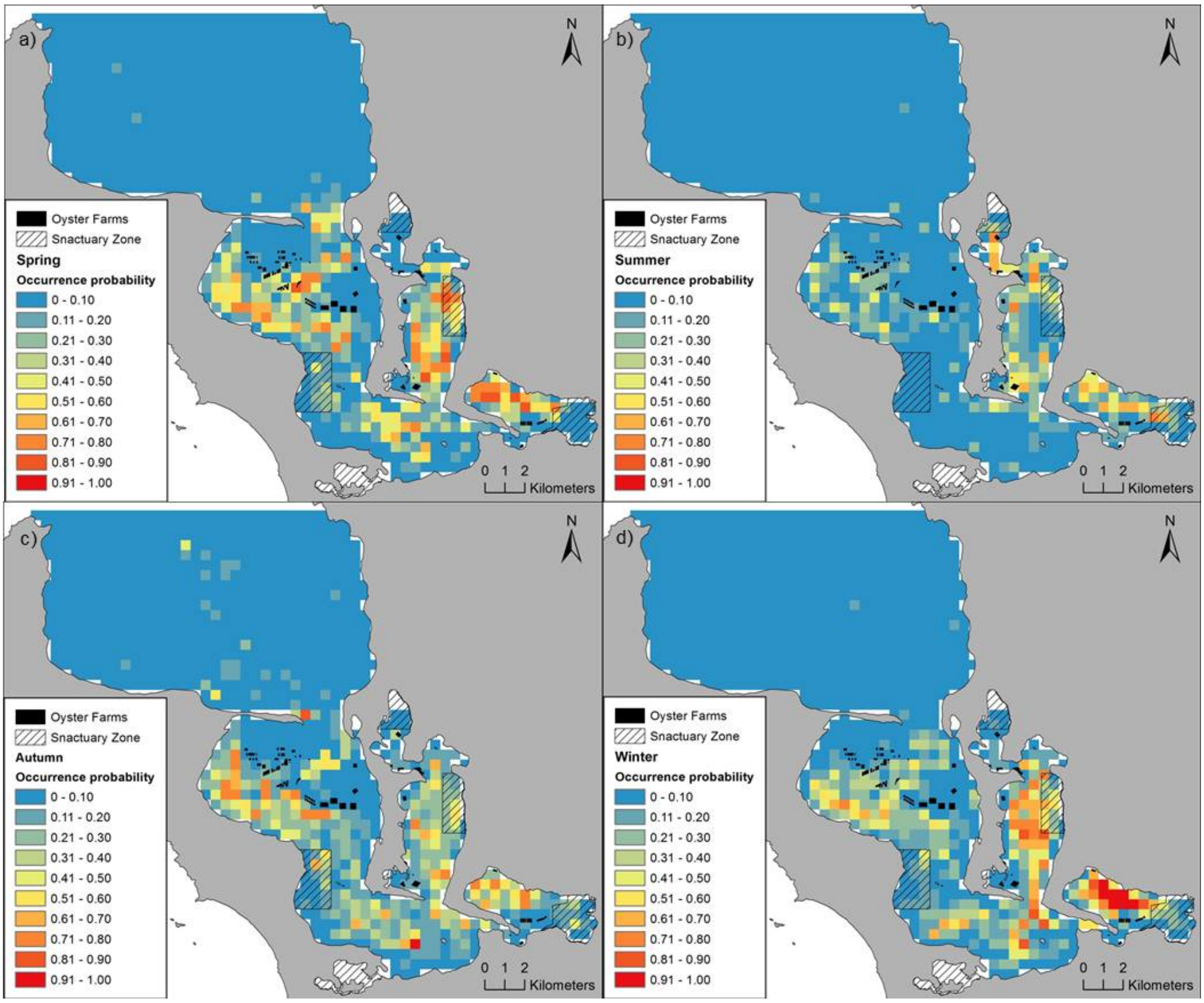

Figure S7. Ensemble model prediction of the probability of occurrence of southern Australian bottlenose dolphin in Coffin Bay per season: a) spring; b) summer; c) autumn; and d) winter.