Demography, habitat use and social structure of Australian humpback dolphins (*Sousa sahulensis*) around the North West Cape, Western Australia: Implications for conservation and management

by

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SUMMARY

Understanding the demography, habitat use and social structure of wildlife populations, particularly those vulnerable to impacts from anthropogenic activities, is fundamental to their conservation and management (Chapter 1). The paucity of information on Australian humpback dolphins (*Sousa sahulensis*) along Western Australia's coastline has hindered adequate environmental impact assessments, as well as assessment of their conservation status. In this study, I used systematic boat-based surveys and photo-identification of humpback dolphins around the North West Cape (NWC), in the northern section of the Ningaloo Marine Park (NMP), to estimate their: abundance, apparent survival, temporary emigration, site fidelity and residence patterns (Chapter 2); distribution and habitat use (Chapter 3); and social structure (Chapter 4). Surveys were undertaken over three ca. six-month field seasons between May 2013 and October 2015, covering a study area of approx. 130 km^2. In Chapter 2, using capture-recapture models, I show that humpback dolphin abundance varied from 65 to 102 individuals around the NWC, with a super-population size of 129 individuals. At approx. one humpback dolphin per km^2, this is the highest density recorded for this species. Temporary emigration was Markovian, suggesting seasonal movement in and out of the study area. Hierarchical clustering showed that 63% of identified individuals exhibited high levels of site fidelity. Analysis of lagged identification rates showed dolphins use the study area regularly, following a movement model characterised by emigration and re-immigration. These patterns of density, site fidelity and residence indicate that the NWC is important habitat toward the south-western limit of this specie's range. In Chapter 3, I used an ensemble species distribution modelling approach, combining the results of six modelling algorithms in relation to ecogeographic variables to identify areas of high probability of humpback dolphin occurrence in the waters of northern NMP. Water depth and distance to coast were identified as important variables influencing humpback dolphin presence, revealing a preference for shallow waters (5-15 m), less than 2 km from the coast. There were areas of high occurrence throughout northern NMP, but they were predominantly outside sanctuary (no take) zones, indicating the need to reconsider zoning boundaries to effectively protect important dolphin habitat. In Chapter 4, I investigated the social structure of humpback dolphins using generalised affiliation indices, and social network techniques to assess dyadic relationships, assortative interactions and social clustering. Results indicated humpback dolphins live in a fission-fusion society, characterised by non-random dyadic relationships. Assortative interactions were identified both within and between sex classes, and were higher amongst members of the same sex, indicating same-sex preferred affiliations and evidence of sexual segregation. Modelling of temporal patterns of association indicated individuals had both strong, long-term preferred associates, as well as casual associates. In Chapter 5, I discuss the implications of these results for the conservation and management of humpback dolphins in the NWC region, and outline future research directions. The NWC represents an important habitat for this population, the methods presented provide a methodological framework for future impact assessments, and the results provide a strong platform for conservation of Australian humpback dolphins.

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

ACKNOWLEDGEMENTS

It’s done! Finally! Almost five years, multiple moves between the south and the north-west of Australia, two kids, and a full-time job later, I’ve finally been able to bring it all together, and bloody hell it feels good!

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[A proportion of the content of this publication was used in Chapter 1 (and figures in Appendix S1) of this thesis, and is permitted for reuse in a thesis under Elsevier License Number 3916151272291].

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[The methodology described in this publication was used in Appendix S4 (section S4.1) relating to Chapter 4 of this thesis. Elsevier allows co-authors the reproduction of up to 10% of the original manuscript for re-use without permission being sought. The lead author of this publication revised section S4.1 in Appendix S4].

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Statement of authorship

I (T.N.H.) am the principal contributor for each chapter. My primary supervisor, Dr Guido J. Parra (G.J.P.), and adjunct-supervisors, Professor Lars Bejder (L.B.) and Dr Simon Allen (S.J.A.), 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. Daniella Hanf (D.H.) is a co-author on the content of the Elsevier *(Advances in Marine Biology*) publication used in Chapter 1. Extensive literature review, data compilation and synthesis, and manuscript writing was split equally between T.N.H and D.H, and reviewed by G.J.P. as senior author. Content of this manuscript is permitted for reuse in a thesis under Elsevier License Number 3916151272291. Please note, however, that only ca. 1,300 words of the ca. 3,500 in Chapter 1 (< 40%) were taken from the Elsevier publication. Chapter 1 does not comprise the entire publication. D.H. is also a co-author in Chapter 2 due to contribution to data collection. Robert Rankin (R.W.R.) is a co-author due to contribution of statistical analysis and advice for Chapter 2.

Chapter 1:

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- Manuscript writing: T.N.H., D.H. & G.J.P. (in part)
- Figure creation (Elsevier publication figures re-produced in Chapter 1): D.H.

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LIST OF FIGURES

Please note: Figures displayed in Supplementary Information are not listed above.

LIST OF TABLES

Please note: Tables displayed in Supplementary Information are not listed above.

CHAPTER 1: GENERAL INTRODUCTION

Approximately two-thirds of the world's population inhabit areas within 150 kilometres (km) from the coastline and, consequently, many coastal zones are overcrowded, over-developed and overexploited (Hinrichsen 1996). As a result, coastal ecosystems are one of the most threatened marine environments (Halpern et al. 2008). In Australia, 85% of the population live within 50 km of the coast, creating a risk of 'loving our coast to death' (Clark & Johnston 2016). This concentration of anthropogenic activities has implications for the marine wildlife that inhabit coastal waterways, particularly those species vulnerable to the variety of threatening processes associated with overlapping human activities (Reeves et al. 2003, Wallace et al. 2011, Davidson et al. 2012, Dulvy et al. 2014).

Marine mammals play important roles in the marine ecosystem as meso- and top-level predators (Heithaus et al. 2008, Estes 2009), but many estuarine and coastal species and populations are under threat from multiple stressors (Davidson et al. 2012, Parsons et al. 2015). Some species, such as the Hector's dolphin (*Cephalorhynchus hectori*), the Yangtze finless porpoise (*Neophocaena asiaeorientalis asiaeorientalis*), and the vaquita (*Phocoena sinus*) are on the brink of extinction (Dawson et al. 2001, Mei et al. 2014, Taylor et al. 2017), while others, such as the Yangtze River dolphin, or baiji (*Lipotes vexillifer*), are already extinct (Turvey et al. 2007). Successful conservation and management of such vulnerable species are fundamentally underpinned by having an understanding of their behaviour and ecology (Caro 1998, Sutherland 1998, Berger-Tal et al. 2011, Snijders et al. 2017).

Marine protected areas (MPAs) offer a tool for marine mammal protection, particularly if their zoning includes large no-take areas (i.e. areas closed to extractive activities) of habitat suitable for the species in question (Gormley et al. 2012, Edgar et al. 2014). Considering the importance of marine mammals as umbrella species and their vulnerability to anthropogenic impacts, the identification of important marine mammal habitat is key to their conservation (Hoyt 2011, di Sciara et al. 2016). However, ensuring the efficacy of MPAs requires a comprehensive understanding of the behaviour and ecology of the species therein (Gregr et al. 2013, Guisan et al. 2013), which is lacking for several existing protected areas (Hooker et al. 2011). In Australian waters, the state of knowledge regarding most marine mammal populations and species is insufficient to assess conservation status and, as such, many such populations are considered Data Deficient (Woinarksi et al. 2014a, 2014b).

Population demographics, distribution, habitat use and social structure are important ecological traits to quantify because they provide the baseline upon which to develop effective species conservation and management strategies. Estimating abundance is critical for ecological studies of the spatial and temporal dynamics of a population and to inform conservation and management efforts (Burgman & Lindenmayer 1998, Williams et al. 2002). Obtaining abundance estimates over sufficient temporal scales enables the determination of population trends over time, knowledge of which is critical for species conservation assessments and triggering conservation actions (Gerrodette 1987, Primack 2006). Furthermore, estimating survival rates facilitates assessing a given population's extinction risk, which is of particular importance for populations of threatened species (Shaffer 1981, Caughley 1994). Further, quantifying the movement patterns of individuals in and out of an area provides insight into the level of site fidelity and residency of a population. In cetaceans, as for many other taxa, those populations that are both small and display high site fidelity and residency to confined areas are, by their very nature, at higher risk from localised threats (Parra et al. 2006a, Gonzalvo et al. 2013, Atkins et al. 2016) than are larger populations with high levels of emigration/immigration. In contrast, populations exhibiting site fidelity and/or residency within or adjacent to MPAs have the benefit of an existing management framework to minimise potential threats, and such frameworks should be used to maintain biodiversity and enhance the conservation of these populations (e.g. Flores & Bazzalo 2004, Gormley et al. 2012, Guerra & Dawson 2016).

Gaining an understanding of species-habitat relationships in space and time (i.e. habitat use), and the underlying processes driving these relationships, are also important to describe and predict habitats that are important to an animal, and to inform marine spatial conservation planning (Redfern et al. 2006). Species may exhibit distinct behaviour-specific habitat preferences (e.g. resting, foraging, socialising) and these may vary by, for example, population or season, so a baseline understanding of these preferences and what drives them under natural conditions (e.g. presence/absence of conspecifics, prey availability, predation risk) is fundamental to identifying how potential conflicts with human activities may arise (Bejder et al. 2009).

In addition to understanding population demographics and habitat use, the patterns of associations and interactions amongst individuals within a population (i.e. social structure; Whitehead 2008a) are also important for conservation and management (Whitehead 1997, Berger-Tal et al. 2011, Snijders et al. 2017). Understanding animal social networks and behaviour allows assessment of 'society's state' through group stability and viability, and therefore provides insight into how this stability may change with external stimuli (Berger-Tal et al. 2011, Snijders et al. 2017). For example, knowledge of social structure can provide important ecological insights into reproductive fitness (Silk et al. 2003, Silk 2007), transfer of genetic material (Chepko-Sade & Halpin 1987, Sugg et al. 1996), and/or the transfer of information or behaviours amongst conspecifics (Lusseau & Newman 2004, Allen et al. 2013). Without such information, it would not be possible to fully describe a species' ecology, nor to identify the potential impacts of human activity (Sutherland 1998, Snijders et al. 2017).

1.1 Study site and species

1.1.1 Western Australia

The Commonwealth Government of Australia recently prioritised northern Australia for further growth in energy export, local human populations and tourist visitation (DPMC 2015). Fuelled by petroleum and mineral industries, Western Australia (WA, Fig. 1.1) is the nation's fastest growing state. The North West Shelf of WA contains highly productive hydrocarbon fields (Fig. 1.2), and the capital city of Perth (Fig. 1.1) is a major service centre for the petroleum industry in south-east Asia (Fig. 1.1; DMP 2014). At the time of writing, the development boom appeared to have been slowing: oil and iron ore prices have dropped; large construction projects have slowed; and unemployment rates have increased. Whilst these may all be signs of a slowing economy, the 'boom' is not necessarily leading to a 'bust' (Edwards 2014). Coastal areas in the Pilbara region are growing at record pace (WAPC 2012), with Karratha (Fig. 1.1) being the first town of northern WA to achieve 'city status' on 1 July 2014. Major construction activities are still occurring in the western Pilbara and this will likely continue, with further exploration planned for the coastal areas around Exmouth and Onslow (Fig. 1.2). The Pilbara coastal waters are also subject to high levels of shipping traffic (Fig. S1.1 in APPENDIX S1) (AMSA 2014). Northern WA is therefore likely to remain an area of intensive anthropogenic activity in the foreseeable future.

The cumulative impacts of coastal development and associated human activities, such as seismic surveys, land reclamation, dredging, blasting, pile driving, increased shipping and the influx of environmental contaminants are recognised as serious threats to Australia's coastal dolphins (Cagnazzi et al. 2013a, Parra & Cagnazzi 2016, Weijs et al. 2016). The northern WA coastline supports a mosaic of habitats, including mangroves, salt flats, seagrasses, sponge gardens, coral reefs and coral-fringed islands (Wilson 2013). Accordingly, this region also supports a diverse assemblage of marine megafauna, including two endemic coastal dolphin species – the Australian snubfin *Orcaella heinsohni* ("snubfin dolphin" hereafter) and the Australian humpback dolphin *Sousa sahulensis* (Parra et al. 2002, 2004). Rapid and wide-scale development along this coastline has occurred without adequate baseline data collection on these species and, therefore, without a precautionary approach to their conservation and management (Allen et al. 2012, Bejder et al. 2012).

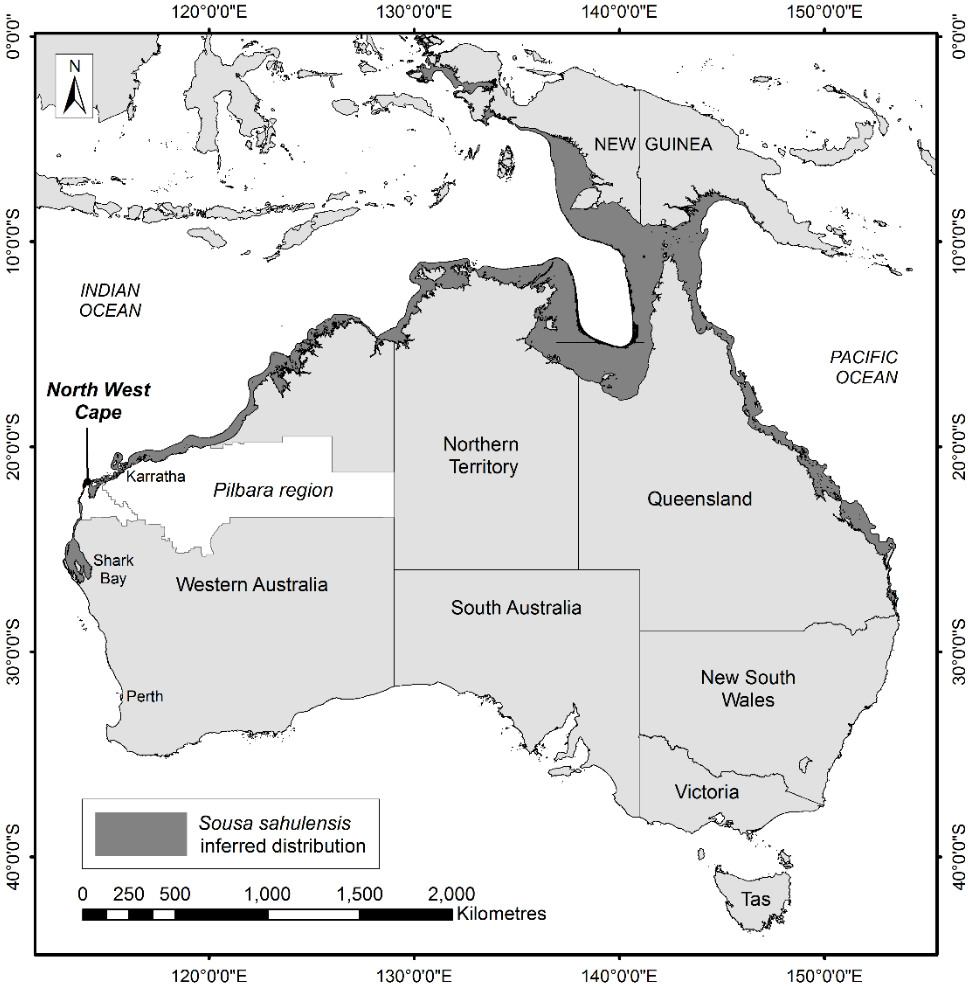

Fig. 1.1. Map of Australia with inferred distribution (to the 30 m isobath) of Australian humpback dolphins (*Sousa sahulensis*) throughout their range in northern Australia and southern New Guinea. The locations of the North West Cape, Pilbara region, Karratha, Shark Bay and Perth in Western Australia are also indicated. Tas = Tasmania.

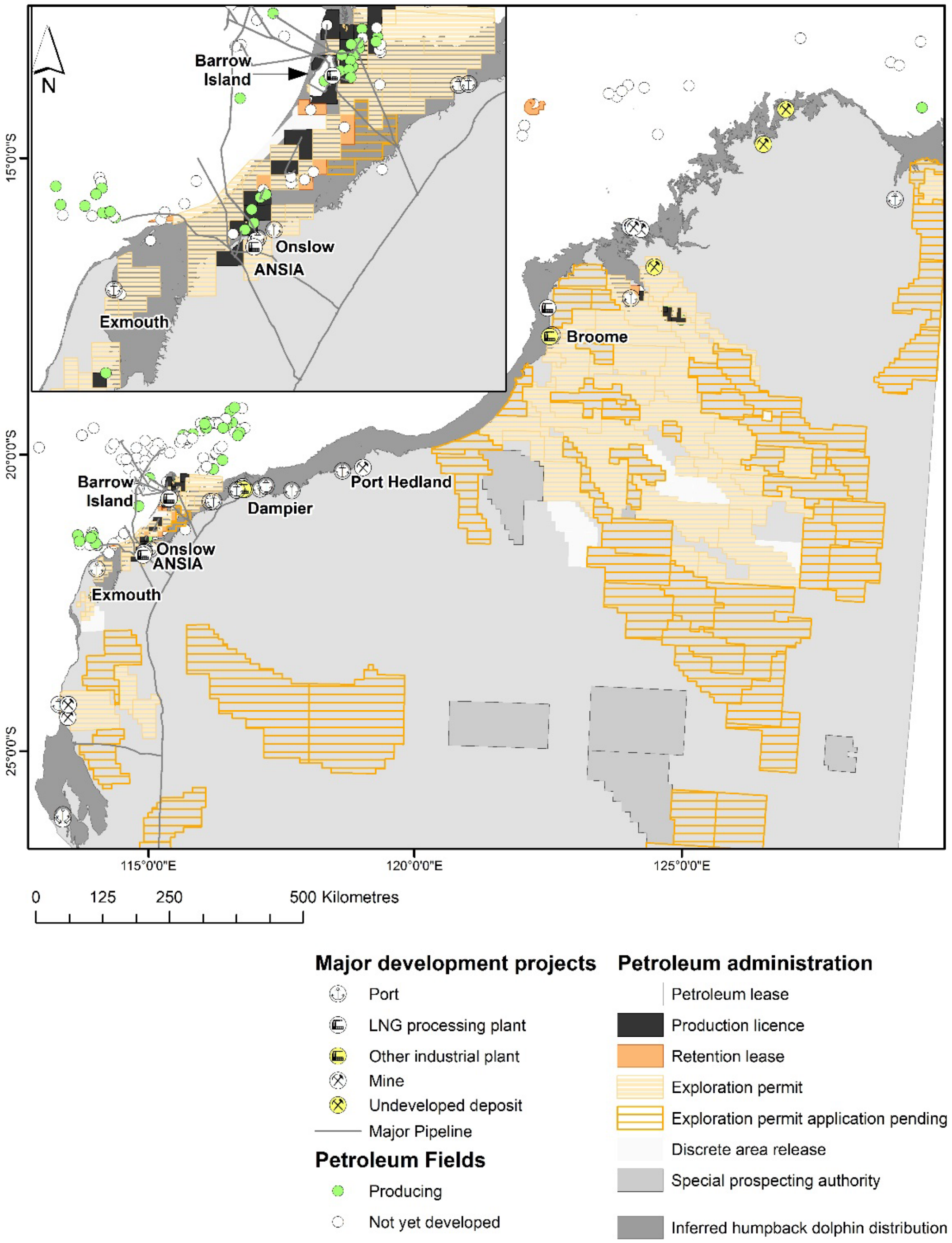

Fig. 1.2. Major developments and administrative areas (DMP 2014) along the northern coastline of Western Australia and their overlap with inferred humpback dolphin distribution. Figure taken from Hanf et al. (2016), reuse permitted in a thesis under Elsevier License Number 3916151272291.

1.1.2 The Australian humpback dolphin and conservation status

The genus *Sousa* is, arguably, one of the most highly variable and locally adapted of small cetaceans (Mendez et al. 2013) and, at the same time, one of the most threatened (Parra & Ross 2009, Jefferson & Curry 2015, Vermeulen et al. 2018). The recently-described Australian humpback dolphin, *Sousa sahulensis* ("humpback dolphin" hereafter), inhabits the tropical and subtropical waters of the Sahul Shelf from northern Australia to southern New Guinea (Fig. 1.1; Jefferson & Rosenbaum 2014). This species' inferred distribution includes coastal waters out to the 30 m isobath, extending from the New South Wales/Queensland border to Shark Bay in WA (Parra & Cagnazzi 2016). Comprehensive studies on the ecology of humpback dolphins have been carried out in selected areas of eastern Queensland (Parra et al. 2004, 2006a, 2006b, Cagnazzi et al. 2011, Parra et al. 2011, Cagnazzi 2013, Parra & Jedensjö 2014). More recently, research has been undertaken in some areas of the Northern Territory (Palmer et al. 2014, 2015, Brooks et al. 2017) and WA (Allen et al. 2012, Brown et al. 2012, 2014, 2016b, this study). Humpback dolphins typically occur in small populations of approximately 50 to 150 individuals, sometimes less, and exhibit high site fidelity, relatively small home ranges (< 300 km²), and relatively fine-scale population structure (summarised in Brown et al. 2016b, Parra & Cagnazzi 2016). This species appears to have a preference for shallow waters (< 20 m depth), close to the mainland coast and islands (Parra & Cagnazzi 2016). These characteristics render humpback dolphin populations sensitive to the cumulative impacts of coastal development and fisheries interactions and, thereby, vulnerable to decline (reviewed in Parra & Cagnazzi 2016).

Under the International Union for Conservation of Nature's (IUCN) Red List criteria, *Sousa sahulensis* were recently (December 2017) listed as "Vulnerable" (Parra et al. 2017). Under Australia's *Environment Protection and Biodiversity Conservation Act 1999*, the species has not been considered for listing as Vulnerable, Endangered or Critically Endangered at the national level due to insufficient data. However, the species is considered "Near Threatened" in 'The Action Plan for Australian Mammals 2012' (Woinarksi et al. 2014a, 2014b) and "Vulnerable" in Queensland under the *Nature Conservation Act 1992*. Now that the status of Vulnerable for *S. sahulensis* has been adopted by the IUCN, it is anticipated that Australian national and state governments will fall in line, enabling increased protection for this endemic species. This has already occurred in other nation states' species listings around the world (see Parsons 2016).

In WA, species facing identified threats or impacts may be listed as "Threatened" or "Specially Protected" under the *Wildlife Conservation Act 1950* but, as with the national listing, data deficiencies currently prevent humpback dolphins from being assessed. Independent of this Act, the Government of WA compiled a Priority Fauna List that ranks native fauna against a priority code from 1 to 5. This List has no legislative basis but, rather, is an internal ranking system to identify fauna in need of research and monitoring. Humpback dolphins remain listed as "Priority 4

Fauna: Taxa which are considered to have been adequately surveyed, or for which sufficient knowledge is available, and which are considered not currently threatened or in need of special protection, but could be if present circumstances change”. Since this designation was assigned (in 1995), coastal development has increased markedly and, contrary to the listing’s claim, humpback dolphins remain inadequately surveyed (Allen et al. 2012, Bejder et al. 2012). Furthermore, a third of the inferred distribution of humpback dolphins in WA overlaps existing or proposed MPAs (Fig. S1.2 in APPENDIX S1), but the efficacy of these marine parks in protecting humpback dolphins remains unproven because knowledge about the distribution and abundance of this species within MPAs is also lacking.

In 2013, cetacean experts and the Commonwealth Government developed the first Coordinated National Research Framework (CNRF) to collect the information required to assess the national conservation status of Australia’s tropical inshore dolphins (DoE 2013). This exercise was carried out in response to increasing concerns over their unknown conservation status and likely susceptibility to impacts from human activity. In 2015, and in light of new knowledge and research efforts, the objectives and priorities of the CNRF were revised, identifying six research objectives and one enabling objective (Fig. 1.3; DoE 2015). The CNRF provided guidance on national research priorities for funding and research that should inform the conservation and management of tropical inshore dolphins. One such high priority research objective was for long-term monitoring to “*gather and use information over long-term timescales to determine trends, mitigate impacts from threats, and support adaptive management and conservation of tropical inshore dolphins*” (Fig. 1.3). The information gathered in this thesis on the demography, habitat use, and social structure provides the ecological baseline needed to inform adaptive management and conservation of humpback dolphins, while also providing a platform on which to assess long-term trends and address other research objectives (see Fig. 1.3). Guidance on sampling protocols and statistical methods to assess occupancy and abundance were also reported as part of the coordinated framework (Brooks et al. 2014), and I have adopted such methods in this thesis, where appropriate (see below).

Similarly, in 2014, the then WA Department of Parks and Wildlife (DPaW; now Parks and Wildlife Service of the Department of Biodiversity, Conservation and Attractions; DBCA) solicited expert opinion from the scientific community in a Prioritisation Framework to identify and confirm priorities for fundamental and applied research on marine mammals in WA, in order to better inform their conservation and management. Humpback (and snubfin) dolphins were considered high priority, with a need to answer fundamental research questions around population demographics (abundance, residency, movement patterns), distribution and habitat use, life history, genetic connectivity and health parameters (DPaW 2014b), particularly in the Pilbara region (DPaW 2014a).

Objectives and priorities of the 2015 Coordinated National Research Framework (DoE, 2015)

Research Objectives

High Priority

1) National distribution data: Provide for access to and analysis of standardised national tropical dolphin data to assess distribution and underpin management and conservation.
2) Long-term monitoring: Gather and use information over long-term timescales to determine trends, mitigate impacts from threats, and support adaptive management and conservation of tropical inshore dolphins.
3) Threat risk assessment: Identify, map and assess threats to tropical inshore dolphins, understand related impacts, and mitigate risks.

Medium Priority

4) Dispersal and movement: Improve understanding (at national, regional and local scales) of dispersal, movement, and genetic connectivity of tropical inshore dolphins to aid conservation and management at appropriate geographic scales.
5) Mortality and life history: Foster collaborative and national approaches to effectively gather mortality, life history and dietary information from stranded and by-caught specimens.
6) Citizen science: Foster community participation in data collection on tropical inshore dolphins and develop a continuous-improvement approach to methods and related programs.

Enabling Objective

1) Indigenous engagement: Foster effective and informed partnerships with Australia's Indigenous communities to enable sustainable conservation management of tropical inshore dolphins.

Fig. 1.3. Objectives and priorities of the 2015 Coordinated National Research Framework for the conservation and management of Australia's tropical inshore dolphins (DoE, 2015). Figure re-produced and modified from Hanf et al. (2016), reuse permitted in a thesis under Elsevier License Number 3916151272291.

Pilot surveys conducted in 2010 by cetacean researchers indicated the North West Cape (NWC), in north-western Australia, was potentially a hotspot for Australian humpback dolphins (Brown et al. 2012). A total of just 18 days of unsystematic photo-identification and biopsy sampling effort in the coastal waters of the NWC in April 2010 yielded a total of 42 group encounters, identifying 54 individuals (calves excluded) around ca. 80 km of coastline (Brown et al. 2012). Despite the relatively low level of effort in the field, the cumulative discovery curve of individuals revealed a consistent increase in the number of individuals identified, with no indication of a levelling off over the study period. The number of individuals identified during this pilot research and relative density of humpback dolphins encountered seemed to indicate that the NWC represented an important habitat and further research into this population was recommended (Brown et al. 2012).

1.1.3 The North West Cape (Ningaloo Marine Park)

The NWC is part of the Pilbara (Fig. 1.1) and one of Australia's fastest growing regions (WAPC 2012). Much of the NWC is encompassed by the Ningaloo Marine Park (NMP) and is part of the Ningaloo Coast World Heritage Area, which was proclaimed in 2011 based on its exceptional marine biodiversity and habitat for threatened species (UNESCO 2011). The NMP covers approximately 2,600 km² along 300 km of coastline (Fig. 3.1 in Chapter 3) and is home to Australia's largest fringing coral reef, Ningaloo Reef (CALM & MPRA 2005). The peak season for human use at NMP and the adjacent Cape Range National Park (CRNP) is April to October (CALM & MPRA 2005, Smallwood et al. 2011). The CRNP receives ca. 300,000 visits annually (DBCA 2017), and given the NMP extends beyond the entrance the CRNP towards the township of Exmouth, it is reasonable to expected that annual visits to the northern part of the marine park would exceed 500,000. Visitor numbers at NMP appear to be increasing (Rob & Barnes 2016); primary attractions include swim-with whale shark tourism, recreational fishing, diving, camping at the adjacent CRNP and, most recently (since August 2016), swim-with humpback whale tourism. The nearby township of Exmouth has a population of ca. 2,500, but can reach up to 10,000 people during the peak visitor season.

The climate in the NWC region is characterised as hot, dry and arid, with an average annual rainfall of ca. 280 mm, and average minimum and maximum temperatures of 18°C and 32°C, respectively. Sea surface temperatures are tropical, ranging from 22°C to 28°C. Outside the primary tourist season (November to April), the NWC is exposed to tropical cyclones, air temperatures of up to 48°C, and water temperatures that can reach in excess of 30°C. The western and northern side of the NWC adjoin the Indian Ocean and the NMP, the latter region being characterised by shallow (< 10 m depth) lagoon waters, with primarily sandy substrates and coral communities within the fringing (sub-tidal) coral reef system (CALM & MPRA 2005, Cassata & Collins 2008). Water depth drops sharply outside the reef towards the continental shelf (Fig. 2.1 in Chapter 2), and the reef is exposed to considerable wave and swell energy (> 2 m) (CALM & MPRA 2005, Cassata & Collins 2008). The eastern side of the NWC faces Exmouth Gulf, an area exposed to low wave energy and dominated by sub-tidal limestone and coral reef/sandy-bottomed habitat that slopes to 20 m depth less than 5 km from the shoreline (Fig. 2.1 in Chapter 2; Bancroft & Sheridan 2000, Kobryn et al. 2013). Approximately two-thirds of the study area lies within the northern section of NMP.

With preliminary evidence of a sizeable dolphin population at the NWC (Brown et al. 2012), accessibility and prospects of major developments in the locality, as well as the adjacent marine protected area of NMP, the NWC was considered by the Australian Commonwealth Department of Environment as one of the key priority areas in northern Australia for conducting research into the ecology of data deficient humpback dolphins to improve the scientific basis for their conservation and management (DoE 2015).

1.2 Aims and research objectives

The overall aim of this thesis was to improve our knowledge about the ecology of Australian humpback dolphins and provide the information (demography, habitat use and social structure) needed to inform decision-making about their conservation and management around the NWC, WA. The specific objectives of the research were to:

1. Estimate the abundance, apparent survival, temporary emigration, site fidelity and residence patterns of humpback dolphins around the NWC (Chapter 2);
2. Investigate the spatio-temporal distribution of humpback dolphins in relation to eco-geographic variables and identify areas of high probability of occurrence in northern NMP (Chapter 3); and,
3. Assess social association patterns among individual humpback dolphins and assortative interactions by sex and geographic location around the NWC (Chapter 4).

1.3 Thesis structure

This thesis is composed of a total of 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 (one published, two currently in review). As such, there is limited but necessary overlap between some sections of each chapter. Chapter 2 is published (Hunt et al. 2017, *Endangered Species Research* 32:71-88), Chapter 3 has been submitted for publication (Hunt et al. in review. *Biodiversity and Conservation*), and Chapter 4 has been submitted for publication (Hunt et al. in review. *Behavioral Ecology*). Tables and figures are integrated in the text of each chapter. For ease of the reader, and to avoid duplication, a single, combined reference list corresponding to all chapters is at the end of this thesis. The Supplementary Information for the chapters is presented as Appendices at the end of the thesis, where each Appendix corresponds to each chapter; i.e. Appendix S1 corresponds to Chapter 1, Appendix S2 corresponds to Chapter 2, and so on. Chapter 5 represents a general discussion, recommendations, and conclusions of the thesis.

CHAPTER 2: DEMOGRAPHIC CHARACTERISTICS OF AUSTRALIAN HUMPBACK DOLPHINS REVEAL IMPORTANT HABITAT TOWARD THE SOUTH-WESTERN LIMIT OF THEIR RANGE

2.1 ABSTRACT

The paucity of information on the recently described Australian humpback dolphin (*Sousa sahulensis*) has hindered assessment of its conservation status. Here, we applied capture-recapture models to photo-identification data collected during boat-based surveys between 2013 and 2015 to estimate the abundance, site fidelity and residence patterns of Australian humpback dolphins around the North West Cape (NWC), Western Australia (WA). Using Pollock's Closed Robust Design, abundance estimates varied from 65 to 102 individuals, and POPAN open modelling yielded a super-population size of 129 individuals in the 130 km^2 study area. At approximately one humpback dolphin per km^2, this density is the highest recorded for this species. Temporary emigration was Markovian, suggesting seasonal movement in and out of the study area. Hierarchical clustering showed that 63% of individuals identified exhibited high levels of site fidelity. Analysis of lagged identification rates indicated dolphins use the study area regularly over time, following a movement model characterised by emigration and re-immigration. These density, site fidelity and residence patterns indicate that the NWC is an important habitat toward the south-western limit of this species' range. Much of the NWC study area lies within a Marine Protected Area, offering a regulatory framework on which to base the management of human activities with the potential to impact this threatened species. Our methods provide a methodological framework to be used in future environmental impact assessments, and our findings represent a baseline from which to develop long-term studies to gain a more complete understanding of Australian humpback dolphin population dynamics.

2.2 INTRODUCTION

Understanding the dynamics of wildlife populations, particularly those exposed to disturbance from anthropogenic activities, is fundamental to successful conservation and management. Quantifying these dynamics can present particular challenges for taxa that are cryptic or otherwise difficult to study and whose populations overlap with human activities. Coastal cetaceans embody this challenge; they are long-lived, slow to reproduce, highly mobile and occupy ecosystems subject to changes as a result of human activities (Lotze et al. 2006, Halpern et al. 2008). As a result, many coastal cetacean populations are exposed to multiple stressors associated with anthropogenic activities (Davidson et al. 2012, Parsons et al. 2015), with some species facing extinction (e.g. Dawson et al. 2001, Jaramillo-Legorreta et al. 2007, Mei et al. 2014).

The ability to implement appropriate conservation and management actions to better protect coastal cetaceans is often limited by the lack of information on local population dynamics and the extent of any threats (e.g. Parra et al. 2006a, Brown et al. 2016b). Two of the three species of tropical inshore dolphins inhabiting the northern Australian coastline, the Australian snubfin dolphin (*Orcaella heinsohni*) and the Australian humpback dolphin (*Sousa sahulensis*) are endemic to the region, and coastal development has been identified as a major threat to the species' persistence (DEWHA 2010, Parra & Cagnazzi 2016). The Australian humpback dolphin (hereafter "humpback dolphin") inhabits the tropical/subtropical waters of the Sahul Shelf across northern Australia and southern Papua New Guinea (Jefferson & Rosenbaum 2014). In Australia, they occur mainly in shallow (< 30 m), inshore waters from the Queensland-New South Wales border to Shark Bay in Western Australia (WA) (Parra & Cagnazzi 2016). Comprehensive studies on their ecology have been carried out in selected areas of eastern Queensland, however, information is still scarce for most populations in the Northern Territory and WA (see reviews in Hanf et al. 2016, Parra & Cagnazzi 2016). These studies have shown that humpback dolphins typically occur in small populations of approximately 50 to 150 individuals (Parra et al. 2006a, Cagnazzi et al. 2011, Palmer et al. 2015), exhibit high site fidelity and relatively small home ranges (< 300 km^2; Parra 2006, Parra et al. 2006a, Cagnazzi et al. 2011), and relatively fine-scale population structure (Cagnazzi et al. 2011, Brown et al. 2014). The ecological characteristics of humpback dolphin populations render them sensitive to the cumulative impacts associated with human activities (Parra et al. 2006b, Cagnazzi et al. 2013a). Their conservation status was recently (December 2017) updated from "Near Threatened" to "Vulnerable" (under the International Union for Conservation of Nature (IUCN) Red List (Parra & Cagnazzi 2016, Parra et al. 2017). Under Australia's national environmental law, the *Environment Protection and Biodiversity Conservation Act 1999*, sufficient data is unavailable to allow assessment against the criteria for listing as threatened species (i.e. "Vulnerable", "Endangered" or "Critically Endangered") under that legislation.

In WA waters, less than 1% of the distribution of humpback dolphins has been surveyed adequately enough to assess their abundance (Hanf et al. 2016). A lack of information on their ecology and population status has hindered adequate environmental impact assessments along WA's changing coastline (Allen et al. 2012, Bejder et al. 2012). Results of a 2010 pilot study around the North West Cape (NWC) suggested that the region might represent an important area for the species (Brown et al. 2012). The NWC is part of one of Australia's fastest growing regions, the Pilbara (Fig. 2.1; WAPC 2012), with major construction and exploration activities associated with oil, gas and mineral extraction industries currently occurring or planned for this region (Hanf et al. 2016), despite a recent down-turn in this sector. Although much of the NWC is part of the Ningaloo Marine Park (NMP), a World-Heritage listed Marine Protected Area (MPA), current and projected coastal developments in the adjacent (non-protected) Pilbara region equate to potential cumulative pressures on humpback dolphins likely increasing in the future. Given the preliminary evidence of a sizeable dolphin population, accessibility and prospects of major developments in the locality, the NWC was considered by the Australian Government Department of Environment as one of the key priority areas in northern Australia for conducting research into the ecology of data deficient humpback dolphins (DoE 2015).

In this study, we present the results of the first comprehensive population assessment of humpback dolphins around the NWC and, indeed, the first in the Pilbara region of WA. We used boat-based surveys and photo-identification techniques to generate sighting histories of naturally marked individuals to estimate abundance, apparent survival, temporary emigration, site fidelity and residence patterns of humpback dolphins. We discuss the implications of our findings for humpback dolphin conservation in the region and suggest areas for further research on this data poor, threatened species. This research contributes towards a more complete understanding of humpback dolphin population dynamics as a basis for future management of this species in Australian waters.

2.3 MATERIALS AND METHODS

2.3.1 Study site

The NWC study site encompasses the northern part of Ningaloo Reef, Australia's largest fringing coral reef (CALM & MPRA 2005) (Fig. 2.1). The western and northern side of the NWC adjoin the Indian Ocean and NMP, the latter region is characterised by shallow (< 10 m depth) lagoon waters, with primarily sandy substrate and coral communities within the fringing (sub-tidal) coral reef system (CALM & MPRA 2005, Cassata & Collins 2008). Water depth drops sharply outside the reef towards the continental shelf (Fig. 2.1), and the reef is exposed to considerable wave and swell energy (> 2 m) (CALM & MPRA 2005, Cassata & Collins 2008). The eastern side of the NWC faces Exmouth Gulf; an area dominated by sub-tidal limestone and coral reef/sandy-bottomed habitat, exposed to low wave energy that slopes to 20 m depth less than 5 km from the shoreline (Fig. 2.1; Bancroft & Sheridan 2000, Kobryn et al. 2013). Approximately two-thirds of the study area is within the MPA of the NMP (Fig. 2.1).

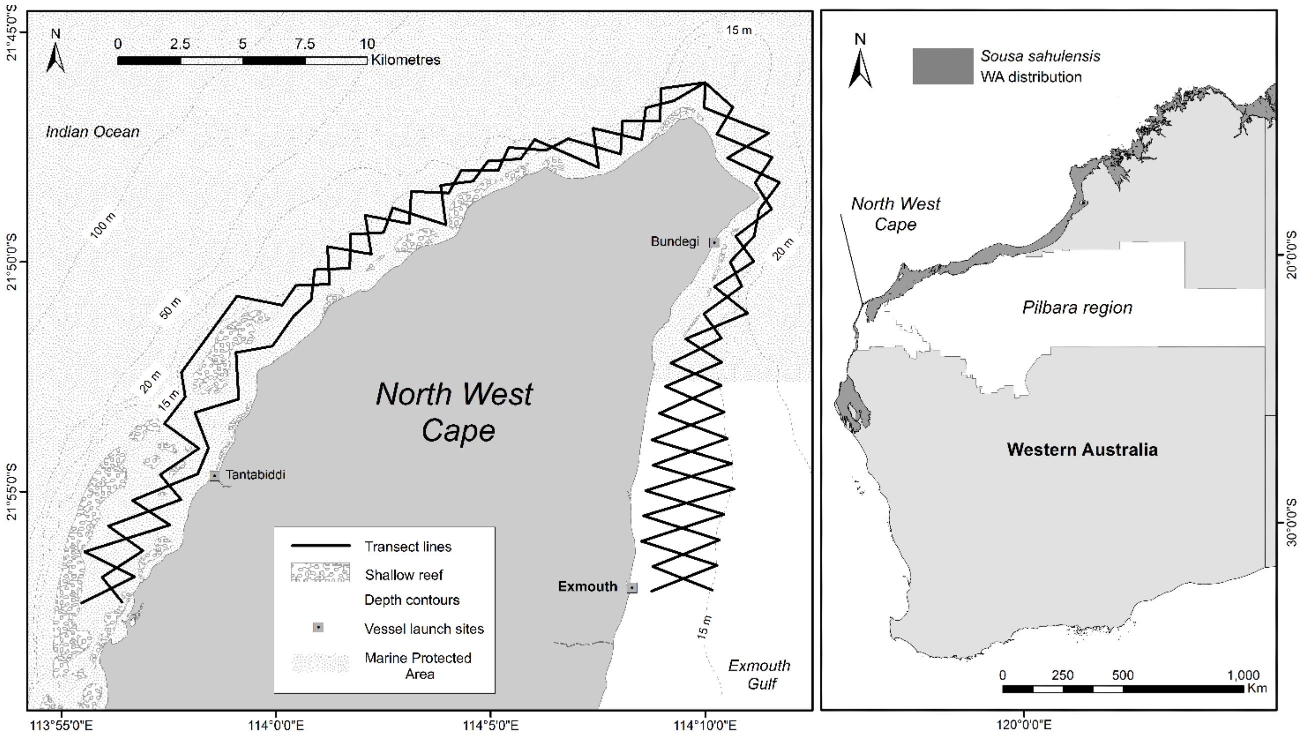

Fig. 2.1. Left: North West Cape (NWC) study site, including vessel launch sites (Tantabiddi, Bundegi, and Exmouth) and opposing zig-zag line transect sampling design (2 x 93 km in length). Right: Western Australia, indicating the location of the NWC, Pilbara region, and Australian humpback dolphin distribution.

2.3.2 Data collection

Boat-based surveys for humpback dolphins were conducted across the study area during May to October 2013, April to October 2014 and May to October 2015. Surveys were conducted following a systematic line transect sampling design (2 x 93 km in length, following opposing, evenly-spaced zig-zag lines; Fig. 2.1). The two pre-determined transect routes covered an area of ca. 130 km^2 and includes waters between 1 and 20 m deep.

Surveys were conducted on board a 5.6 m research vessel powered by a 100 HP outboard motor at speeds of 10 to 12 km/hr and only in good sighting conditions (Beaufort Sea State ≤ 3 and no rain). Survey effort was continuous from 07:00 to 18:00 h, depending on suitable conditions. A crew of three to five (mode = four) observers systematically searched for dolphins forward of the vessel's beam with the naked eye and 7 x 50 binoculars. Once a school of dolphins was sighted, on-transect effort was suspended and dolphins were approached slowly (< 5 knots) to within 10 to 30 m to record GPS location, species identification, school size, school age composition (calf, juvenile, adult), predominant school behaviour (as per Mann 1999) and to collect photo-identification data. Schools were defined as dolphins with relatively close spatial cohesion (i.e. each member within 100 m of any other member) involved in similar (often the same) behavioural activities (modified from Connor et al. 1998). Age class categories used in school composition were the same as those defined by Parra et al. (2006a). Photographs of individual animals were taken using Nikon digital SLR cameras (D600 and D70S) fitted with Nikkor telephoto zoom lenses (80-400 mm and 70-300 mm). After all or most individuals in the school were photographed, or we lost sight of the dolphins, transect effort resumed from the location on the transect line where the dolphins were first sighted.

2.3.3 Photo-identification

Individual humpback dolphins were identified based on the unique natural marks on their dorsal fins (Würsig & Jefferson 1990). All photographs taken were examined and subject to a strict quality (Q) and distinctiveness (D) grading protocol (modified from Urian et al. 1999, 2015) to minimise misidentification. Only high quality photographs of distinctive individuals were used in analyses. For full details of the photo-identification protocol used in this study see S2.1 in APPENDIX S2.

2.3.4 Estimating abundance, survival and temporary emigration

Capture-recapture records of distinctive individuals were used to estimate abundance, apparent survival and temporary emigration under Pollock's Closed Robust Design ('PCRD'; Pollock 1982, Kendall & Nichols 1995, Kendall et al. 1995, Kendall et al. 1997) implemented in program MARK v6.1 (White & Burnham 1999). Under PCRD, photographic 'captures' occur within a hierarchical sampling design, including: (1) primary periods (P-periods) between which the population is considered open to gains and losses, and (2) several secondary periods (s-periods) per P-period, in which the population is assumed closed to demographic change. Closed population models can be used to estimate capture probabilities and abundance within each P-period, while the open-population portion allows the accommodation of temporary emigration and apparent survival between P-periods (Pollock et al. 1990, Kendall 1997). The PCRD for this study consisted of a total of six ca. three-month P-periods (37 s-periods), separated by a minimum of 21 days (Table 2.1). s-periods were defined as the time required to complete a single replicate of the 93 km transect (Fig. 2.1) within a P-period, which ranged from a minimum of three to a maximum of 31 days (median = 11; Table 2.1).

In this study, inference about population abundance ($\widehat{N}$), and demographic processes were based on a multi-model-inference capture-recapture paradigm (Burnham & Anderson 2002). Specifically, we averaged parameter estimates based on posterior model probabilities (as approximated by weights of Akaike's Information Criterion with the small sample-size correction; AICc; Link & Barker 2006). Model averaging is advantageous because a PCRD analysis typically involves considerable 'model uncertainty' in the form of many plausible parameterisations of survival (Φ), capture probability (p), recapture probability (c), probability of becoming a temporary migrant (γ''), and the probability of remaining a temporary migrant (γ'). Many of the more complex PCRD models are desirable in order to incorporate ecologically realistic process variation (such as time-varying survival $\Phi(t)$ vs. time-invariant survival $\Phi(\bullet)$). Unfortunately, such complex models are data-demanding and often yield unreliable estimates (especially singularities and boundary-value estimates; Rankin et al. 2016). Part of the post-modelling exercise was to find a candidate set of models with reliable Maximum-Likelihood Estimates (MLE), and then use this set for AICc-based averaging. Candidate models were screened based on parameter counts, singularities and boundary-value estimates before averaging, so that unreliable parameter estimates were not included. The PCRD models considered for multi-model inference of humpback dolphin abundance, apparent survival and temporary emigration, while taking into account different combinations of parameter specifications, are summarised in Fig. 2.2.

$$\begin{array}{ccccccc} \text{Survival}^{a} & & \text{Temporary Migration}^{b} & & \text{Capture \& Recapture Probabilities}^{f} & & \text{Capture Heterogeneity}^{h} \\ \begin{Bmatrix}\phi(\bullet)\\ \phi(t)\end{Bmatrix} & \times & \left\{\begin{array}{c} \gamma''(\bullet)=\gamma'(\bullet)^{c}\\ \gamma''(season)=\gamma'(season)^{c}\\ \gamma''(t)=\gamma'(t)^{c}\\ \begin{pmatrix}\gamma''(\bullet)\\ \gamma''(season)\\ \gamma''(t)\end{pmatrix}\times\begin{pmatrix}\gamma'(\bullet)\\ \gamma'(season)\\ \gamma'(t)\end{pmatrix}^{d}\\ \gamma''=\gamma'=0^{e}\end{array}\right\} & \times & \left\{\begin{array}{c} p(\bullet,\bullet)=c(\bullet,\bullet)\\ p(t,\bullet)=c(t,\bullet)\\ p(t,s)=c(t,s)\\ \begin{pmatrix}p(\bullet,\bullet)\\ p(t,\bullet)\\ p(t,s)\end{pmatrix}\times\begin{pmatrix}c(\bullet,\bullet)\\ c(t,\bullet)\end{pmatrix}\\ \begin{pmatrix}p(\bullet,\bullet)\\ p(t,\bullet)\end{pmatrix}\times c(t,s)\\ \text{logit}(p)=\text{logit}(c(t,s))+z^{g}\end{array}\right\} & \times & \begin{Bmatrix}\pi=1\\ \pi(\bullet)\\ \pi(t)\end{Bmatrix}\end{array}$$

^{a} ϕ apparent survival between primary periods

^{b} γ'' probability of leaving study area between primary periods; γ' probability of staying outside study area

^{c} Random temporary emigration $\gamma'' = \gamma'$

^{d} Markovian temporary emigration $\gamma'' \neq \gamma'$

^{e} No temporary emigration $\gamma = 0$

^{f} p intial capture probability; c recapture probability

^{g} z "additive offset" modelling recapture probability as a function of capture probability

^{h} π two-point finite mixture parameter, allowing heterogeneity in p and c; $\pi = 1$ enforces no heterogeneity

Fig. 2.2. Idealised full set of Pollock's Closed Robust Design (PCRD) models considered for multi-model inference of Australian humpback dolphins around the North West Cape, Western Australia. The models are represented as different combinations of parameter specifications, accounting for temporal variation, behavioural responses, and variation among individuals. The notation '•' indicates that a given parameter was kept constant, '*t*' indicates that a given parameter was allowed to vary with primary period, *'season'* indicates a temporary migration parameter was allowed to vary by austral seasons 'Autumn-Winter' (April to July) and 'Winter-Spring' (August to October), and '*s*' indicates capture (*p)* and/or recapture (*c*) probability was allowed to vary by secondary period within primary periods. Parameterisations in grey consistently resulted in singularities and boundary-value estimates for *p* and *c*, and were discarded from the model-averaging exercise.

Given that mortality and permanent emigration are confounded (Pledger et al. 2003), we estimated apparent survival (*Φ*) (Lebreton et al. 1992), and considered time-varying and time-invariant alternatives (Fig. 2.2). The intervals between P-periods were specified in decimal years between their mid-dates to obtain consistent per annum estimates of apparent survival (as per Tezanos-Pinto et al. 2013, Palmer et al. 2015).

For temporary emigration, we considered: constant migration probabilities *γ(•),* probabilities varying by P-periods *γ(t),* and probabilities varying by austral seasons 'Autumn-Winter' (April to July; P1, P3 & P5) and 'Winter-Spring' (August to October; P2, P4, & P6), or *γ(season)* (Fig. 2.2). Note that P1 is not considered in PCRD temporary emigration (or apparent survival) parameter estimates since it is the first sampling occasion with no previous sampling occasion from which to derive an estimate. P1 is considered in abundance estimation. For each of these specifications, we also considered: random movement ($\gamma'' = \gamma'$), when the probability that an animal temporarily emigrates is independent of its state during the previous occasion; and Markovian movement ($\gamma'' \neq \gamma'$), when the probability that an animal temporarily emigrates is dependent on its state during the previous occasion (Kendall et al. 1997). Finally, we also considered a no movement model ($\gamma'' = \gamma' = 0$).

For the capture (*p*) and recapture (*c*) probabilities, we considered a large variety of specifications (Fig. 2.2) given the large influence that such decisions have on abundance estimates (Carothers 1973, Burnham & Overton 1978, Rankin et al. 2016). In particular, the agglomerative hierarchical clustering analysis suggests there may be heterogeneity in migration and resighting patterns, which motivates the *a priori* consideration of individual heterogeneity models. Unfortunately, the data did not support complex models with independent capture and recapture probabilities ($p \neq c$), or individual heterogeneity in capture probabilities using two-point finite mixture models (Pledger 2000). Models with equality in capture probabilities ($p = c$) were supported (Fig. 2.2) and for each, the effective detection probability per P-period (p_P) was also calculated as $p_P = 1 - (1-p_{s1})(1-p_{s2})...(1-p_K)$, where s1, s2,... sK, are the s-period capture probabilities in each P-period (Cooch & White 2014, Rankin et al. 2016).

We used AICc to rank models (Burnham & Anderson 2002). To account for model selection uncertainty (Buckland et al. 1997), weighted model averaging was applied across all suitable models (i.e. models with cumulative AICc weight > 99.9%) to produce model-averaged estimates of population parameters. All model outputs generated used the full parameterisation of maximum likelihood available in MARK.

2.3.5 Estimating 'super-population' size

To determine the total number of animals that theoretically used the study area during the course of the study we used the Schwarz and Arnason (1996) 'super-population' parameterisation of the Jolly-Seber model (i.e. POPAN) as implemented in MARK. Beside the estimation of a 'super-population' parameter, POPAN models also provide estimates of apparent survival, capture probabilities per sampling period, and the probability of entry of animals from the super-population into the sampled population between sampling periods (Arnason & Schwarz 1995). For

POPAN models, each s-period within a P-period was pooled to form a single capture event, for a total of six sampling periods. Per annum estimates of apparent survival were derived (as per PCRD models). A total of six POPAN models were examined to allow for fixed (•) or time-varying (*t*) effects on apparent survival rates (Φ), capture probabilities (*p*), and entry probabilities (*pent)* of humpback dolphins in the study area throughout the survey period. As for the PCRD models, we applied weighted model averaging by AICc across suitable models to produce model-averaged estimates of population parameters.

2.3.6 Proportion of marked individuals in the population

Abundance estimates from capture-recapture models were adjusted to take into account the proportion of marked (i.e. distinct) individuals in the study population (Williams et al. 2002). The proportion of marked individuals in the population ($\hat{\theta}$) was estimated using a school sightings based-method (modified from Nicholson et al. 2012). Marked proportion, total population size, associated standard errors and log-normal 95% confidence intervals were calculated using formulas in S2.2 in APPENDIX S2.

2.3.7 Goodness-of-fit tests and validation of model assumptions

There is no formal goodness-of-fit (GOF) test for PCRD. By collapsing the s-periods we determined the GOF across the six primary sampling periods using program RELEASE in MARK (Lebreton et al. 1992) and the software U-CARE V2.3.2 (Choquet et al. 2009). We estimated the variance inflation factor $\hat{c}$ (a measure to quantify over-dispersion) by using the chi-square statistic divided by its degrees of freedom.

PCRD and POPAN models have a number of assumptions; the violation of which can lead to bias in population estimates (Pollock 1982, Pollock et al. 1990, Williams et al. 2002). We used information on the biology of humpback dolphins and specific tests to validate assumptions of PCRD and POPAN analyses (S2.3 in APPENDIX S2).

2.3.8 Site fidelity

We investigated the tendency of humpback dolphins to return to the study site by calculating the following descriptive statistics of resighting rates: (1) monthly sighting rate: the number of months a given dolphin was identified as a proportion of the total number of months of survey effort, (2) P sighting rate: the number of P-periods in which a given dolphin was identified as a proportion of the total number of P-periods, and (3) yearly sighting rate: the number of calendar years when a given dolphin was identified as a proportion of the total years surveyed. Monthly sighting rates could range between 0.05 (i.e. animals sighted in only one month out of 19 surveyed) and 1 for an individual sighted in all months. Similarly, P sighting rates could range between 0.17 and 1, and yearly sighting rates could be either 0.33, 0.66 or 1 (i.e. sighted in one, two or all three years of study). Additionally, site fidelity indices were calculated as the ratio between the number of recaptures for each individual and the number of s-periods from an individual's first capture to its last capture (modified from Simpfendorfer et al. 2011, Bond et al. 2012). A site fidelity index value of 1 indicates an individual was captured in all sampling periods from its first capture to its last capture. Conversely, a value of zero indicates an animal was only sighted once during the sampling period.

To assess if distinctive "clusters" of individuals with similar degrees of site fidelity could be identified based on monthly and yearly sighting rates, and site fidelity indices, we used agglomerative hierarchical clustering (AHC; Legendre & Legendre 2012) to construct a dendrogram using Euclidean distance as our dissimilarity measure and Ward's Method (minimum variance) as our clustering algorithm due to its robustness (Ward Jr 1963, Cao et al. 1997, Singh et al. 2011, Murtagh & Legendre 2014). Approximately unbiased (AU) *p*-values were generated for each cluster using a multiscale bootstrap resampling technique (1000 bootstrap replications per cluster; Suzuki & Shimodaira 2006). High AU *p*-values indicate high confidence in the clusters and were used to specify a cut-off point along the dendrogram (a dissimilarity threshold) to represent the most appropriate number of clusters (as per Singh et al. 2011). To test the overall efficiency of the clustering we calculated the cophenetic correlation coefficient (CPCC). This is a measure of how faithfully clusters in the dendrogram represent the dissimilarities among observations (Sokal & Rohlf 1962), with a CPCC-value > 0.8 indicating a reliable representation of the data (Bridge 1993). AHC analysis was performed in Excel add-in software '*statistXL*' v1.11 (Roberts & Withers 2009) and in R (R Core Team 2015) using the '*pvclust*' package (Suzuki & Shimodaira 2009).

Finally, to explore long-term site fidelity, we cross-checked the 54 distinctive individuals identified around the NWC during the 2010 pilot study with our photo-identification catalogue from this study (as per protocol described above).

2.3.9 Residency

To estimate residency patterns, we calculated lagged identification rates (LIR), i.e. the probability that, if an individual was identified in the study area at any time, it was identified during any single identification made in the area some time lag later (Whitehead 2001). We compared observed LIR rates to expected LIR from exponential mathematical models of no movement, emigration/mortality, emigration + re-immigration, and emigration + re-immigration + mortality (Whitehead 2001, 2007). To consider movements within yearly survey periods, (and hence exclude the ca. 6 month time period between these yearly survey periods) a maximum time lag (Whitehead 2009) was set at 177 days. This period was the longest possible time between the first capture and last capture of an individual in any yearly survey period. Applying this restriction allowed the models to consider overall residency patterns across the three years surveyed while removing consideration of movement patterns between yearly survey periods. LIR models were set to 1000 bootstrap replications, and start parameters were explored against default values for each model to check the fit and test suitability of model parameter outputs (Whitehead 2009). Model selection was based on the Quasi-Akaike Information Criterion (QAIC) value, with the most supported model having the lowest QAIC value. Computation of LIR and model fitting was carried out using the computer software SOCPROG 2.6.

2.4 RESULTS

2.4.1 Survey effort, photo-identification and proportion of marked individuals

A total of 330 hours (h) of survey effort (ca. 3,450 km) was completed across our six primary periods (P-periods) and 37 secondary periods (s-periods; Table 2.1). The majority (79%) of the survey effort across the study period occurred in Beaufort Sea State (BSS) 2 (153 h) and 3 (108 h), and to a lesser extent in BSS 1 (65 h, 20%) and BSS 0 (4 h, 1%). Similarly, the majority (66-87 %) of survey effort within each P-period occurred in BSS 2 and 3. Differences in BSS are likely to cause differences in capture-probability, which, if unaccounted for, would increase the error in abundance estimates. We accommodate such differences, to a certain extent, in the *p(t,s)* models.

Our surveys resulted in a total of 145 sightings of humpback dolphin schools with an encounter rate of 0.04 schools, or 0.17 individuals (including calves) per km of transect surveyed. Schools varied in size from one to 19 animals, with a mean school size (± SD) of 4.6 ± 3.2. A total of 98 marked individuals (86 adults and 12 juveniles) were identified, of which 26 (27%) were sighted once and 49 (50%) were sighted four or more times (mean = 4.1 ± 3.0 SD, range 1-15). The cumulative number of marked individuals identified (Fig. 2.3) over the study period showed a steady increase indicating that not all individuals using the study area had been identified.

Table 2.1. Survey effort, number of schools of Australian humpback dolphins sighted and number of marked animals identified per primary period (P) around the North West Cape, Western Australia, during the 2013 (May-October), 2014 (April-October) and 2015 (May-October) survey periods. Dates are shown as dd/mm/yyyy. Values for total effort are approximate to the nearest kilometre. d = days, h = hours.

Primary period (P)	Time period	Total effort (km)	Length (d) (or part thereof)	Survey effort (h)	No. of secondary sampling periods	Average (± SD) length of secondary sampling periods (d)	Schools sighted	Individual animals identified
P1	28/05/2013 – 05/08/2013	374	22	37.6	4	15.75 ± 10.37	21	34
P2	26/08/2013 – 21/10/2013	465	35	44.3	5	18.40 ± 3.9	20	38
P3	09/04/2014 – 06/07/2014	747	38	70.4	8	9.88 ± 4.49	34	52
P4	31/07/2014 – 07/10/2014	746	39	69.9	8	8.13 ± 3.48	30	47
P5	03/05/2015 – 05/07/2015	466	28	42.6	5	8.80 ± 2.39	16	43
P6	29/07/2015 – 26/10/2015	652	33	65.5	7	12.14 ± 3.67	24	39
	Total	3450	195	330.3	37	11.57 ± 5.71	145	98

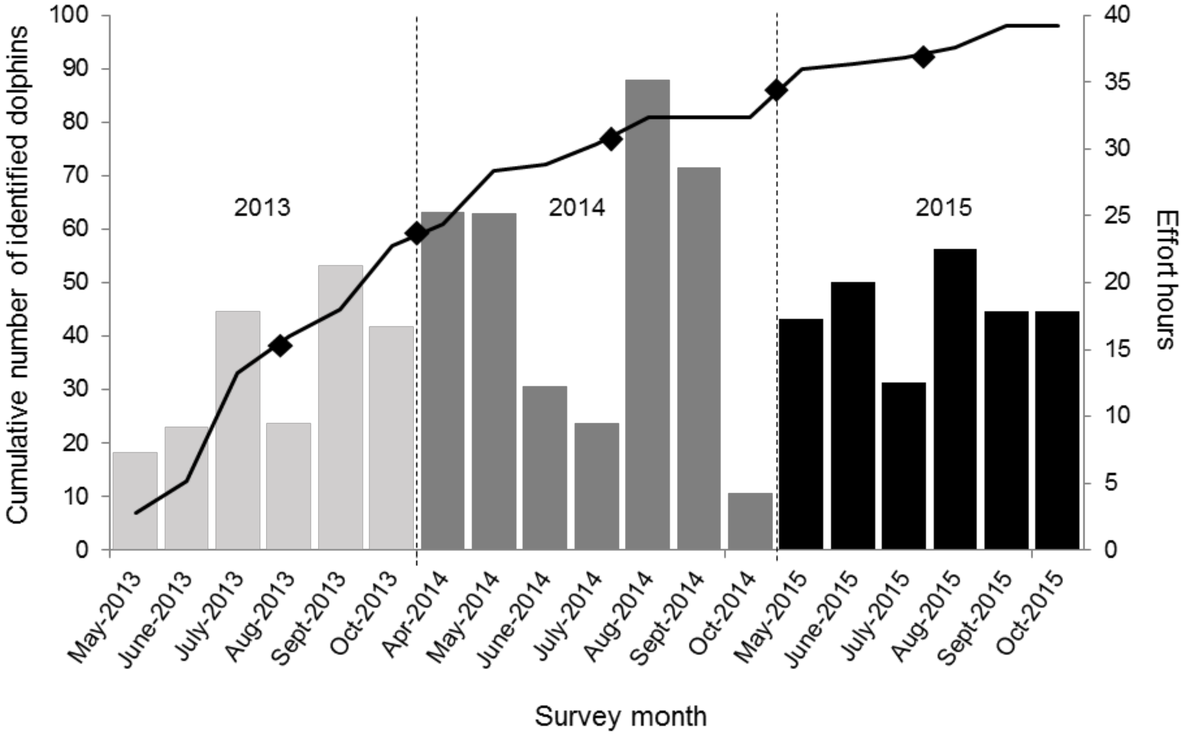

Fig. 2.3. Cumulative discovery curve of identified Australian humpback dolphins (n = 98) within the North West Cape study area over the 2013 (May-October), 2014 (April-October) and 2015 (May-October) survey periods (total 195 days). Vertical bars represent the number of survey effort hours during each month of study. Diamond symbols indicate separation of the six primary periods throughout the entire survey period. Vertical dotted lines indicate separation of yearly survey periods.

2.4.2 Estimates of abundance, survival and temporary emigration

In this section, we detail the model-selection and model-averaging techniques used to estimate abundance, survival and temporary emigration by capture-recapture. The models considered are detailed in Fig. 2.2. Some ecologically desirable specifications were excluded (finite mixture models and *p≠c* models) because of severe symptoms of over-parameterisation, including MLEs at boundary values ($\hat{p}$ = 0, or $\hat{p}$ = 1, or $\widehat{N}_t = M_t$; where M_t = no. of captured individual dolphins per P-period). Among the models used for estimation, some estimates of apparent survival and temporary emigration were likewise at boundary values (e.g. $\hat{\phi}$ = 1 or $\hat{\gamma}'' = 0$). These results indicate data sparseness and over-parameterisation, and are common among temporary-emigration models (see Discussion). The full reduced set of 22 PCRD models is shown in Table S2.1 in APPENDIX S2.

The PCRD model most supported by AICc included Markovian temporary emigration, where γ'' varied by season, and γ' and apparent survival were constant (Table 2.2). The next two models with high support (AICc weight = 0.47) were: (1) Markovian temporary emigration, whereby the only difference from the top model was that γ' varied by season, and (2) random emigration, where apparent survival was constant throughout the survey period, and both γ'' and γ' varied by season (Table 2.2). All 22 PCRD models were averaged by AICc weights to obtain estimates of abundance and apparent survival (Table 2.3), temporary emigration parameters (Table 2.4), and capture probability (Table S2.2 in APPENDIX S2). The proportion of distinctively marked individuals within the study population ($\hat{\theta}$) was estimated at 0.83 and estimates of abundance were adjusted accordingly. Original parameter estimates from the top three PCRD models are given in Tables S2.3, S2.4, and S2.5 in APPENDIX S2.

Model-averaged capture probabilities were variable across the survey period (per s-period), ranging from 0.01 to 0.40, with a mean value of 0.17 (95% CI 0.00-0.55; Table S2.2 in APPENDIX S2). Effective detection probability per P-period ranged from 0.50 to 0.86, with a mean value of 0.67 (Table S2.2 in APPENDIX S2). Model-averaged estimates of the total number of humpback dolphins using the study area ranged from 65 to 102 with comparatively higher abundance estimates (*N* = 75-102) in Autumn-Winter (i.e. P1, P3 and P5) than in Winter-Spring (*N* = 65-69 in P2, P4 and P6; Table 2.3).

Model-averaged apparent survival rates across all P-periods were high, with estimates ranging 0.86 to 0.97 (95% CI 0.05-1.00). Temporary emigration rates (γ'' and γ') were variable but values were consistent across 'season' (i.e. Autumn-Winter vs. Winter-Spring; Table 2.4). The probability of an individual emigrating out of the study area (γ'') was low, while the conditional probability of an individual staying out of the study area (γ') was relatively high (Table 2.4). Estimates of γ' in Autumn-Winter indicate that if an animal was outside the study area in the previous season, there is a ca. 50% probability that it will re-enter the study area (Table 2.4). The top four models all considered temporary emigration parameters by season, and accounted for 85% of AICc weight, with the top two models supporting Markovian emigration and accounting for 65% of AICc weight (Table 2.2).

Table 2.2. Summary of most supported Pollock's Closed Robust Design (PCRD) models fitted to the capture histories of Australian humpback dolphins to estimate population size (*N*), apparent survival rate (*Φ*), emigration (*γ″*, *γ′*) and capture probability (*p*). The top 10 models shown account for > 96% cumulative AICc weight (AICc = Akaike's Information Criterion with the small sample-size correction). The notation '•' indicates that a given parameter was kept constant, '*t*' indicates that a given parameter was allowed to vary with time, and '*season'* indicates that emigration parameters were allowed to vary by seasons Autumn-Winter (P1, P3 & P5) and Winter-Spring (P2, P4, & P6). Capture probability was allowed to vary with time among and within primary sampling periods (*t,s*). Recapture probability (*c*) was set equal to *p* and therefore is not included in the model description. The top three ranked models are shown in **bold.** For details of the full 22 (reduced) PCRD model set see Table S2.1 in APPENDIX S2.

Model	Rank	Δ AICc	AICc weight	Cumulative AICc weight (%)	Number of parameters
Φ(.) γ"(season) ≠ γ'(•) p(t,s)	**1**	**0.0**	**0.33**	**33.1%**	**47**
Φ(.) γ"(season) ≠ γ'(season) p(t,s)	**2**	**0.1**	**0.32**	**64.9%**	**48**
Φ(.) γ"(season) = γ'(season) p(t,s)	**3**	**1.5**	**0.15**	**80.3%**	**46**
Φ(t) γ"(season) = γ'(season) p(t,s)	4	4.0	0.05	84.9%	50
Φ(.) γ"(t) ≠ γ'(•) p(t,s)	5	4.6	0.03	88.2%	50
Φ(t) γ"(•) = γ'(•) p(t,s)	6	4.7	0.03	91.4%	49
Φ(.) γ"(•) ≠ γ'(•) p(t,s)	7	6.0	0.02	93.1%	46
Φ(t) γ"(season) ≠ γ'(•) p(t,s)	8	6.5	0.01	94.3%	51
Φ(t) γ"0 = γ'0 p(t,s)	9	6.6	0.01	95.5%	48
Φ(t) γ"(•) ≠ γ'(•) p(t,s)	10	7.2	0.01	96.5%	50

Table 2.3. Model-averaged estimates of abundance (*N*) and apparent survival (*Φ*) of Australian humpback dolphins for 22 Pollock's Closed Robust Design (PCRD) models. P-period = primary sampling period; AW = Autumn-Winter season; WS = Winter-Spring season; N_m = estimate of number of marked animals in the population; N_{total} = estimate of total population size after correcting for proportion of identifiable individuals (= 0.83). CI = Lower and Upper 95% Confidence Intervals. Note that P1 values for apparent survival (*Φ*) cannot be obtained since there is no previous sampling occasion from which to derive an estimate. For details of the 22 PCRD models averaged see Table S2.1 in APPENDIX S2.

P-period (season)	N_m (95% CI)	N_{total} (95% CI)	Apparent survival *Φ* (95% CI)
1 (AW)	62 (33-90)	75 (47-118)	-
2 (WS)	57 (41-73)	69 (51-91)	0.90 (0.09-1.00)
3 (AW)	73 (58-87)	88 (72-107)	0.97 (0.11-1.00)
4 (WS)	54 (47-62)	65 (56-75)	0.93 (0.11-1.00)
5 (AW)	85 (58-112)	102 (74-140)	0.97 (0.09-1.00)
6 (WS)	55 (40-69)	66 (51-86)	0.86 (0.05-1.00)

Table 2.4. Model-averaged estimates of temporary emigration (γ'', γ') rates of Australian humpback dolphins for 22 Pollock's Closed Robust Design (PCRD) models fitted to capture-recapture data. γ'' is the probability of emigration from the study area given an individual was present in the previous primary (P) period, and γ' is the probability of staying out of the study area given an individual was absent in the previous P-period. Temporary emigration patterns considered were either random ($\gamma'' = \gamma'$), Markovian ($\gamma'' \neq \gamma'$), or no temporary migration ($\gamma'' = \gamma' = 0$), and were either kept constant (•), allowed to vary with time (*t*), or by '*season'*, i.e. Autumn-Winter (P3 & P5) or Winter-Spring (P2, P4, & P6). CI = Lower and Upper 95% Confidence Intervals. Note that emigration parameters for P1 cannot be obtained since it is the first sampling occasion from which to derive an estimate. γ' for P2 cannot be estimated given there are no animals to be considered in P2 that were outside the study area in P1 (i.e. they had not been captured yet). For details of the 22 PCRD models averaged see Table S2.1 in APPENDIX S2.

P-period	Season	Temporary emigration γ'' (95% CI)	Temporary emigration γ' (95% CI)
P2	Winter-Spring	0.30 (0.15-0.51)	-
P3	Autumn-Winter	0.01 (1.2×10^{-5}-0.94)	0.52 (0.06-0.94)
P4	Winter-Spring	0.30 (0.15-0.50)	0.73 (0.09-0.99)
P5	Autumn-Winter	0.01 (6.6×10^{-6}-0.96)	0.52 (0.06-0.94)
P6	Winter-Spring	0.29 (0.11-0.56)	0.71 (0.08-0.99)

2.4.3 Estimate of 'super-population' size

The POPAN model with most support was one in which probability of capture of individuals remained constant, and the apparent survival rate and probability of individuals entering the study population varied across all six sampling periods (Table S2.6 in APPENDIX S2). The next model with high support (AICc weight = 0.40) differed from the top model only in that *p* varied across all six sampling periods (Table S2.6 in APPENDIX S2). The top four models with most support were weight-averaged to obtain estimates of super-population size (N_{super}), apparent survival (Φ), capture probabilities (*p*) and entry probabilities (*pent*). The total super-population size estimate was 129 humpback dolphins (95% CI 117-141; Table 2.5). Estimates of apparent survival varied from 0.45 to 0.96, with capture probability relatively high (range 0.56 to 0.80), and probability of entry generally low (range 0.03 to 0.22; Table 2.5).

Table 2.5. Model-averaged POPAN estimates of Australian humpback dolphin super population size (N_{super}), apparent survival (Φ), capture probability (p) and probability of entry into the study area (*pent*) for the four most supported POPAN models. N_m = estimate of number of marked animals in the population; N_{super} = estimate of total population size over the study period after correcting for proportion of identifiable individuals (= 0.83). AW = Autumn-Winter season, WS = Winter-Spring season. CI = 95% Lower and Upper Confidence Intervals. Note that the first sampling period parameters of Φ and *pent* cannot be obtained given no previous sampling occasion from which to derive an estimate. In fully time dependent models, (i.e. Φ *(t) p(t) pent(t)*), the final Φ and *p,* and the initial *pent* parameters are confounded. Parameter estimates provided are those averaged where the fully time dependent model has been removed. For details of all POPAN models averaged see Table S2.6 in APPENDIX S2.

Models averaged	Sampling period (season)	N_m (95% CI)	N_{super} (95% CI)	Φ (95% CI)	p (95% CI)	*pent* (95% CI)
$\Phi(t)\ p(\bullet)\ pent(t)$ (Rank 1) $\Phi(t)\ p(t)\ pent(t)$ (Rank 2) $\Phi(.)\ p(t)\ pent(t)$ (Rank 3) $\Phi(\bullet)\ p(\bullet)\ pent(t)$ (Rank 4)	1 (AW)	107 (98-116)	129 (117-141)	-	0.80 (0.26-0.98)	-
	2 (WS)			0.50 (0.15-0.84)	0.57 (0.40-0.72)	0.22 (0.06-0.55)^{b}
	3 (AW)			0.96 (0.30-1.00)	0.65 (0.50-0.78)	0.08 (0.01-0.52)
	4 (WS)			0.69 (0.32-0.92)	0.63 (0.50-0.75)	0.03 (0.00-0.52)
	5 (AW)			0.93 (0.38-1.00)	0.56 (0.44-0.70)	0.13 (0.05-0.29)
	6 (WS)			0.45 (0.09-0.88)^{b}	0.58 (0.44-0.71)	0.05 (0.01-0.24)

2.4.4 Goodness-of-fit tests and model validation

GOF tests for the six primary sampling periods conducted in program RELEASE and U-CARE indicated a $\hat{c}$ value of 0.92 and 1.33, respectively; suggesting there is not strong evidence of lack of fit. Results from the Otis et al. (1978) closure test indicated no strong evidence of gains (births or immigration) or losses (deaths or emigration) of individuals from the population for all primary periods in the PCRD analysis (*p*-values > 0.11). GOF tests run in U-CARE showed some suggested difference (*p*-value = 0.05) in expected time of first recapture between ’new’ and ‘old’ individuals seen at least once (TEST 3.SM), but in general showed no strong evidence of ‘‘trap-happy’’ or ‘‘trap-shy’’ behaviour (TEST 2.CT), transience effect (TEST 3.SR) or overall heterogeneity in capture probabilities (Test 2 + 3) (Table S2.7 in APPENDIX S2).

2.4.5 Site fidelity

Mean (± SD) monthly and yearly sighting rates indicated individuals were sighted in three separate months (0.18 ± 0.12) and over two separate years (0.65 ± 0.27) across the study period. The mean P-period sighting rate was 0.43 (± 0.25), indicating that individuals were typically sighted in three out of six P-periods. Site fidelity indices ranged from 0 to 0.5, with a mean value of 0.15 (± 0.12), indicating that most individuals were not captured in all sampling periods from their first capture to their last capture, but had at least three recaptures spread over more than two consecutive P-periods (i.e. 1-2 years).

AHC analysis separated individuals into three main clusters (dissimilarity threshold = 2.5) according to monthly and yearly sighting rates, and site fidelity indices (Fig. 2.4; Table 2.6). The values of CPCC (0.82) and AU *p*-values (0.89-0.97) indicated clusters in the dendrogram are a good representation of the dissimilarities among observations. Group A (n = 30) consisted of individuals sighted in the study area over all three years and a minimum of three separate months (mean = six months; Table 2.6), and were thus considered long-term residents. Group B (n = 32) consisted of individuals sighted in the study area in two separate years and a minimum of two separate months (mean = three months; Table 2.6), and were considered part-time residents. Group C (n = 36) were considered occasional residents, and were comprised of individuals sighted in a single year of the study and a minimum of one separate month (mean = one month; Table 2.6). Group A and B individuals displayed stronger levels of site fidelity to the study area than those in Group C (Table 2.6). This finding was further supported by their primary cluster being derived from the same ‘root’ in the dendrogram tree (AU *p*-value = 0.76; Fig. 2.4).

Of the 54 humpback dolphins identified in the study area in 2010, 34 individuals (65%) were resighted during this study, indicating long-term site fidelity of some individuals to the study area. The majority of individuals (n = 30) were resighted across two or more years of this study, and four individuals were resighted in 2015 only.

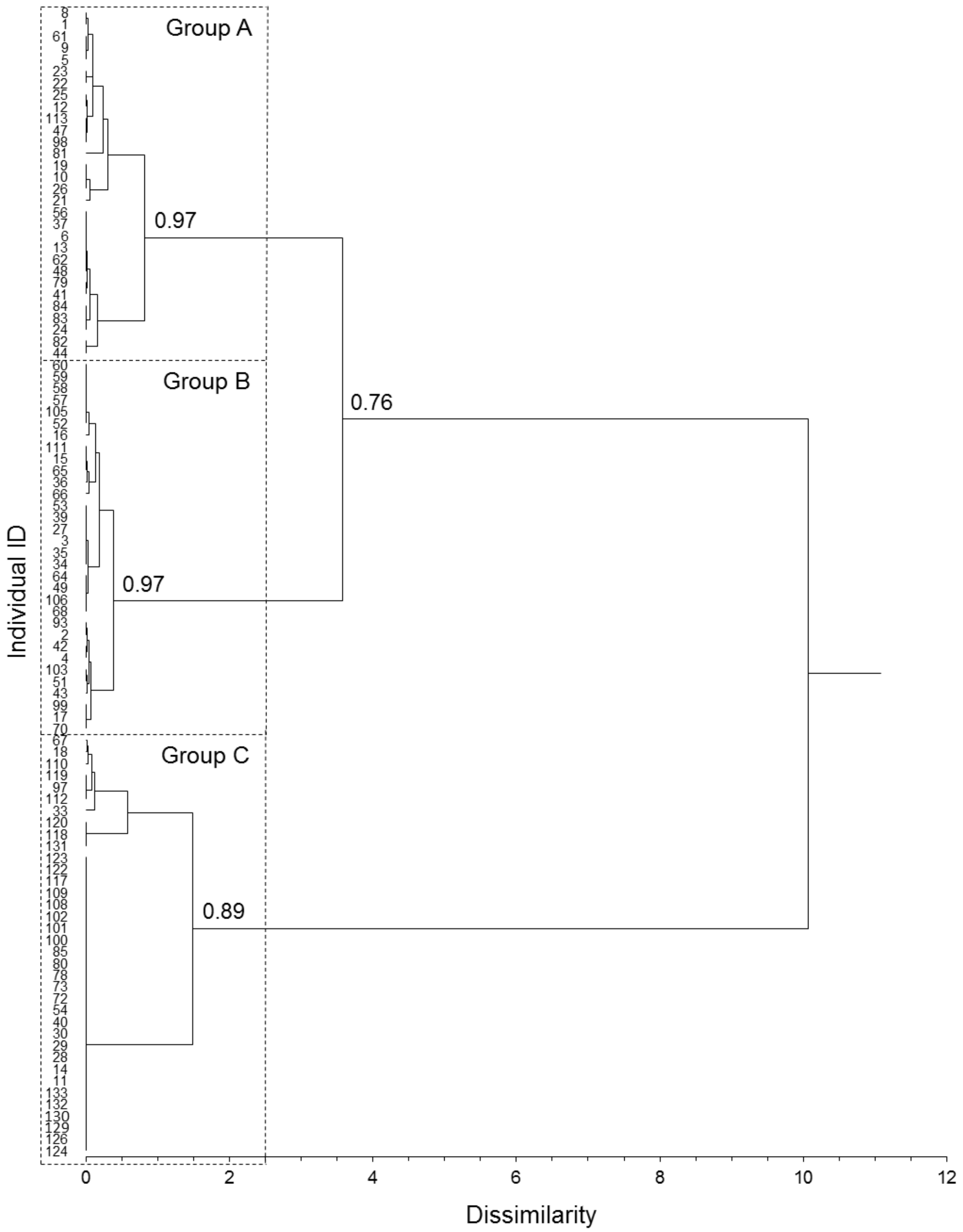

Fig. 2.4. Dendrogram of the agglomerative hierarchical clustering (AHC) analysis separating clusters of Australian humpback dolphins based on three measures of site fidelity: monthly sighting rate, yearly sighting rate, and site fidelity indices. Dashed rectangles indicate three clusters (dissimilarity threshold = 2.5): Group A (long-term residents), Group B (part-time residents) and Group C (occasional residents). Approximately unbiased (AU) probability values for each group and main cluster are indicated on the dendrogram.

Table 2.6. Monthly sighting rate, yearly sighting rate and site fidelity (SF) indices of three clusters (A, B and C; see Fig. 2.4) of Australian humpback dolphins in the North West Cape study area as determined by agglomerative hierarchical clustering (AHC) analysis. SD = standard deviation of mean, CI = 95% Lower and Upper Confidence Intervals.

	Group A (n = 30)					Group B (n = 32)					Group C (n = 36)				
Sighting rate	Mean	SD	Mode	Median	95% CI	Mean	SD	Mode	Median	95% CI	Mean	SD	Mode	Median	95% CI
Monthly	0.32	0.09	0.26	0.32	0.28 – 0.35	0.17	0.05	0.21	0.16	0.16 – 0.19	0.07	0.04	0.05	0.05	0.06 – 0.08
Yearly	1.00	0.00	1.00	1.00	1.00 – 1.00	0.67	0.00	0.67	0.67	0.67 – 0.67	0.33	0.00	0.33	0.33	0.33 – 0.33
SF Index	0.22	0.08	0.20	0.20	0.19 – 0.24	0.16	0.06	0.20	0.16	0.14 – 0.18	0.08	0.16	0.00	0.00	0.03 – 0.13

2.4.6 Residency

LIR began to fall after periods of 1 to 142 days (Fig. 2.5), indicating that some individuals spend very short amounts of time in the study area, while others remain within the study area for most of each yearly survey period. LIR, in general, levelled above zero, suggesting that some animals are residents while others re-immigrate into the study area after long time lags. The most supported model was that of emigration/mortality (QAIC = 2437.8; Fig. 2.5; Table S2.8 in APPENDIX S2). The mean number of humpback dolphins in the study area at any one time, derived from this model, was 57 (95% CI 47-69). The mean residence time of individuals in the study area was 288.4 days (95% CI 162-778), with a low emigration rate of 0.003 (95% CI 0.001-0.006). The model of emigration + reimmigration + mortality (QAIC = 2440.0, ΔQAIC = 2.2) was also well supported (Fig. 2.5; Table S2.8 in APPENDIX S2).

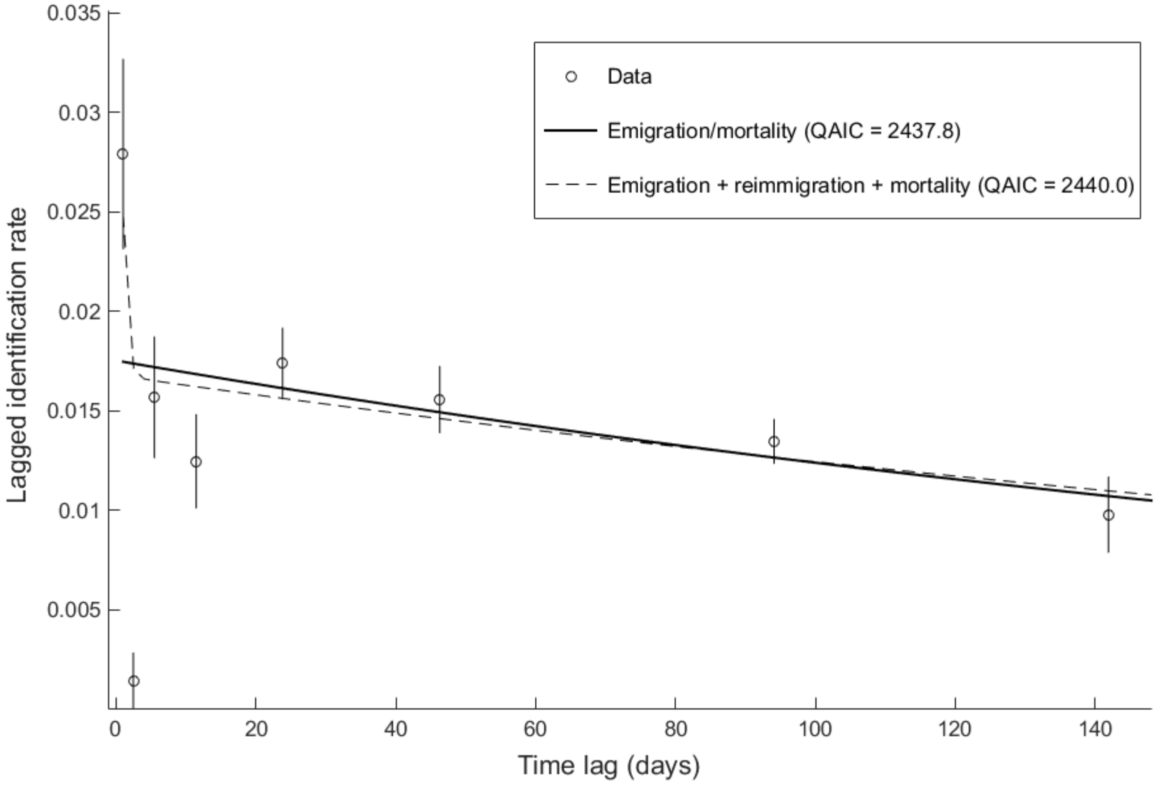

Fig. 2.5. Lagged identification rates (circles) and estimated standard errors (bars) of individual Australian humpback dolphins sighted in the North West Cape study area with the best (emigration/mortality) and second best (emigration + reimmigration + mortality) fitting models of movement. Maximum time lag was set to 177 days (i.e. longest period of time between the first capture and last capture of an individual in any yearly survey period) in order to consider movements within yearly survey periods (and exclude the ca. 6 month time period between these yearly survey periods).

2.5 DISCUSSION

2.5.1 Abundance and density

This study provides the first comprehensive assessment of the population demographics of Australian humpback dolphins inhabiting the waters around the NWC in WA, including the first reported abundance estimate for this species along the ca. 1000 km Pilbara coastline. Population capture-recapture models are powerful techniques for estimating abundance, rates of apparent survival and temporary emigration, but the validity of the estimates depend on the validation of model assumptions underlying this methodology. We acknowledge there was difficulty in precisely quantifying the survival and migration processes, likely due to the sensitivity of PCRD to low-detection probabilities, data-sparseness, transience, and individual heterogeneity. Despite these limitations, we believe our estimates are supported by the amount of data that we have (in addition to being backed by the GOF tests, and that the assumptions of the PCRD and POPAN mark–recapture models were satisfied (S2.3 in APPENDIX S2).

About 60 to 100 animals used the NWC study area at any one time, with a total of ca. 129 individuals (95% CI 117-141 individuals) using the area over the three-year study. These estimates are broadly comparable to those reported for other humpback dolphin populations across northern Australia, which average 54 to 89 individuals and 0.10 to 0.19 individuals/km^2 (see reviews in Brown et al. 2016b, Parra & Cagnazzi 2016). At 0.90 to 1.09 individuals/km^2, the NWC represents the highest density recorded for this species. This high density, together with the high levels of site fidelity and residence patterns observed, indicates that the NWC represents an important habitat towards the south-western limit of this species' range.

Abundance estimates on the NWC tended to be slightly higher during the Autumn-Winter (P1, P3, P5) than the Winter-Spring (P2, P4, P6) sampling periods. This variation in abundance suggests some seasonality in movement in and out of the study area. The influx of individuals into the study area during the Autumn-Winter periods is supported by our findings of Markovian temporary emigration from PCRD analysis, with 50% return rate of temporary emigrants, and marginally higher probability of entry (*pent*) values during Autumn-Winter from POPAN models. This result suggests that the NWC study population is open to emigration/immigration, and that the NWC study area likely represents a portion of the home range of humpback dolphins in this region. It seems likely that the full extent of the home range of individuals in this population extends further into the Exmouth Gulf and Ningaloo Reef regions, given that representative ranges of humpback dolphins elsewhere range from 190 to 325 km^2 (Parra et al. 2006a, Cagnazzi et al. 2011) and that individually-identified humpback dolphins seen in our 130 km^2 study area were also were sighted opportunistically beyond that region (Hunt, unpub. data). Study areas typically cover a subset of inshore dolphins' home ranges; some individuals will have large parts of their home range covered within the study area, and some will be on the peripheral of the study area. These ranges may vary temporally, and be influenced by ecological and social factors (e.g. Ballance 1992, Sprogis et al. 2016b). Future capture-recapture studies including simultaneous surveys inside and outside the NWC study area, coupled with genetic analyses and multi-state models (Brownie et al. 1993), could be employed to estimate movement probabilities between areas, individual home ranges, and better define population boundaries and population structure.

2.5.2 Apparent survival and temporary emigration

Survival is a key demographic process, but is difficult to estimate from capture-recapture data, given that mortality and permanent emigration can be confounded (Pledger et al. 2003). This difficulty is amplified when dealing with short study periods relative to the subject's longevity (in this instance, only a few years for a species that may live to > 50 years). The PCRD apparent survival estimates reported here for humpback dolphins (0.86-0.97) are comparable to those reported for other coastal delphinids both around Australia (e.g. Nicholson et al. 2012, Palmer et al. 2015, Sprogis et al. 2016a, Brooks et al. 2017) and globally. This estimate suggests low levels of permanent emigration and/or mortality, and high levels of site fidelity and residency of the local population over the study period. Considering the relatively small study area, the variable POPAN apparent survival rates reported are likely a result of movement patterns (e.g. "transient" animals that are sighted and then never, or infrequently, seen again; Silva et al. 2009), and do not reflect differences in true survival (see Brooks & Pollock 2015, Palmer et al. 2015).

Temporary emigration of humpback dolphins from the study area seems to follow a Markovian model, indicating it was dependent on animals being absent or present in the previous sampling season. The probability of temporary emigration for dolphins that had been absent in a previous season was higher than the temporary emigration rates of dolphins that were present in the previous season, suggesting that a high proportion (30 to 50 %) of individual dolphins return to the study area after being absent for a season. The high probability ($1-\gamma'' = 0.99$) of animals being present in the study area in Autumn-Winter if they were present in Winter-Spring, despite there being a ca. six-month Summer-Autumn period in between (i.e. November to March), suggests dolphins may remain around the NWC during the Summer-Autumn period. Year-round residency with temporary movement in and out of the study area is suspected for humpback dolphins around the NWC based on opportunistic sightings (Hunt, unpub. data), and studies of this species in eastern Australia (Parra et al. 2006a, Cagnazzi 2011, Cagnazzi et al. 2011). Future studies including surveys over the Summer-Autumn period are needed to confirm year-round residency of this population at the NWC.

Despite the inability of GOF tests to detect heterogeneity, transience and trap-behaviour responses, we note that there was considerable support for mark-recapture models that included heterogeneity. However, data sparseness prevented us from including these models in our model-averaging set. Therefore, the predictable consequence of not accounting for individual heterogeneity is a slight negative-bias in abundance estimates (Carothers 1973, Burnham & Overton 1978, Rankin et al. 2016). Given our data, this is justified by the classic “bias-variance” trade-off in model-selection. By selecting simple models, we deliberately favour slightly-biased estimates that are low-variance, rather than the unbiased, high-variance estimates from more complex models (which suffer singularities and boundary-value estimates). Thus our abundance estimates may be slightly downward-biased as a result of ignoring individual heterogeneity, but are more likely to be closer to the truth than the wildly-varying estimates from the over-parameterised mixture-models. Our estimates represent a comprehensive attempt at better understanding the population demographics of humpback dolphins on the NWC. Future studies should prioritise: (1) increasing the number of resightings and the effective capture probabilities at the study-design through a targeted increase in survey effort (e.g. use of two boats to simultaneously cover the study area), or (2) using recently developed individual-heterogeneity Bayesian models to circumvent MLE issues with model fitting, such as parameter singularities (albeit, with more injection of prior information; Rankin et al. 2016), and (3) better accounting for sub-populations with different site-fidelity (as per our cluster analysis).

Sparse data have another immediate consequence for temporary-migration models, in that there is an almost unavoidable correlation between survival and migration parameters. This is particularly true when effective detection probabilities are low within primary sampling periods. These correlations can manifest as boundary-value parameter estimates (i.e. 0 or 1) and singularities, and very wide 95% CIs (Rankin et al. 2016). In this study, wide CIs are evident for apparent survival and some temporary emigration estimates (Tables 2.3 & 2.4). These are inherent issues of temporary-migration models, such that one cannot effectively separate individuals remaining in the 'unobservable state' and death, especially under low capture probabilities (Kendall et al. 1995, Rankin et al. 2016). Limitations are therefore placed on our ability to interpret survival estimates under sparse data and low-detection probabilities (Bailey et al. 2010). Despite these limitations, we assert that our PCRD models provide evidence of relatively high levels of site fidelity and regular movement in and out of the area for humpback dolphins in the NWC population. This was well supported by our site fidelity and residence analysis.

2.5.3 Site fidelity and residency

Overall, humpback dolphins inhabiting the NWC showed high levels of site fidelity and residency, further emphasizing the importance of this area for this population. Most individuals identified were resighted on multiple occasions across all months and years surveyed. Two-thirds (65%) of the individuals identified in 2010 (Brown et al. 2012) were resighted during this study. The site fidelity groups identified from agglomerative hierarchical clustering indicated individual variability in site fidelity, with the majority of individuals (63%, sighted in two or more years) considered long-term and part-time residents, and some occasional residents. Individual variability in site fidelity has also been found in other Australian humpback dolphin populations (Parra et al. 2006a, Cagnazzi 2011, Cagnazzi et al. 2011), as well as in other humpback dolphin species elsewhere (e.g. Karczmarski et al. 1999, Stensland et al. 2006, Xu et al. 2012).

Site fidelity patterns are largely influenced by resource availability and predation risks (Greenwood 1980, Switzer 1993). Two-thirds of the study area is within the boundaries of NMP, with the majority (86%) of humpback dolphin sightings occurring within the MPA (Hunt, unpub. data). We hypothesise that the predominant high site fidelity patterns to the NWC may be driven by high-quality, heterogeneous and productive habitat within the MPA. A total of six sanctuary zones (no fishing zones) are within the boundaries of the MPA in the study area (see DPaW DoF 2014). Fitzpatrick et al. (2015) found that, within NMP, fish assemblages at sanctuary zones had higher biomass and abundance than at sites where fishing is permitted. Given that protected areas in general can increase overall abundance and biomass of fish assemblages, and that humpback dolphins are thought to be opportunistic feeders (Parra & Jedensjö 2014), consistent prey availability may be influencing regular use of NMP by humpback dolphins, compared to the adjacent (unprotected) Exmouth Gulf. Tiger sharks (*Galeocerdo cuvier*) and white sharks (*Carcharodon carcharias*) are known to occur in the NWC region (Hunt, pers. obs.; Fitzpatrick et al. 2006). These sharks are known to prey on dolphins (Heithaus 2001) and likely pose predation risks to humpback dolphins in this region. Future studies on seasonality in prey and predator abundance and biomass (e.g. Heithaus & Dill 2006, Fearnbach et al. 2011, McCluskey et al. 2016) and sociality (e.g. Smith et al. 2016) are needed to determine their influence on humpback dolphin site fidelity and abundance patterns.

Evidence of Markovian temporary emigration suggests that dolphins do not reside permanently in the study area, but move in and out of the study area regularly. Modelling of sighting patterns support this assertion, with data supporting movement models characterised by emigration/mortality, and emigration + reimmigration + mortality. Similar movement patterns were observed for humpback dolphins in Cleveland Bay, northern Queensland (Parra et al. 2006a). The mortality aspect of the lagged identification rate movement models may be driven by permanent emigration and/or transients, which corresponds to the wide CIs and variable values in our estimates of apparent survival rates. It may also be indicative of a larger temporal scale (years) of temporary emigration, which is supported by the identification of individuals in 2015 that were first sighted in 2010, but not sighted in 2013 or 2014. This evidence of long-term site fidelity further supports the NWC as important habitat for humpback dolphins.

2.5.4 Implications for conservation and management

The high density, site fidelity and residency of humpback dolphins in our study area highlight the importance of the NWC to this endemic, poorly known species of conservation concern. Reviews of available data from across their range suggest that density is generally lower elsewhere, considerably so in most cases (Brown et al. 2016b, Parra & Cagnazzi 2016), suggesting this NWC population is of high conservation value. For example, less than 20 individually identifiable humpback dolphins were recorded in each of five, ca. 130 km^2 study sites across the adjacent Kimberley region of WA (Brown et al. 2016b).

The identification of a sizeable humpback dolphin population within a MPA offers two potential benefits for this species' conservation: (1) a regulatory management framework on which to base conservation strategies and the management of human activities with the potential to impact this threatened species, and (2) a logistically and ecologically suitable site for long-term research and monitoring, with the potential to provide important information on this species' life history traits and behavioural ecology. Humpback dolphins are already a recognised value within NMP (CALM & MPRA 2005), but the efficacy of this marine park (and other MPAs) in protecting humpback dolphins (and other marine mammals) is uncertain. Management agencies have a unique opportunity to target research and conservation objectives of a threatened species within this MPA, and to use the knowledge gained to better manage and protect humpback dolphin populations outside MPAs.

Although the NWC area remains relatively undeveloped to date, its proximity to ongoing petroleum interests in the region means that there is potential for it to be affected by exploration and coastal development (Hanf et al. 2016). The cumulative impact of activities associated with exploration and coastal development (e.g. seismic surveys, dredging, pile driving, vessel traffic, and pollution) have been recognised as major threats to this species (Parra & Cagnazzi 2016). The methods presented in the present study provide a methodological framework that should be used by those conducting future environmental impact assessments. Our results provide a robust demographic baseline of inshore delphinids on which to base environmental impact decisions, and a strong platform for the design and implementation of Before-After-Control-Impact studies. Specifically, the NWC study area can serve as a quasi-control site, and we emphasise the importance of surveying adjacent areas to better understand populations that do not occur in protected areas and may be subject to the cumulative pressures associated with future coastal development. Through the development of long-term studies, we can gain a more complete understanding of Australian humpback dolphin population dynamics as a basis for their future management in Australian waters.

CHAPTER 3: IDENTIFYING PRIORITY HABITAT FOR CONSERVATION AND MANAGEMENT OF AUSTRALIAN HUMPBACK DOLPHINS WITHIN A MARINE PROTECTED AREA

3.1 ABSTRACT

Increasing human activities along the coast has amplified the extinction risk of inshore delphinids. Despite some populations occurring within large marine protected areas (MPAs), a comprehensive understanding of their distribution and habitat relationships therein is lacking, preventing informed prioritisation and selection of areas for their conservation. In this study, we used an ensemble species distribution modelling approach; combining results of six modelling algorithms to identify areas of high probability of Australian humpback dolphin occurrence in the waters of northern Ningaloo Marine Park (NMP) in north-western Australia. Model outputs were based on sighting data collected during systematic, boat-based surveys between May 2013 and October 2015, and in relation to a variety of ecogeographic variables. Water depth and distance to coast were identified as the most important variables influencing dolphin presence, with dolphins showing a preference for shallow waters (5-15 m) less than 2 km from the coast. The location of areas of high dolphin occurrence throughout the majority of the coastal region of the NMP study area highlight the importance of shallow, coastal waters for Australian humpback dolphins. Areas of high probability (> 0.6) of dolphin occurrence were poorly represented in sanctuary zones (no-take zones), with over 90% of them occurring in multiple use areas, where extractive human activities are permitted. This spatial mismatch emphasises the need for future spatial planning and marine park management plan reviews to consider the preferred habitats identified here as priority areas for conservation of this Vulnerable species.

3.2 INTRODUCTION

Coastal marine environments are most heavily impacted by anthropogenic activities (Halpern et al. 2008). As a result, those species that reside, migrate, forage, or breed along the coast, particularly long-lived, slow-reproducing species, are becoming increasingly endangered (Reeves et al. 2003, Wallace et al. 2011, Davidson et al. 2012, Dulvy et al. 2014). Small odontocetes found in coastal and riverine habitats are examples of such vulnerability, with several species currently under threat (Slooten & Davies 2012, Cagnazzi et al. 2013b, Parra & Cagnazzi 2016) and others already extinct (Nichols et al. 2007, Turvey et al. 2007), or on the brink of extinction (Taylor et al. 2017) as a result of human activities. Marine protected areas (MPAs) can be an effective tool for protecting threatened marine species, particularly if their zoning includes large no-take areas (i.e. areas closed to extractive activities) of highly suitable habitat for target species (Gormley et al. 2012, Edgar et al. 2014). Considering marine mammals' vulnerability and role as umbrella species, the identification of important marine mammal habitat is key for their conservation, but also has the potential to contribute towards the protection of broader ecosystem communities and support the delineation of no-take zones within MPA's (Hoyt 2011, di Sciara et al. 2016). However, ensuring the efficacy of such protected areas requires a comprehensive understanding of species distribution and habitat relationships therein (Gregr et al. 2013, Guisan et al. 2013), which is lacking for several existing protected areas (Hooker et al. 2011).

Lack of spatially explicit information on species distributions and habitat preferences can compromise the protection of marine threatened species, even when the target species occurs within designated MPAs (Dryden et al. 2008, Cleguer et al. 2015, Oh et al. 2017). Although the implementation of MPAs has grown exponentially since the 1960s (Worm 2017); only a small proportion contain no-take zones, and overall the global tendency is for MPAs to be located in remote or unpromising areas for extractive activities, which has led to questioning of their effectiveness for conservation (Wood et al. 2008, Devillers et al. 2015). The north-west marine region of Western Australia (WA) is home to several threatened marine megafauna species and Australia's largest fringing reef in Ningaloo Marine Park (NMP). The NMP is a multiple-use MPA part of the Ningaloo Coast World Heritage Area that was proclaimed based on its exceptional marine biodiversity and habitat for threatened species, including a myriad of marine megafauna, many of which have been recognised as ecological values (CALM & MPRA 2005, UNESCO 2011). However, our understanding of the distribution and space use of most of these marine megafauna, including threatened species such as the recently described Australian humpback dolphin (*Sousa sahulensis*), remains limited, hampering conservation and management efforts (Hanf et al. 2016).

The Australian humpback dolphin (hereafter "humpback dolphin") is endemic to shallow (typically < 30 m) coastal waters of tropical northern Australia and southern Papua New Guinea (Jefferson & Rosenbaum 2014). Ecological studies in selected areas throughout the Australian range of humpback dolphins indicate that populations are small (typically 50 to 150 individuals; Parra et al. 2006a, Cagnazzi et al. 2011, Palmer et al. 2015, Brown et al. 2016b, Brooks et al. 2017, Chapter 2/Hunt et al. 2017), with limited gene flow between populations (Cagnazzi et al. 2011, Brown et al. 2014), and relatively small home ranges (< 300 km^2; Parra et al. 2006a, Cagnazzi et al. 2011). The IUCN Red List of Threatened Species recently (December 2017) listed the Australian humpback dolphin as 'Vulnerable' (Parra et al. 2017) due to the species' small population sizes and cumulative exposure to human activities (Parra & Cagnazzi 2016).

MPAs cover a third of Australian humpback dolphins inferred distribution[1] in WA, but the efficacy of these reserves in protecting local cetacean populations is unknown (Hanf et al. 2016). The North West Cape (NWC), located in the northern NMP (Fig. 3.1), supports the highest density of humpback dolphins (one dolphin per km^2) recorded to date in Australia (Chapter 2/Hunt et al. 2017). This population (ca. 130 individuals) is characterised by high levels of site fidelity and residency, with some seasonality of movement in and out of the study area (Chapter 2/Hunt et al. 2017). Despite the apparent importance of this area for humpback dolphins in WA, our understanding of their habitat use in this region is limited. Species distribution models (SDMs, presence-only) for this species using opportunistic data collected during dugong surveys in the western Pilbara, north and east of the NMP, showed a potential preference for intertidal areas, however, the models were limited by a low sample size and lack of environmental predictor data (Hanf 2015).

Australian humpback dolphins are a recognised ecological value of many MPAs in WA, including the NMP (CALM & MPRA 2005). In light of increasing anthropogenic activities across their range in WA, a better understanding of their distribution and habitat use is needed for robust environmental impact assessments, and the effective implementation and management of protected areas for their conservation (Allen et al. 2012, Bejder et al. 2012, Hanf et al. 2016). In

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[1] Inferred distribution is from the coastline and islands to the 30 m depth contour (see Parra & Cagnazzi, 2016)

this study, we used an ensemble modelling approach (i.e. combination of single model predictions; Araújo & New 2007) to model the distribution of humpback dolphins within the northern section of the NMP and identify areas of high probability of dolphin occurrence and preferred habitats. Demographic analysis from Chapter 2/Hunt et al. (2017) indicated that there was some seasonality of movement in and out of the study area, so models have been split temporally into corresponding seasons to determine if these demographic characteristics are reflected in changes in the probability of occurrence and habitat preferences. Furthermore, we evaluate the suitability/efficacy of the current sanctuary zones within the study area (i.e. zones where extractive activities like recreational and commercial fishing, and collecting, are not permitted; CALM & MPRA 2005) for the protection of humpback dolphins.

3.3 MATERIALS AND METHODS

3.3.1 Study site

The study site is within the northern section of the NMP, extending from the northern NMP boundary in Exmouth Gulf around the tip of the NWC, and south to Mangrove Bay (inside lagoon) and South Passage (outside reef; Fig. 3.1). The area is characterised by shallow (< 5 m depth) lagoon waters, with primarily sandy substrate and coral communities within the fringing (sub-tidal) coral reef system (CALM & MPRA 2005, Cassata & Collins 2008). Water depth on the western side of the NWC drops sharply outside the reef crest towards the continental shelf, with maximum tidal ranges extending up to 2.5 m.

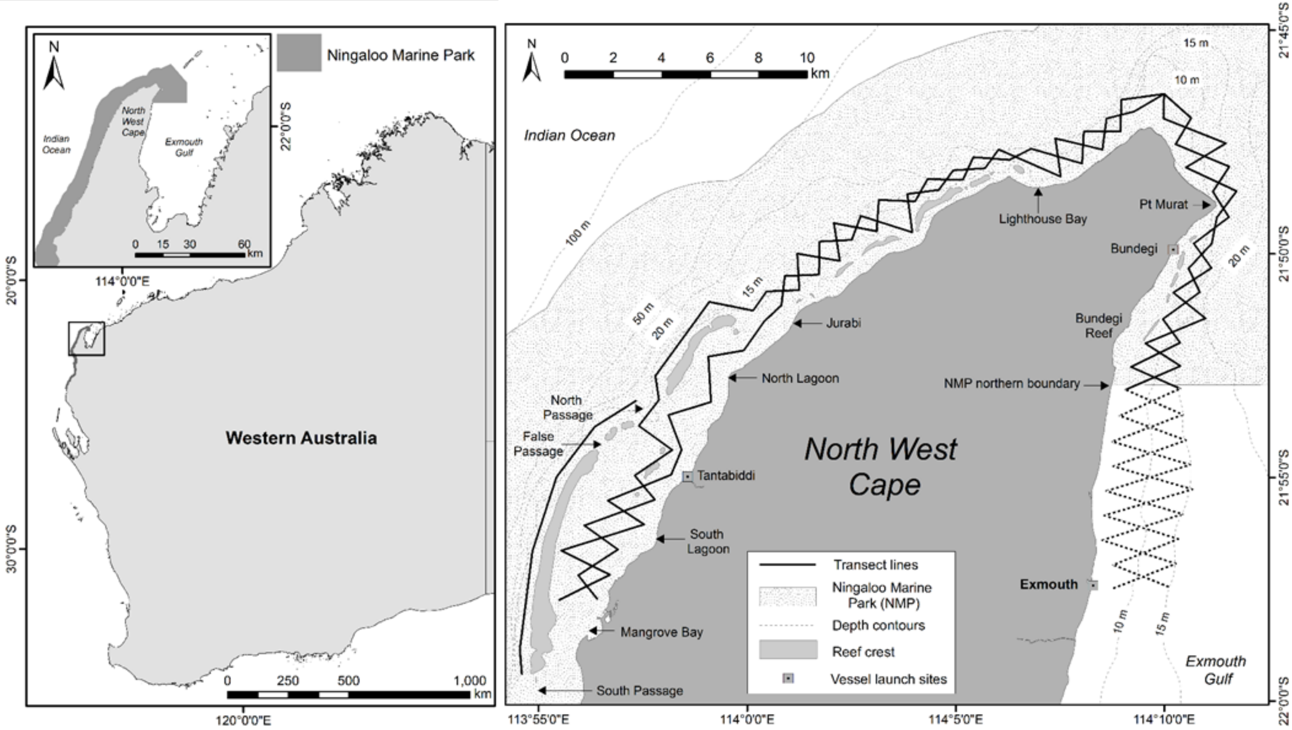


Fig. 3.1. Left: Western Australia, indicating extent of Ningaloo Marine Park and location of North West Cape (NWC). Right: NWC study site, including northern Ningaloo Marine Park (NMP) boundary, location names, depth contours, vessel launch sites (Tantabiddi, Bundegi, and Exmouth boat ramps) and opposing zig-zag line transect sampling design. Dotted transect lines indicate the area south of the NMP boundary that were excluded from analyses.

3.3.2 Survey design and data collection

Boat-based surveys for humpback dolphins were conducted around the NWC during May to October 2013, April to October 2014 and May to October 2015. Surveys were conducted following a systematic line transect sampling design (2 x 93 km in length, opposing, evenly-spaced zig-zag lines; and 1 x 13 km single line; Fig. 3.1). Only survey effort and dolphin sighting information collected within the boundaries of the NMP (169 sightings out of 193) was considered for species distribution modelling analyses. The area south of the NMP boundary (as indicated by dotted transect lines; Fig. 3.1) was excluded from analysis because spatial data on benthic habitat is not available for the area outside NMP. The NMP study area equated to systematic line transect lengths of 2 x 68 km opposing zig-zag lines, and 1 x 13 km single line (as indicated by bold line in Fig. 3.1). The study area covered approximately 150 km^2 along ca. 50 km of coastline, and extended up to 5 km offshore, encompassing water depths between 1 m and 45 m.

Surveys were conducted on board a 5.6 m research vessel powered by a 100 HP outboard motor at speeds of 10 to 12 km/hr and only in good sighting conditions (Beaufort Sea State ≤ 3 and no rain). Survey effort was continuous from 07:00 to 18:00 h, depending on suitable sighting conditions. A crew of three to five (mode = four) observers searched for dolphins forward of the vessel's beam with the naked eye and 7 x 50 binoculars. Once a school of dolphins was sighted, search effort was suspended and dolphins were approached to within 10 to 30 m to record their GPS location, school size, school age composition (calf, juvenile, adult; as defined in Parra et al. 2006a), and predominant school behaviour (i.e. behavioural state in which more than 50% of the animals in a school are involved, Mann 1999). Schools were defined as dolphins with relatively close spatial cohesion (i.e. each member within 100 m of any other member) involved in similar (often the same) behavioural activities (modified from Connor et al. 1998).

Environmental measurements of water depth and sea surface temperature (SST) were recorded *in situ* at dolphin sighting locations, at the beginning/end point of transects (n = 87, termed 'Transect Environmental Station, or 'TES'), and every 60 min of transect survey effort (termed 'ES', see Fig. S3.1 in APPENDIX S3). Water depth was recorded using the research vessel's depth sounder, and SST was recorded using an Oakton handheld multi-parameter.

3.3.3 Ecogeographic predictor variables

Ecogeographic variables considered in modelling humpback dolphin distribution were either biotic (i.e. benthic habitat type), abiotic (i.e. water depth, slope, seabed complexity, SST, distance to coast, distance to reef crest), or anthropogenic (i.e. distance to sanctuary zone, distance to passage, and distance to boat ramp, which were used as a proxy for human activity) (Table 3.1, Table S3.1 in APPENDIX S3). Previous research indicates that some of these biotic and abiotic ecogeographic variables likely influence dolphin distribution (Redfern et al. 2006). Digital environmental layers of water depth and SST were created and explored using environmental data collected *in situ* at TES, ES and dolphin school sightings (including sightings of Indo-Pacific bottlenose dolphins *Tursiops aduncus*). In deriving digital layers, a mean TES value from each of the 87 fixed locations was obtained for the entire survey period, and by 'season' (see below), where *n* per TES ranged from 2 to 30, total *n* = up to 1,582).

Benthic habitat data covering the entire spatial extent of the study area was obtained through the Western Australian Government Parks and Wildlife Service. This habitat data was derived from the broad scale marine habitat study of the NMP, outlined in Bancroft and Sheridan (2000). Habitat types within the study area included ‘coral reef communities (subtidal)’, ‘subtidal reef (low relief - seaward)’, ‘subtidal reef (low relief - lagoonal)’, ‘coral reef communities (intertidal or shallow/limestone)’, sand, macroalgae (limestone reef), shoreline reef, salt marsh, mangroves, mudflats, and ‘deep water mixed filter feeding and soft bottom communities’ (see Table S3.2 for definitions; Fig. S3.2 in APPENDIX S3). Water depth across the study area was obtained from hyperspectral image (see Kobryn et al. 2013), then cross-checked and validated using a combination of *in situ* measurements of water depth (from TES, ES and dolphin sightings, see above, see also Fig. S3.1 in APPENDIX S3), and bathymetric grids from (Geoscience Australia 2008, 2009) (Table 3.1).

All ecogeographic variables were sampled at a 500 x 500 m grid resolution using ArcMap 10.3.1 in ESRI’s ArcGIS© (ESRI, Redlands, California) and the Universal Transverse Mercator projection Zone 50 South based on the WGS 1984 datum (Fig. S3.3 in APPENDIX S3). This resolution ensured sufficient detail of each variable throughout the study area, and corresponded with the sampled scale of the dolphin presence-absence data (see below). We used the Spatial Analyst extension in ArcMap to calculate the Euclidean distance (the shortest straight line distance) for distance to coast, and the Cost distance tool (the shortest distance factoring in land given the study area wraps around a peninsula) for distance to reef crest, distance to sanctuary zone, distance to boat ramp, and distance to passage (see Table 3.1; Table S3.1 & Fig. S3.3 in APPENDIX S3). SST was calculated by season (see definitions below) using the Ordinary Kriging interpolation tool with a spherical semivariogram model (500 m cell size, 12 point variable search radius size) in the Spatial Analyst extension in ArcMap (see Table 3.1; Table S3.1 & Fig. S3.4 in APPENDIX S3).

3.3.4 Data exploration

Ecogeographic predictor variables considered for SDMs were grouped according to three temporal periods (as per Chapter 2/Hunt et al. 2017): 1) the entire survey period from May 2013 to October 2015 (i.e. an overall SDM, using all fixed predictor variables outlined in Table 3.1); 2) Autumn-Winter season (AW, April to July inclusive), and 3) Winter-Spring (WS, August to October inclusive). For AW and WS seasons, we considered SST in addition to all other fixed predictor variables. The purpose of such seasonal groups is to examine whether the seasonality in humpback dolphin movement patterns observed in Hunt et al. (2017) (Chapter 2) are reflected in changes of probability of occurrence and habitat preferences (i.e. relative strength of predictor variables). Surveys were not conducted during the summer period (i.e. November to March), due to the region being exposed to strong winds and tropical cyclones during this time. Prior to running the SDMs, collinearity (correlation between environmental variables) was investigated in R v3.3.1 (R Core Team 2015) using multi-panel scatterplots, Pearson's correlation coefficient (r) and variance inflation factors (VIFs) for all combinations of variables in the overall and seasonal models (Zuur et al. 2010). Highly correlated variables were identified using the stepwise procedures *vifcor* and *vifstep* in the package '*usdm*' in R (Naimi et al. 2014). Using the *vifcor* procedure, whenever the maximum linear correlation between two variables was greater than the threshold (r = 0.7; Zuur et al. 2010), that variable with the highest VIF is excluded. This step was repeated until no variable remained with an r-value greater than the threshold. Similarly, using *vifstep*, the variable with the highest VIF, and greater than the threshold (VIF = 3; Zuur et al. 2010), was excluded; this step was also repeated until no variable with a VIF greater than the threshold remained (Naimi et al. 2014).

Table 3.1. Summary of ecogeographic predictor variables used in species distribution modelling of Australian humpback dolphins in northern Ningaloo Marine Park. All predictor variables, excluding SST, were considered fixed (i.e. did not vary temporally). For full description of variables see Table S3.1 in APPENDIX S3.

Predictor variable	Variable type	Variable abbreviation	Data source
Benthic habitat type	Biotic (fixed)	Habitat	Habitat categories as outlined in Bancroft and Sheridan (2000). See also Fig. S3.2 and Table S3.2 in APPENDIX S3.
Water depth	Abiotic (fixed)	Depth	Derived from Kobryn et al. (2013), *in situ* measurements of depth (n = 1,467; from TES, ES and dolphin sightings; Fig. S3.1), and bathymetric grids from Geoscience Australia (2008, 2009). See also Fig. S3.3 in APPENDIX S1.
Slope	Abiotic (fixed)	Slope	Derived from the depth layer (see MacLeod 2013). See also Fig. S3.3 in APPENDIX S3.
Seabed complexity	Abiotic (fixed)	Complexity	Derived from calculating the standard deviation of the slope layer (see MacLeod 2013). See also Fig. S3.3 in APPENDIX S3.
Sea surface temperature	Abiotic (temporal)	SST	Derived from *in situ* measurements of SST (n = 405 for AW, and 521 for WS at TES, ES and dolphin sightings; Fig. S3.1). See also Fig. S3.4 in APPENDIX S3.
Distance to coast	Abiotic (fixed)	Dist_coast	Derived using Euclidean distance tool. See also Fig. S3.3 in APPENDIX S3.
Distance to reef crest	Abiotic (fixed)	Dist_reef	Modified from Smallwood et al. (2012) and the Bancroft and Sheridan (2000) 'Coral reef communities (intertidal or shallow/limestone)' layer, and nautical charts and author's knowledge of the study area. Derived using Cost distance tool. See also Fig. S3.3 in in APPENDIX S3.
Distance to sanctuary zone	Anthropogenic (fixed)	Dist_sz	Sanctuary zone polygons in the study area (n = 6) obtained from Western Australian Government Parks and Wildlife Service (see DPaW DoF 2014). Derived using Cost distance tool. See also Fig. S3.2 and Fig S3.3 in APPENDIX S3.
Distance to passage	Anthropogenic (fixed)	Dist_passage	North Passage, False Passage, and South Passage (Fig. 3.1) are well-known 'passages' in the study area. Derived using Cost distance tool. See also Fig S3.3 in APPENDIX S3.
Distance to boat ramp	Anthropogenic (fixed)	Dist_ramp	Tantabiddi and Bundegi boat ramps are established vessel launch sites in the study area (Fig. 3.1). Derived using Cost distance tool. See also Fig S3.3 in APPENDIX S3.

3.3.5 Response variable

The presence-absence of humpback dolphins (schools or single animals) was used as the response variable for ensemble species distribution modelling. The locations of dolphin sightings obtained on survey effort, and the associated survey tracks, were imported into ArcMap, and binary presence-absence grids were prepared for the overall and seasonal periods (AW, WS). Survey coverage was quantified by adding a 250 m buffer either side of each survey track line, which was the average distance to which dolphins could be reliably observed from the boat under a variety of sea conditions (e.g. Zanardo et al. 2017). Survey effort was then quantified by intersecting track lines with the 500 x 500 m gridded area of survey coverage and calculating the length of survey effort track (km) per grid cell (MacLeod 2013). Each 500 x 500 m grid cell was classified as either 1 (dolphin presence) or 0 (dolphin absence), and was also characterised by each of the environmental predictor variables (Table 3.1).

To reduce false absences in SDMs (i.e. a species is considered absent from an area when it may in fact occur in that area; see Gu & Swihart 2004, Barbet-Massin et al. 2010), absence cells were defined based on areas of highest survey effort (Phillips et al. 2009). To determine this, grid cells within the study area were ranked from highest to lowest effort, and cells with the highest survey effort and no dolphin presence (for the overall and seasonal SDMs) were considered most likely to represent true absences and were thus defined as absence cells (as per Zanardo et al. 2017). The total number of absence cells was made equal to the total number of presence cells when considering ensemble SDMs. The survey effort thresholds (converted to m per grid cell) for defining true absences were: 8,727 m for the overall model (highest was 24,274 m); 6,739 m for AW (highest was 11,817 m); and 6,778 m for WS (highest was 17,586 m). Survey effort in presence cells across all SDMs ranged from 0 m to 30,831 m per grid cell.

3.3.6 Ensemble species distribution modelling

Species-habitat relationships are often investigated using correlative models to predict species distributions by combining known occurrence records with digital layers of ecogeographic variables expected to affect the species' distribution (Guisan & Zimmermann 2000). SDMs encompass a variety of modelling algorithms with differences in predictive performance, depending on sample size, data structure (e.g. presence-only, presence-absence, presence/pseudo-absence), and the underlying fitted functions (Guisan & Zimmermann 2000, Elith

& Graham 2009, Marmion et al. 2009). Ensemble modelling (EM) is an approach by which single-model predictions are combined (Araújo & New 2007, Franklin 2010), yielding a higher level of accuracy and less bias than separate, single models (Marmion et al. 2009, Grenouillet et al. 2011, Zanardo et al. 2017). EM approaches have been used across terrestrial species (e.g. Sun 2016), and a variety of marine species (e.g. Oppel et al. 2012, Gårdmark et al. 2013, Pikesley et al. 2015), including coastal dolphins (Pérez-Jorge et al. 2015, Zanardo et al. 2017).

We used an EM approach implemented in the '*biomod2*' R package (Thuiller et al. 2009) to predict the presence-absence of humpback dolphins with respect to the ecogeographic predictor variables (Table 3.1). This approach used six different modelling algorithms under three different modelling methods: two regression methods, generalised additive models (GAMS, Guisan et al. 2002) and generalised boosted models (GBMs, Friedman et al. 2000); two classification methods, classification tree analysis (CTA, De'ath & Fabricius 2000) and flexible discriminant analysis (FDA, Hastie et al. 1994); and two machine learning methods, random forest (RF, Breiman 2001) and maximum entropy (MAXENT, Phillips et al. 2006).

SDMs were developed for the entire survey period and for both the AW and WS seasonal periods, using a binomial error distribution and the logit link function. Data for each SDM was split 75/25% for model calibration and testing, respectively (Thuiller et al. 2009). A total of 60 different statistical models calibrated for each SDM dataset resulted from a 10-fold cross validation process. A randomisation procedure in *biomod2* based on 10 permutation runs was subsequently implemented to assess the importance of the environmental predictor variables (Thuiller et al. 2009). This procedure is independent of the modelling technique, and calculates the correlation between the standard predictions (i.e. fitted values) and predictions where one variable has been randomly permutated. Subsequently, this allows direct comparison between models regardless of the modelling method. The mean correlation coefficient was then used to rank the variables from zero to one; where zero indicates the variable has no influence in the model, and one indicates the variable is most influential in the model (Thuiller et al. 2009).

SDMs that utilise presence-absence data are subject to false positives (predicting species occurrence in areas where the species does not occur) or false negatives (failing to predict species presence where the species does occur) (Franklin 2010). To assess SDM predictive performance and compare individual modelling algorithms, we used the area under the curve (AUC) metric of the receiver operating characteristics plot (Fielding & Bell 1997) calculated in R using *biomod2*. The AUC is a measure of the ratio between the observed presence-absence values and the model predictions; values range from zero to one, with values above 0.5 indicative of models with predictions performing better than what would be expected by chance (Fielding & Bell 1997).

Lastly, we combined the six individual SDMs (modelling algorithms) to obtain an ensemble prediction of dolphin presence across the study area for the overall, and the two seasonal SDM periods (Thuiller et al. 2009). Of the individual models, only those with AUC values above 0.5 were considered, and their contribution to the ensemble model was weighted based on their predictive accuracy (the higher the evaluation score the more weight assigned to the model) (Marmion et al. 2009). Ensemble model outputs were then imported into ArcMap, providing a visual output of probability of species occurrence, where values ranged from zero to one; zero indicating no probability and one indicating a very high probability of dolphin presence. Finally, following Marmion et al. (2009), we used AUC values to compare the performance of the ensemble models with the performance of the individual models in each of the overall and seasonal SDM periods.

3.3.7 Dolphin occurrence and sanctuary zones

To evaluate the relevance of the six current sanctuary zones in the northern NMP for the protection of humpback dolphins, we assessed whether areas of high dolphin occurrence (i.e. > 0.6) fell within sanctuary zones more often than would be expected by chance using a randomisation test in PopTools v3.2.5 (Hood 2011). To do this, we calculated an observed index for each of the overall and seasonal ensemble outputs (i.e. total number of high dolphin occurrence cells that were located within sanctuary zones) and compared this index with a random index (i.e. total number of times high dolphin occurrence cells fell within sanctuary zones as they were randomly distributed across the study area), obtained from 5,000 permutations. The significance (*P*-value ≥ 0.05) was calculated as the proportion the random index that was greater than or equal to the observed index (Manly 2007).

3.4 RESULTS

A total of 238 days (or part thereof) of survey effort, covering approximately 330 h and 3,627 km were completed between May 2013 and October 2015 (Table 3.2, Fig. 3.2). Survey effort varied slightly by season because of variable weather conditions (Table 3.2, Fig. 3.2). We encountered 169 humpback dolphin schools over the study period (Table 3.2, Fig. 3.2).

Table 3.2. Summary of survey effort, number of dolphin schools encountered and number of 500 x 500 m grid cells with dolphin presences used to model dolphin distribution within northern Ningaloo Marine Park between May 2013 and October 2015. Autumn-Winter season refers to April to July (inclusive), and Winter-Spring refers to August to October (inclusive). h = hours.

	Total	Autumn-Winter	Winter-Spring
Survey days (or part thereof)	238	106	132
Survey effort (h)	330	151	179
Survey effort (km)	3,627	1,658	1,969
No. of dolphin schools	169	73	96
No. of grid cells with dolphin presences	130	62	85

3.4.1 Model performance

Collinearity was evident only between distance to reef crest and distance to passage (r = 0.9); thus distance to passage was removed from SDM analysis. Consequently, a total of eight predictor variables were considered in the entire survey period (overall) SDM, and nine predictor variables in each of the two seasonal SDMs (Table 3.3). All single SDMs across all three dataset periods performed better than random models, and the ensemble models performed better than single models (Fig. 3.3). The median AUC for single SDMs across the three dataset periods ranged from 0.71 to 0.75, while AUC of ensemble models ranged from 0.75 to 0.82 (Fig. 3.3). When considering the mean of means across all datasets, water depth was the most important variable predicting humpback dolphin distribution (Table 3.3).

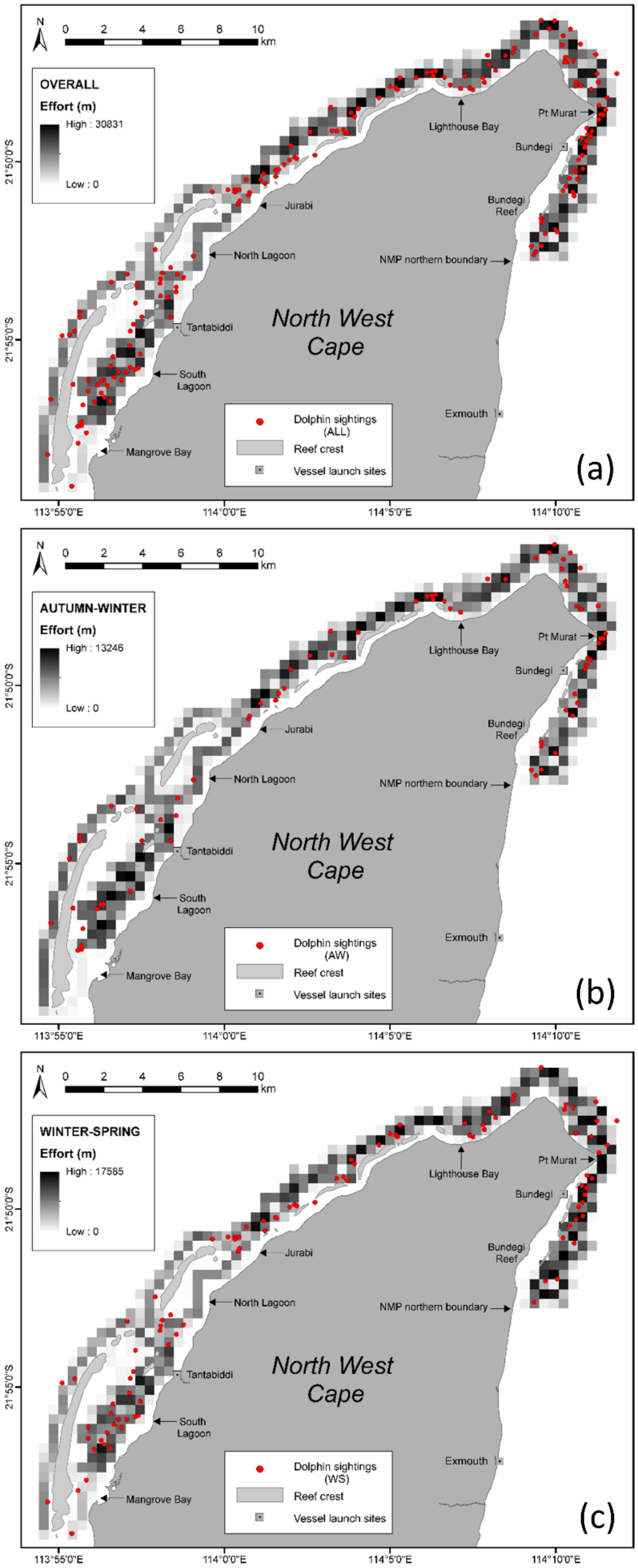


Fig. 3.2. Survey effort and sightings of Australian humpback dolphins during boat-based surveys in northern Ningaloo Marine Park (NMP) during the a) overall survey period (May 2013 – October 2015, n = 169 sightings), b) Autumn-Winter (AW) period (April-July, n = 73 sightings), and c) Winter-Spring (WS) period (August-October, n = 96 sightings). Effort represented as m of survey track lines per 500 x 500 m grid cell. Dolphin sightings represent single or schools of animals.

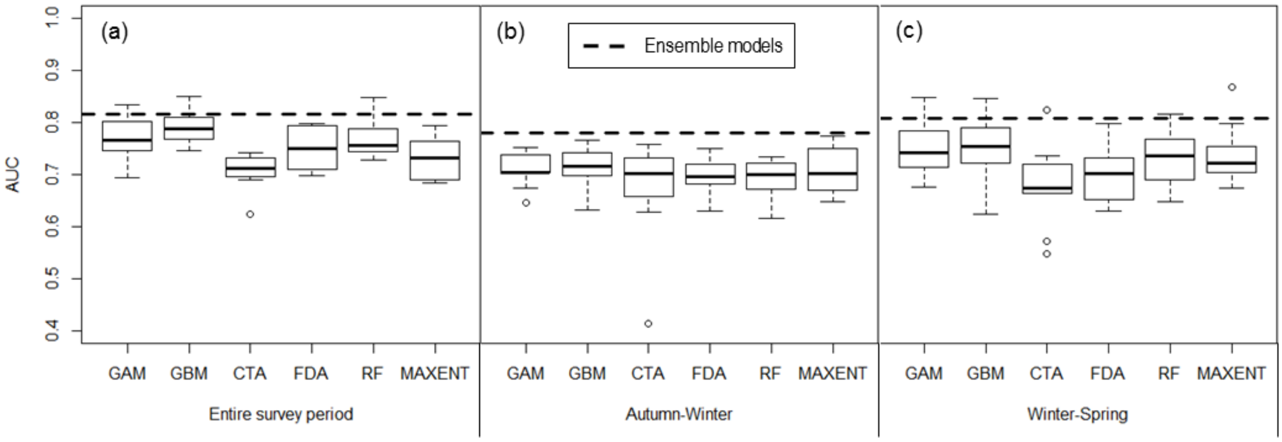


Fig. 3.3. Performance of species distribution models of Australian humpback dolphins in northern Ningaloo Marine Park, Western Australia, built with datasets for a) the entire survey period (May 2013 - October 2015), b) Autumn-Winter period (April-July), and c) Winter-Spring period (August to October). Performance assessed using the AUC (area under the curve of the receiver operating characteristics plot) between the 10 cross-validation runs of each modelling algorithm (box–whisker plot); GAM = generalised additive model, GBM = generalised boosted model, CTA = classification tree analysis, FDA = flexible discriminant analysis, RF = random forest, MAXENT = maximum entropy. Dashed line indicates the predictive performance (AUC) of ensemble models for each of the SDM datasets. AUC values above 0.5 indicate that the model predictions performed better than random.

3.4.2 Dolphin occurrence across the entire survey period

Across all individual SDMs for the overall dataset, water depth and distance to coast were the two most important ecogeographic variables predicting dolphin occurrence, followed by slope and seabed complexity (Table 3.3). The response curves across most individual models indicated that the probability of dolphin occurrence was higher in water depths ranging from 5 to 15 m and less than 2000 m from the coast (Fig. S3.5 in APPENDIX S3). Accordingly, the ensemble model predicted high (> 0.6) dolphin presence in shallow waters (mean ± SD = 10.6 ± 4.6; range 4-20 m;) within 2000 m from the coast between Bundegi Reef in the east and Jurabi in the west, and in the area between North Passage and Tantabiddi, and South Lagoon in the west (Fig. 3.4). Dolphin occurrence generally increased with increasing slope and seabed complexity (Fig. S3.5 in APPENDIX S3). After depth and distance to coast, benthic habitat was the next most important variable in the GAM (Table 3.3), specifically categories of 'coral reef communities (subtidal)', sand, and 'subtidal reef' (both lagoonal and seaward). For habitat type definitions see Table S3.2 in APPENDIX S3.

3.4.3 Dolphin occurrence across seasons

For the AW and WS datasets, across all individual SDMs (with the exception of WS GAM indicating slope), water depth and distance to coast were again the two most important variables (Table 3.3). This was followed, in general, by slope, seabed complexity, distance to reef crest, and benthic habitat (Table 3.3). Across both seasons, the response curves indicated higher probability of dolphin presence in depths 8 to 12 m and at a distance less than 2000 m from the coast (Fig. S3.6 & Fig. S3.7 in APPENDIX S3). The ensemble model for both seasons indicated a consistent high probability of dolphin occurrence in waters less than 2000 m from the coast, from the NMP northern boundary in the east (i.e. edge of study area), around the NWC to Jurabi in the west (Fig. 3.4). High occurrence was also evident in areas around and inshore of North Passage, and the South Lagoon, but was more prominent in WS than in AW (Fig. 3.4). Dolphin presence was generally higher in shallower waters in WS (mean depth ± SD = 9.2 ± 0.9) than in AW (mean depth ± SD = 12.2 ± 2.6). In AW, dolphin presence was generally higher at a slope less than one (Fig. S3.6 in APPENDIX S3), but in WS tended to increase as slope increased (Fig. S3.7 in APPENDIX S3). Dolphin presence in AW increased with seabed complexity, but conversely in WS, decreased with an increase in seabed complexity.

Table 3.3. Importance of ecogeographic predictor variables used in species distribution models (SDMs) of Australian humpback dolphins in northern Ningaloo Marine Park over the entire survey period (May 2013 - October 2015), Autumn-Winter (April-July) and Winter-Spring (August-October). Variable importance is presented as the mean parameter estimate over 10 cross-validation runs of each modelling algorithm, and the mean of means; GAM = generalised additive model, GBM = generalised boosted model, CTA = classification tree analysis, FDA = flexible discriminant analysis, RF = random forest, MAXENT = maximum entropy. Environmental variables of greatest influence are highlighted in **bold**. For variable definitions see Table 3.1 and Table S3.1 in APPENDIX S3.

SDM period	Model	Ecogeographic predictor variables								
		Habitat	Depth	Slope	Complexity	Dist_coast	Dist_ramp	Dist_reef	Dist_sz	SST[1]
Entire	GAM	0.179	**0.412**	0.23	0.116	**0.412**	0.051	0.094	0.019	-
	GBM	0.037	**0.499**	0.129	0.085	0.266	0.02	0.045	0.004	-
	CTA	0.085	0.556	0.328	0.211	**0.566**	0.074	0.141	0.054	-
	FDA	0.051	**0.737**	0.108	0.057	0.184	0.000	0.046	0.003	-
	RF	0.046	**0.239**	0.139	0.091	0.176	0.041	0.055	0.022	-
	MAXENT	0.069	0.326	0.205	0.108	**0.428**	0.093	0.169	0.097	-
	Mean of means	0.078	**0.462**	0.190	0.111	0.339	0.047	0.092	0.033	-
Autumn-Winter	GAM	0.278	0.465	0.089	0.105	**0.477**	0.102	0.242	0.074	0.077
	GBM	0.025	**0.356**	0.179	0.032	0.236	0.064	0.149	0.008	0.071
	CTA	0	0.618	0.141	0.094	**0.667**	0.142	0.104	0.024	0.386
	FDA	0.041	**0.777**	0.103	0.000	0.161	0.000	0.081	0.000	0.028
	RF	0.019	**0.206**	0.124	0.055	0.122	0.081	0.097	0.019	0.056
	MAXENT	0.075	**0.405**	0.089	0.04	0.276	0.02	0.073	0.041	0.013
	Mean of means	0.073	**0.471**	0.121	0.054	0.323	0.068	0.124	0.028	0.105
Winter-Spring	GAM	0.215	0.356	**0.401**	0.279	0.389	0.115	0.186	0.063	0.067
	GBM	0.073	**0.499**	0.152	0.204	0.118	0.056	0.062	0.021	0.082
	CTA	0.118	**0.714**	0.154	0.198	0.209	0.117	0.163	0.058	0.213
	FDA	0.064	**0.797**	0.032	0.073	0.135	0.127	0.137	0.083	0.000
	RF	0.049	**0.280**	0.110	0.109	0.086	0.057	0.042	0.024	0.057
	MAXENT	0.059	**0.400**	0.166	0.161	0.215	0.069	0.152	0.040	0.041
	Mean of means	0.096	**0.508**	0.169	0.171	0.192	0.090	0.124	0.048	0.076

[1] Sea surface temperature (SST) is a temporal variable and not included in the entire survey period SDM dataset.

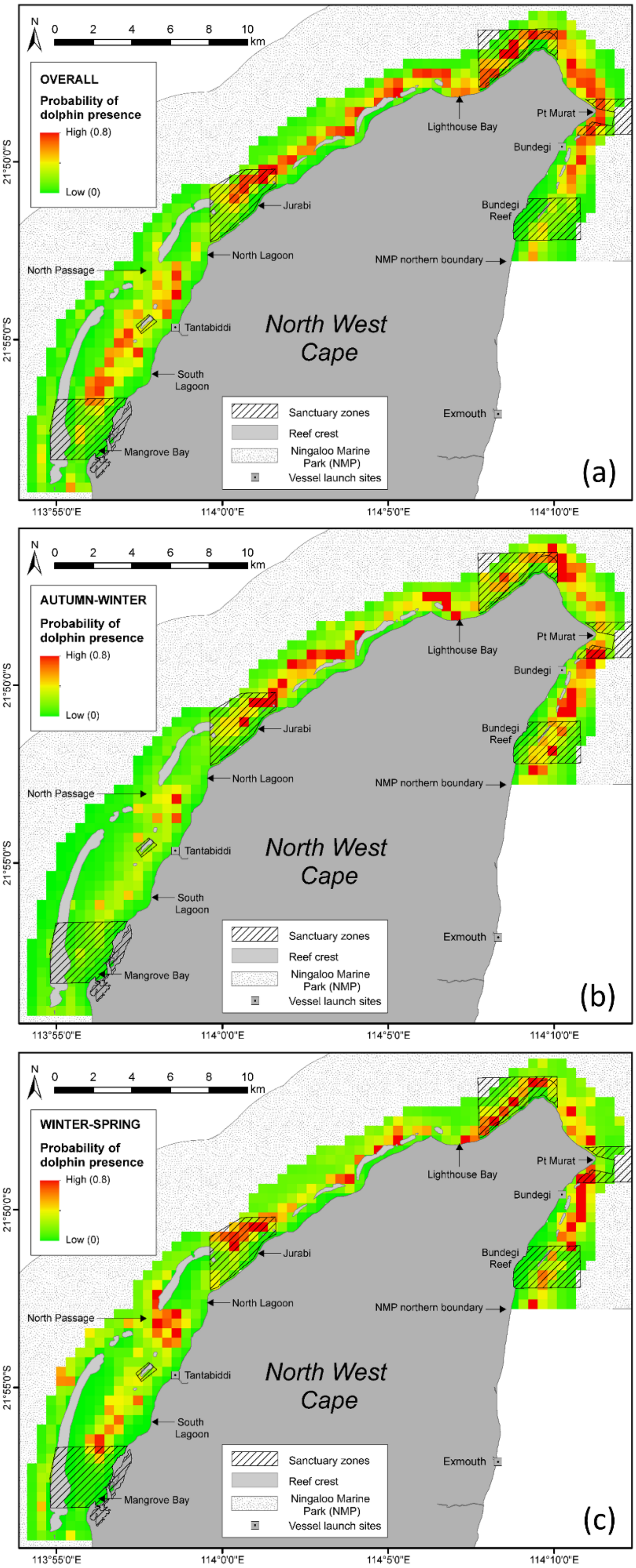


Fig. 3.4. Ensemble model outputs indicating probability of occurrence of Australian humpback dolphins in northern Ningaloo Marine Park (NMP) during the a) overall survey period (May 2013 – October 2015), b) Autumn-Winter period (April-July), and c) Winter-Spring period (August-October). Sanctuary zones and locations are also indicated.

3.4.4 Dolphin occurrence in sanctuary zones

Sanctuary zones made up 26% of the entire study area, but distance to sanctuary zone was not considered an important variable influencing humpback dolphin occurrence (Table 3.3). Overall, the probability of dolphin occurrence inside sanctuary zones was low (combined mean < 0.3; Table 3.4, Fig. 3.4). Dolphin probability of occurrence was generally highest in Jurabi, Lighthouse Bay and Point Murat sanctuary zones across all three dataset periods (mean range = 0.18-0.37) (Table 3.4, Fig. 3.4). The mean probabilities of dolphin occurrence were higher in these three sanctuary zones than outside (outside mean range = 0.14-0.22). Across all dataset periods, sanctuary zones only covered a small proportion of areas of high probability (> 0.6) of dolphin occurrence (range 1-11%; Table 3.5). Randomisation tests indicated that areas of high dolphin occurrence probability did not occur within sanctuary zones more often than would be expected by chance, regardless of dataset periods (*P*-value = 0.25 for overall, 0.84 for AW, and 0.42 for WS).

Table 3.4. Probability of Australian humpback dolphin occurrence in six sanctuary zones of northern Ningaloo Marine Park predicted by ensemble models for the overall survey period (May 2013-October 2015), and seasons Autumn-Winter (April-July) and Winter-Spring (August-October). Values shown indicate mean (± SD), median, and range of occurrence probability for the total number of 500 x 500 m grid cells occupying each sanctuary zone, sanctuary zone grids combined, or grids outside sanctuary zones. See Fig. 3.4 for visual representation of the probability of dolphin occurrence in sanctuary zones.

			Dolphin occurrence probability		
Sanctuary zone	Area (km²)	No. of grid cells	*Overall* (mean ± SD) (median) (range)	*Autumn-Winter* (mean ± SD) (median) (range)	*Winter-Spring* (mean ± SD) (median) (range)
Mangrove Bay	11.4	48	0.13 ± 0.13 0.06 0.04 - 0.58	0.06 ± 0.04 0.05 0.02 - 0.19	0.07 ± 0.10 0.04 0.03 - 0.55
Tantabiddi	0.5	2	0.32 ± 0.04 0.32 0.28 - 0.35	0.12 ± 0.01 0.12 0.11 - 0.13	0.19 ± 0.07 0.14 0.14 - 0.24
Jurabi	7.5	36	0.30 ± 0.23 0.25 0.03 - 0.73	0.18 ± 0.16 0.14 0.02 - 0.58	0.26 ± 0.19 0.21 0.03 - 0.75
Lighthouse Bay	7.6	30	0.34 ± 0.27 0.23 0.03 - 0.76	0.18 ± 0.12 0.14 0.03 - 0.43	0.26 ± 0.21 0.20 0.03 - 0.74
Point Murat	4.7	9	0.37 ± 0.21 0.33 0.07 - 0.70	0.25 ± 0.19 0.17 0.07 - 0.63	0.25 ± 0.26 0.15 0.06 - 0.77
Bundegi Reef	7	32	0.14 ± 0.11 0.14 0.04 - 0.43	0.17 ± 0.13 0.12 0.02 - 0.55	0.16 ± 0.16 0.07 0.03 - 0.70
Combined	38.7	157	0.23 ± 0.21 0.15 0.03 - 0.76	0.15 ± 0.13 0.10 0.02 - 0.63	0.18 ± 0.19 0.09 0.03 - 0.77
Outside	111.8	445	0.22 ± 0.20 0.13 0.04 - 0.74	0.14 ± 0.13 0.09 0.02 - 0.70	0.18 ± 0.15 0.12 0.03-0.80

Table 3.5. Summary of Australian humpback dolphin probability of occurrence throughout the entire study area, and six sanctuary zones in northern Ningaloo Marine Park, for the overall survey period (May 2013-October 2015), and seasons Autumn-Winter (April-July) and Winter-Spring (August-October). Values shown represent the proportion of low (< 0.3), medium (0.31-0.6) and high (> 0.6) occurrence probability in each area and temporal period.

Dolphin occurrence probability	*Overall*		*Autumn-Winter*		*Winter-Spring*	
	Entire study area	Sanctuary zones	Entire study area	Sanctuary zones	Entire study area	Sanctuary zones
Low (< 0.3)	72%	71%	89%	87%	84%	79%
Medium (0.31-0.6)	18%	17%	10%	11%	13%	16%
High (> 0.6)	11%	11%	1%	1%	3%	4%

3.5 DISCUSSION

Ensuring the efficacy of MPAs in protecting mobile marine megafauna requires an understanding of their distribution and habitat preferences. Our study identified shallow waters (5-15 m), close to the coast (< 2 km) as the areas of highest probability of humpback dolphin occurrence within the northern section of the NMP. Nevertheless, the majority of areas of high probability of dolphin occurrence were located outside sanctuary zones. These findings, in combination with the recent and forecast increases in human activities in the marine park (e.g. Rob & Barnes 2016), suggest that the shallow, inshore areas identified here need to be prioritised to better protect this important area for Australian humpback dolphins. We recommend that future spatial planning and marine park management plan reviews consider the preferred habitat areas identified in this study to mitigate potential impacts from increasing human activities for this resident humpback dolphin population.

3.5.1 Ecogeographic predictors of humpback dolphin distribution

Our study, which involved survey effort up to 5 km offshore and in depths to 45 m, supports the preference Australian humpback dolphins have for shallow inshore waters. Although sightings occurred in waters toward the offshore survey limits, they were uncommon. Records throughout the range of humpback dolphins indicate they occur typically in shallow waters < 20 m deep, located close to the mainland and islands (Parra & Cagnazzi 2016). Along the east coast of

Queensland, for example, humpback dolphins occurred primarily in waters of < 15 m depth (Parra et al. 2006b, Cagnazzi 2011, 2013). There are records of humpback dolphins occurring as far as 55 km from the coast and in waters up to 50 m deep, but these were uncommon and likely due to the broad, shallow physiography of the continental shelf, and abundance of shallow reefs, sand flats and continental islands; with dolphins remaining in shallow water and not necessarily far from the nearest coast (i.e. mainland or island; Corkeron et al. 1997, Parra et al. 2004). Similarly in WA, humpback dolphins have been observed some 70 km from the mainland coast at the Montebello Islands Marine Park (Hanf 2015, Raudino et al. 2018), but water depth within and around these islands is shallow (i.e. < 10 m). In the Northern Territory of Australia, humpback dolphins are known to occur within 20 km of major tidal rivers, and as far as 50 km upstream (Palmer et al. 2014). In southern Papua New Guinea (the Kikori Delta), humpback dolphins were sighted in coastal waters < 12 m water depth (Beasley et al. 2016). These observations suggest water depth could be a limiting factor for the distribution of this species (discussed in more detail below). Water depth and distance to coast appear to be strong predictors of the occurrence of other S*ousa* spp., indicating their preference for < 30 m coastal waters (reviewed in Jefferson & Curry 2015, see also summary in Koper et al. 2016).

We note, however, that the majority of boat-based survey effort around Australia, as in this study (see Fig. S3.8 & Fig. S3.9 in APPENDIX S3), has occurred in shallow, coastal waters (e.g. Parra et al. 2006a, Cagnazzi 2011, Palmer 2014, Brown et al. 2016b). There may thus be a bias toward distance to coast being a strong predictor variable. The SDMs applied in this study take into account survey effort, however, and despite multiple years of commercial tour (aerial and vessel platforms) and research operations, there have been few confirmed reports of this species in deeper waters (i.e. > 30 m) within and beyond the NMP.

3.5.2 Drivers of humpback dolphin habitat use

Food availability, predation risk and anthropogenic activities influence habitat use by delphinids (Heithaus & Dill 2002, Benoit-Bird et al. 2013, Pirotta et al. 2015). Australian humpback dolphins feed on a wide variety of fish associated with shallow coastal-estuarine environments (Parra & Jedensjö 2014), and these feeding habits may explain their preference for shallow coastal waters and the shift in humpback dolphin use of the Tantabiddi/South Lagoon area in the WS period (from slightly deeper non-lagoonal waters north of Jurabi in the AW period). Reef structures in the study area are located close to shore and coincide with areas of high dolphin occurrence (e.g. Bundegi Reef to Point Murat, channel from Tantabiddi to North Passage). Benthic habitat type including 'coral reef communities (subtidal)', sand, and 'subtidal reef' (both lagoonal and seaward) showed some importance in the analyses across all three dataset periods. In Queensland, humpback dolphins also showed preferences for reef (coral and fringing) habitat type, as well as seagrass flats, mangroves and dredged channels (Parra 2006, Cagnazzi 2011, 2013). Downie et al. (2013) found that the density of herbivorous fish assemblages in Ningaloo Reef was greater around coral reef structures, and that these assemblages included unicorn fish (*Naso fageni*). Humpback dolphins were observed feeding on unicorn fish (*Naso* spp.) in the study area (Hunt, pers. obs.), so these inshore reefs may serve as important foraging areas for this population.

Fish assemblages at sanctuary zones in NMP have higher biomass and abundance than at sites where fishing is permitted (Fitzpatrick et al. 2015). Hunt et al. (2017) (Chapter 2) hypothesised that consistent prey availability may be influencing regular use of NMP by humpback dolphins. Despite distance to sanctuary zone not being identified as a strong predictor of dolphin occurrence, we cannot rule out their importance for promoting food availability and thus influence on dolphin distribution. Hence, sanctuary zones should be expanded to better encompass identified areas of high dolphin occurrence, and mitigate potential impacts from high recreational fishing pressure (discussed in further detail below).

The prevalence of shark bites on tropical inshore dolphins in the Kimberley region of north-west Australia were among the highest recorded (Smith et al. 2018), suggesting that predation risk is likely a strong influence on habitat use (Heithaus & Dill 2002, Smith et al. 2018). A number of animals in the study population show evidence of shark bites (Hunt, unpub. data) and predation risk may be influencing humpback dolphin habitat use in the northern section of NMP. Humpback dolphin preference for coastal, shallow waters may provide protection from potential predators in the NMP such as tiger sharks and killer whales, which are known to occur in the area (Fitzpatrick et al. 2006, Pitman et al. 2015). Future studies and modelling approaches involving prey availability and predator presence are needed to determine their influence on humpback dolphin occurrence.

Temporal patterns of anthropogenic activity may also be influencing dolphin occurrence (e.g. Pirotta et al. 2015). There was a distinct difference in the use of the North Passage/Tantabiddi to South Lagoon area in WS that was largely absent in AW, where areas of occurrence were more prominent north of Jurabi. This may be attributed to the higher commercial and recreational vessel use in AW that occurs as a result of the whale shark season (March to July), and Easter and school holidays (April and July, respectively). The total number of passengers on whale shark tours in the NMP saw an almost 150% increase from 2007 to 2016 (10,993 to 27,700; Rob & Barnes 2016), indicating substantial vessel traffic during this AW period. The high use of Tantabiddi and South Lagoon areas during AW may result in humpback dolphins using other areas, before returning in WS when human activity is less prevalent. Shifts in habitat use (and numbers) as a result of vessel activity have been reported for dolphin species elsewhere (e.g. Bejder et al. 2006, Lusseau & Bejder 2007, Culloch et al. 2016), although none of these studies quantified prey movements. With the commencement of swim-with humpback whale tours in NMP in 2016 from the August to November period (and continuing in 2017 and 2018; Government of Western Australia 2017, Zaunmayr 2017a), it is unknown what potential impact this persistent vessel activity will have on local humpback dolphin occurrence. Quantifying this vessel activity and its associated acoustic footprint and incorporating it as a predictor variable in future SDMs will help elucidate the influence of vessel traffic on humpback dolphins.

3.5.3 SDM considerations and future studies

The performance of SDMs are influenced by deficiencies and biases in the ecogeographic variables used to build the models (e.g. Best et al. 2012). Ideally, species observations and ecogeographic variables, such as benthic habitat type, are measured at the same spatial and temporal resolution. The benthic habitat spatial layer used in this study (i.e. Bancroft & Sheridan 2000) was developed in 1999, but is currently the only benthic habitat spatial data available for the whole northern NMP. Although benthic habitat was not deemed a primary variable of importance, validation of the different habitat types would have been ideal, but was beyond the scope of this study.

There were some discrepancies between single model outputs in regards to the relative importance of certain ecogeographic variables on humpback dolphin occurrence. The EM approach we used overcame these predictive uncertainties, with all EMs performing better than single models. To this end, we concur with Zanardo et al. (2017) in encouraging the use of EM approaches in future studies assessing cetacean distribution and habitat use.

SDMs of marine mammals offer correlative analyses of observed species−environment associations, but often do not take into account environmental and behavioural processes that are important drivers of animal distributions, such as prey availability, predation risk, intra- and inter-specific interactions, and animal behaviour (Palacios et al. 2013). These factors are generally not included in models of marine mammal distributions because a) they are difficult to sample (e.g. long-term, comprehensive datasets are needed, particularly in the case of inferring influence of oceanographic features), and b) because they do not always offer better model performance. For example, Torres et al. (2008) found that relying on prey distribution data alone was insufficient, and that fine scale models of marine predator habitat selection in coastal habitats will be more successful if environmental variables are used as proxies of both prey and predator distribution. Although behavioural data was collected during the present study, the paucity of data prevented its use for building behaviour-specific models of occurrence (e.g. Hastie et al. 2004), or for using kernel density estimates of behaviours to investigate overlap with areas of high dolphin occurrence (e.g. Zanardo et al. 2017). Further studies focusing on the collection of focal behavioural data will help address how these behavioural processes influence humpback dolphin distribution in the NMP region.

Considering all the above, it would be beneficial to examine and compare dolphin occurrence and habitat preference during the November to March period as humpback dolphin distribution patterns may be different during this time. However, this is a period of strong winds, tropical cyclones, and hot weather conditions (up to 48°C) which may pose difficulties for conducting surveys.

3.5.4 Implications for conservation and management

The almost continuous high areas of occurrence for much of the northern NMP study area corroborate that the NWC is an important habitat for Australian humpback dolphins (Chapter 2/Hunt et al. 2017). However, the majority of areas of high probability of dolphin occurrence (> 90%) identified in this study were outside sanctuary zones, in multiple use areas, where extractive activities such as recreational fishing are allowed. The NMP was initially gazetted in 1987, with the current sanctuary zones gazetted in 2004. The management plan for the NMP (the Plan) has gone beyond its 10-year management period, and under the *Conservation and Land Management Act 1984* is due for review "*as soon as possible*" (CALM & MPRA 2005). The forthcoming management plan review represents an opportunity to utilise the adaptive management framework of the Plan to review current or proposed zoning that takes into consideration the high areas of humpback dolphin occurrence identified here in order to minimise disturbance and/or displacement from human activities.

The areas around Tantabiddi and North Passage are characterised by high probability of dolphin occurrence, and have also been identified as part of a core area of very high recreational fishing pressure in NMP (Mitchell et al. 2018). The impact this overlap may have on dolphins in the short and long-term is unknown and needs to be assessed. Another area of high dolphin occurrence is the Bundegi/Pt Murat area, which coincides with high recreational boat use (CALM & MPRA 2005). Further, areas of medium-high dolphin use around North Passage, Tantabiddi, and South Lagoon align with areas of known boat traffic and high recreational use (Smallwood et al. 2011). Given these spatial overlaps and the potential risk of boat strike and/or disturbance to dolphins, consideration should be given to proclaiming 'go slow' areas, as has been adopted in marine parks in Queensland (see Moreton Bay Marine Park Zoning Plan 2008, Great Sandy Marine Park Zoning Plan 2017). A more immediate, interim management measure could include the development of educational and interpretive material (e.g. signage at boat ramps, key messages in tourism brochures) highlighting the areas identified as important habitat for humpback dolphins and a recommendation to slow down and maintain appropriate distances between vessels and surfacing wildlife.

When proclaiming the Ningaloo Coast in 2011, the World Heritage Committee identified that additional management efforts would be required as tourist numbers increased (UNESCO 2011). Given the evidence of increasing human use within the NMP and the conservation value this marine park can provide for future management of this protected species, we recommend that future marine spatial planning reviews consider increasing the area of current sanctuary zones (or establishes new ones) to better encompass areas of high humpback dolphin occurrence. With evidence of fine-scale habitat use being driven by fish density over vessel density (Pine et al. 2017), changes in prey availability (from increased recreational fishing) in important habitat for NWC humpback dolphins is of concern. We argue that the fishing restrictions imposed by sanctuary zones promotes consistent prey availability for this species, and thus their expansion is warranted. Davies et al. (2016) suggests increases in sanctuary zone areas within NMP (e.g. around Bundegi and Jurabi) are needed to better encompass areas critical for resilience to climate change induced disturbance. Encompassing these areas can likely also have indirect benefits to humpback dolphins within the marine park through preservation of important habitat.

Given their conservation status and the important habitat that the northern NMP represents for Australian humpback dolphins, consideration should be given to proclaiming this region as an Important Marine Mammal Area (IMMA) – *"discrete portions of habitat, important to one or more marine mammal species, which have the potential to be delineated and managed for conservation"* (di Sciara et al. 2016). This would raise the profile of this species for conservation purposes both inside and outside the marine park and also contribute to the conservation of associated coastal species and ecosystems.

CHAPTER 4: ASSOCIATION PATTERNS OF AUSTRALIAN HUMPBACK DOLPHINS REVEAL A DYNAMIC FISSION-FUSION SOCIETY WITH ASSORTATIVE INTERACTIONS

4.1 ABSTRACT

Understanding the individual interactions within a community or population provides valuable insight into its social system, ecology and, ultimately, resilience against external stimuli. Here, we used photo-identification data, generalised affiliation indices and social network techniques to investigate dyadic relationships, assortative interactions and social clustering in a poorly known delphinid, the Australian humpback dolphin (*Sousa sahulensis*). Photo-identification data was collected during boat-based surveys between May 2013 and October 2015 around the North West Cape, Western Australia. Our results indicated a fission-fusion society, characterised by non-random dyadic relationships. Assortative interactions were identified both within and between sex classes, and were higher amongst members of the same sex, indicating same-sex preferred affiliations and evidence of sexual segregation. Assortative interactions by geographic locations were also identified, but there was no evidence of distinct social communities or clusters, or affiliations based on residency status. We noted high residency amongst females. Models of temporal patterns of association demonstrated variable levels of stability, including stable (preferred companionships) as well as fluid (casual acquaintances) associations over time. We also demonstrated some social avoidance. Furthering our understanding of these assortative interactions is important to inform effective conservation and management of this resident population. Our results point to more social complexity than previously recognised for humpback dolphins, and provide the necessary baseline information upon which to assess the influence of increasing human activities on the social structure of this endemic, Vulnerable species.

4.2 INTRODUCTION

Non-random patterns of association have been well documented across group living taxa, including guppies, *Poecilia reticulata* (Croft et al. 2004); sleepy lizards, *Tiliqua rugosa* (Leu et al. 2016); African elephants, *Loxodonta africana* (Wittemyer et al. 2005); chimpanzees, *Pan troglodytes* (Wakefield 2013); and bottlenose dolphins, *Tursiops* spp. (Connor et al. 1992, Lusseau 2003). These non-random social associations amongst individuals may be influenced by different phenotypic (e.g. sex, body size), ecological, or behavioural factors (Croft et al. 2005, Croft et al. 2009). Individuals may form strong social bonds (preferred associates) or show avoidance of conspecifics, but the drivers of these association patterns are poorly understood (Strickland et al. 2017). Some animal societies, despite being non-random in structure, are characterised as fission-fusion, i.e. made up of casual groups of variable size and composition that associate, break-up, and re-associate regularly (Conradt & Roper 2005). Others consist of distinct social communities or units with long-term, stable associations (e.g. Christal et al. 1998). Delphinid societies epitomise this variability: from killer whales, that form long-term stable bonds of matrilineal groups with no dispersal by either sex (Baird & Whitehead 2000); to bottlenose dolphins, that live in both random and non-random fission-fusion societies of varying temporal associations (Connor et al. 2000). Understanding the individual interactions within a population can provide valuable insights into its social system (e.g. transfer of information or behaviours amongst conspecifics; Lusseau & Newman 2004, Allen et al. 2013), ecology (eg. reproductive fitness; Silk et al. 2003, Silk 2007), genetic population structure (e.g. through transfer of genetic material; Chepko-Sade & Halpin 1987, Sugg et al. 1996), and, ultimately, how the population might respond to external stimuli, whether they are of biological, environmental and/or anthropogenic origin (reviewed in Blumstein 2010). Thus, knowledge of social behaviour is an important component in both species ecology and conservation.

The analysis of animal social networks using association indices is perhaps the most common and robust tool to describe animal social structure (Farine & Whitehead 2015). The incorporation of structural factors that may be influencing true association patterns amongst individuals within a population (e.g. gregariousness, spatial home range overlap, and temporal overlap) is important, but few studies on delphinid sociality take these into account (e.g. Frère et al. 2010, Cantor et al. 2012, Titcomb et al. 2015). The recent development of generalised affiliation indices (GAI) has enabled control for these factors in social network analyses (Whitehead & James 2015). Sex, age structure and genetic relatedness are also important variables to consider when analysing social structure, but are often difficult to account for without obtaining biological material via, for example, biopsy sampling (e.g. Krützen et al. 2002, Bilgmann et al. 2007). Collecting biopsy samples from free-ranging small cetaceans can be difficult and, thus, novel, non-invasive methods for sex determination using, for example, visual assessments of dorsal fin characteristics offer a promising alternative (e.g. Rowe & Dawson 2009, Brown et al. 2016a, Wright et al. 2017). The ability to incorporate structural factors and phenotypic traits can provide insight into understanding the complexity evident among delphinid societies.

Factors influencing delphinid social structure include food availability, predation risk, life history, dispersal patterns, kin associations, sex-specific relationships, and human activities (reviewed in Gowans et al. 2007, Möller 2012). Knowledge of the social complexity of this family and the factors influencing it come primarily from long-term studies of bottlenose dolphins, *Tursiops* spp. (e.g. Wells 1991, Connor et al. 2000, Wiszniewski et al. 2009), and killer whales, *Orcinus orca* (e.g. Baird & Whitehead 2000, Parsons et al. 2009). The social structure of lesser-known species, such as humpback dolphins (Genus *Sousa*), on the other hand, is poorly understood. *Sousa* typically occur in small groups of up to 10 individuals, and exhibit a fluid social structure characterised by casual and short-term affiliations (Karczmarski 1999, Jefferson 2000, Jefferson & Karczmarski 2001, Parra et al. 2011, Xu et al. 2012). Some populations of Indo-Pacific humpback dolphins (*Sousa chinensis*), however, form distinct social communities, with evidence of strong, stable, long-term associations (Dungan et al. 2012, Wang et al. 2015, Dungan et al. 2016). Gowans et al. (2007) suggested that *Sousa* social structure is likely driven primarily by resource availability, mating opportunities for males, and the parental needs of nursing females. The extent to which assortative interactions based on phenotypic characteristics (e.g. sex) influence network structure, however, remains largely unexplored in *Sousa*.

Our understanding of Australian humpback dolphin (*Sousa sahulensis,* “humpback dolphin” hereafter) social structure is essentially limited to two studies from eastern Queensland (i.e. Cagnazzi et al. 2011, Parra et al. 2011). These studies showed that individual humpback dolphins have preferred associates, fission-fusion grouping patterns, as well as defined social communities. The presence of non-random associates with temporally loose bonds among humpback dolphins could reflect marked sex differences in association, but the effects of sex-specific relationships on the grouping and association patterns of humpback dolphins is as yet unknown (Parra et al. 2011). Recent research in waters around the North West Cape (NWC), Western Australia (WA), indicated this area represents an important habitat for this species, with dolphins occurring in high density and showing high levels of site fidelity and residency (Chapter 2/Hunt et al. 2017). The characteristics of this population, together with the advent of generalised affiliation indices and non-invasive methods for sex determination, provides an opportunity to better understand the social dynamics of this threatened species.

Here, we use sighting histories of adult humpback dolphins identified around the NWC between 2013 and 2015 to investigate their social structure and assess: association patterns (random/non-random); assortative associations (by sex, geographic location, and residency); social clustering; and temporal stability of associations. Given the findings of previous research (e.g. Parra et al. 2011), we hypothesised that associations amongst individual humpback dolphins would be non-random, with both long-term and casual associations, and, further, that close associations would vary depending on spatial location and sex. Lastly, considering residency clusters identified in Chapter 2/Hunt et al. (2017), we hypothesise that long-term residents would be more closely associated than part-time and occasional residents, given more regular use of the same space and, therefore, a higher chance of associating (e.g. Karczmarski et al. 2005, Frère et al. 2010).

4.3 MATERIALS AND METHODS

4.3.1 Study site and data collection

Western Australia's NWC adjoins the Indian Ocean and Ningaloo Marine Park (NMP) to the west and north, and Exmouth Gulf to the east (Fig. 4.1). Approximately two-thirds of the NWC study area is within the Marine Protected Area (MPA) of NMP (Fig. 4.1). For further details on study site characteristics, see Chapters 2 (Hunt et al. 2017) and 3 (Hunt et al. in review).

Between May 2013 and October 2015, boat-based surveys for humpback dolphins were conducted across the study area and followed a systematic, line transect sampling design (opposing, evenly-spaced zig-zag lines; Fig. 4.1). Once a school of dolphins was sighted, they were approached to record GPS location, school size, school age composition (calf, juvenile, adult), predominant school behaviour (as per Mann 1999), and to collect photo-identification data (Würsig & Jefferson 1990). The three age/body size class categories used in school composition were the same as those used in Chapter 2/Hunt et al. (2017), defined by Parra et al. (2006a), where: 'adults' are about 2 to 3 m long; 'juveniles' are approximately 2/3 the length of an adult, usually swimming in close association with an adult (often beside), but sometimes swimming independently; and 'calves' are ≤ 1/2 the length of an adult with light grey skin colour, in close association with an adult, and swimming regularly beside or slightly behind an adult in 'infant position'. Individual humpback dolphins were identified based on the unique natural marks on their dorsal fins (as per Parra et al. 2006a). All photographs taken were examined and subjected to a strict quality (Q) and distinctiveness (D) grading protocol (modified from Urian et al. 1999, 2015) to minimise misidentification (see S2.1 in APPENDIX S2). Only high quality photographs of distinctly marked individuals were used in social analyses. For full details, see Chapter 2/Hunt et al. (2017).

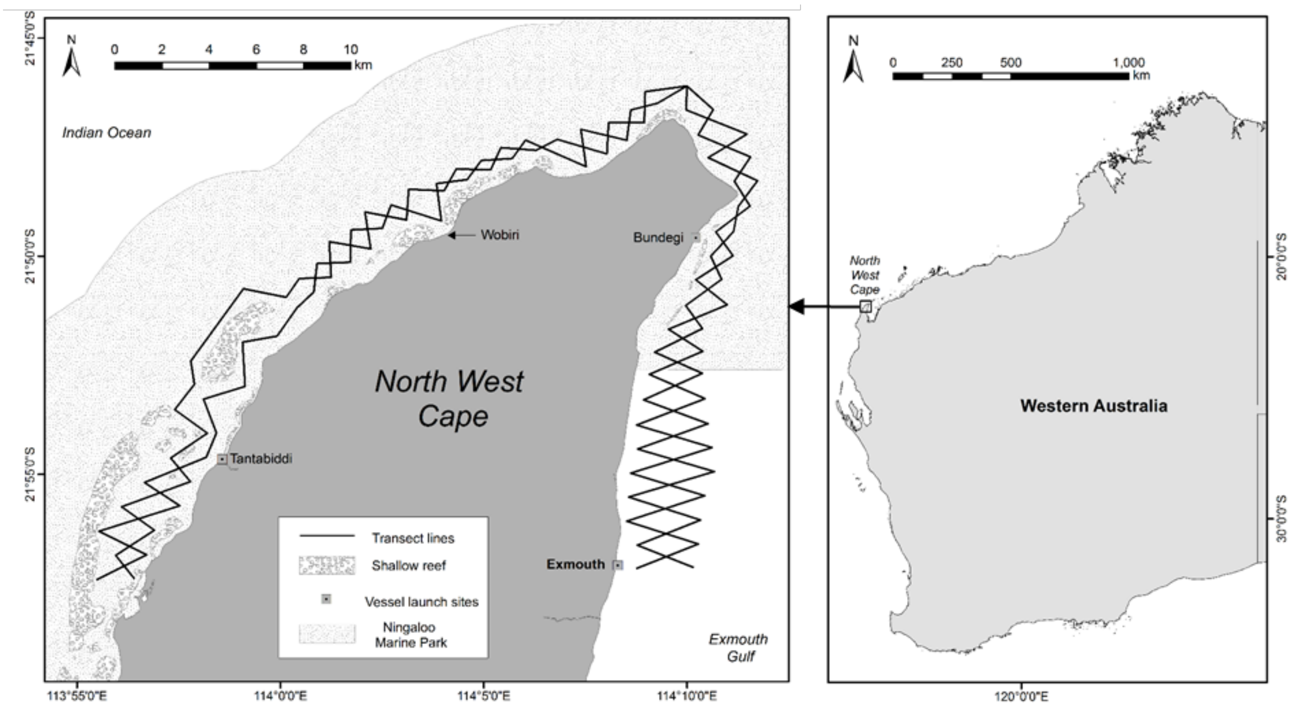


Fig. 4.1. Left: Map of the North West Cape (NWC) study site, including vessel launch sites (Tantabiddi, Bundegi, and Exmouth), opposing zig-zag line transect sampling design (2 x 93 km in length) and extent of northern Ningaloo Marine Park. Right: Map of Western Australia, indicating the location of the NWC.

4.3.2 Sex determination

Sex of individual adult dolphins was determined from one of four methods: 1) molecular analysis from skin samples collected by remote biopsy sampling (e.g. Krützen et al. 2002); 2) visual observation of genital area from high quality photographs; 3) regular association with the same individual calf/juvenile to infer sex of mature females (e.g. Smolker et al. 1992); and 4) logistic regression analyses using spotting and loss of pigmentation (LOP) on the dorsal fin (Brown et al.

2016a; see also section S4.1 in APPENDIX S4). For breakdown of sex determination for the 49 individuals by the above methods, including definitions, see Table 4.1.

Table 4.1. Definitions of methods employed in the sex determination of 49 individual Australian humpback dolphins around the North West Cape, Western Australia.

Method	Definition	Number of females	Number of males	Total individuals
Molecular analysis	Skin samples collected by remote biopsy sampling during opportunistic surveys conducted in 2010 (Allen et al. 2012, Brown et al. 2012). Animals biopsied and sexed from molecular analysis were cross-checked against animals identified in this study using photo-identification protocols described above.	3	5	8
Visual observation	Ventral surface of individual photographed and genital area examined for presence of mammary slits. High-quality photographs of genital area and corresponding individual dorsal fin sequences confirmed match.	1	0	1
Regular association with dependent calf/juvenile	Individuals deemed mature female based on regular sightings with the same identified calf or juvenile in 'infant position' (where 'regular' is defined as > 50% of total individual sightings over entire three-year study period; or, in the case of individuals sighted a total of only five times, a minimum three of those were with the same dependent).	22	0	22
Logistic regression analyses	High-quality images of individual dorsal fins were quantitatively assessed for extent of upper loss of pigmentation (i.e. LOP) and qualitatively assessed based on level of dorsal spotting, as per Brown et al. (2016a). These dorsal fin characteristics were included in a regression model that used a discriminant function to predict the probability that a particular individual is male. For details, see section S4.1 in APPENDIX S4.	13	5	18
	Total	39	10	49

4.3.3 Defining associations and estimating affiliation indices

Note that, unless specified otherwise, all social analyses mentioned herein were calculated in SOCPROG 2.7 (Whitehead 2009). All dolphins sighted within a school were considered associated (Whitehead 2008a). Schools were defined as dolphins with relatively close spatial cohesion (i.e. each member within 100 m of any other member) involved in similar (often the same) behavioural activities (modified from Connor et al. 1998). Only the first sighting of each individual within a school, per day, was used for association analysis. To reduce potential downward bias in association indices, only schools in which ≥ 50% of individuals were identified (based on visually estimated group size) were included in analyses (as per Parra et al. 2011). Only adults sighted on five or more separate days over the entire study period were included in association analyses. We chose this threshold as it approximates the median number of sightings of all individuals identified (see Results) and, thus, minimises the potential for false null associations between pairs of individuals with very low sighting frequencies. Furthermore, fewer than five samples will inherently develop inaccuracies in association indices (Whitehead 2008a); it is comparable to other delphinid association analyses (e.g. Parra et al. 2011, Brown 2016, Chabanne et al. 2017); and it is the minimum required to calculate areas of home range overlap for use in estimation of generalised affiliation indices (GAI, see below). This threshold was also justified through comparison of estimates of social differentiation (*S*), and correlation between true and estimated association indices (*r*) using the likelihood method based on a matrix of associations using half-weight indices (HWI; Cairns & Schwager 1987). *S* is a measure of social complexity amongst individuals in a population and is the coefficient of variation of the true association indices; i.e. the proportion of time dyads (individuals) spend together (Whitehead 2008b). Pearson's correlation coefficient (*r*) is a measure of the quality and power of the data to detect true social complexity (Whitehead 2008b).

An $S \sim 0.2$ indicates that a population is poorly differentiated (i.e. homogenous societies), an $S > 0.5$ indicates well differentiated societies within a population, and an $S > \sim 2$ indicates that a society is extremely differentiated, with varying association strengths between individuals (Whitehead 2009). An *r* value near 1 indicates that the data representation is excellent and has strong power to detect the true social system, an $r \sim 0.8$ indicates a good representation, while $r \sim 0.4$ indicates a moderate representation (Whitehead 2008b). Exploration of individual sighting thresholds (one to ten) revealed that social complexity remained well differentiated regardless of sighting threshold (*S* ranged from 1.0 to 1.2), and the representation of the data remained consistently moderate ($r >$

0.3) (Table S4.2 & Fig. S4.2 in APPENDIX S4). Thus, the chosen five sighting threshold was deemed valid.

The strength of the associations between pairs of individuals (dyads) was estimated using generalised affiliation indices (GAIs; Whitehead & James 2015). GAIs uses a modelling framework to account for structural factors (e.g. gregariousness, spatial and/or temporal overlap, sex) that may be influencing affiliation patterns amongst individuals (Whitehead & James 2015). GAIs are calculated as the residuals of a generalised linear model, where association indices are the dependent variable, and potential predictors of association are the structural factors (Whitehead & James 2015). We considered three predictor structural factors that could be affecting association patterns: gregariousness; spatial home range overlap; and temporal overlap.

Gregariousness is a measure of the tendency of an individual to associate with other individuals (Godde et al. 2013). Areas of spatial home range overlap between individuals were calculated using the '*adehabitatHR*' package (Calenge 2006) in R v 3.3.1 (R Core Team 2015), following the kernel based utilization distribution overlap index method (UDOI) (Fieberg et al. 2005). This UDOI provides a single measure of overlap (based on 95% UD) between two individuals, where values range from zero (no overlap) to one (uniformly distributed and 100% overlap). We adjusted the smoothing factor, *h*, to best account for the shape of the NWC coastline. This involved manually testing different values of *h* (in increments of 100, from 500 to 2,000) by plotting each in ArcMap 10.3 to visually assess which had smooth individual home ranges with minimal to no overlap on land. An *h*-value of 1,000 was deemed the most appropriate for consideration in GAI analyses. Temporal overlap was calculated by considering each austral season as a single sampling period, and whether pairs of individuals were identified during these sampling periods, but not necessarily associated. A total of six seasonal sampling periods were considered (as per Chapter 2/Hunt et al. 2017): three Autumn-Winter (April-July) and three Winter-Spring (August to October). We calculated a matrix of co-occurrence based on the proportion of time that two individuals were seen together in a season. Individuals seen together in all seasons had a value of one, those never observed together in a season had a value of zero, and those with intermediate values corresponded to individuals seen together in some, but not all, seasons. Lastly, we created a matrix of associations based on HWI (Cairns & Schwager 1987), and used multiple regression quadratic assignment procedures (MRQAP) to test the significance (correlation) of each predictor variable on association indices. Those structural predictor variables with a non-significant correlation (i.e. no influence on association) were removed from GAI calculations (Whitehead & James 2015).

4.3.4 Analysis of affiliation patterns and assortative associations as a function of sex, geographic location and residency

Mean GAI and standard deviation of the observed affiliations were estimated for all individuals in the population. We used permutation tests to assess whether individuals (all, and by sex class) associate randomly or have preferred/avoided affiliates (Bejder et al. 1998, Whitehead et al. 2005), and accounted for demographic effects (births, deaths, and migration) by permuting within daily sampling periods (Whitehead 2008a). The number of permutations was increased across multiple tests until the *p*-value stabilised (Bejder et al. 1998). The standard deviation (SD) of the observed associations is expected to be significantly higher ($p < 0.05$) than the permuted dataset if associations occur more often than expected by chance over the sampling period (Whitehead 2009).

To visualise social structure in the form of a social network diagram, we used the spring embedding method in NETDRAW software (v 2.158) (Borgatti 2002). Networks were defined by links representing GAIs (also referred to as "edges") between individuals (also referred to as "nodes"). GAI uses the residuals of the generalised linear model and, therefore, the links amongst individuals can be both positive and negative, creating signed networks (Whitehead & James 2015). We further investigated preferred, casual and avoided companionships in the population by converting raw residuals of the GAIs into deviance residuals, where values greater than 2.0 were considered preferred companions, those between 2.0 and -2.0 casual pairs, and those below -2.0 avoided affiliates (Whitehead 2009, Whitehead & James 2015). Sex-specific affiliations were summarised for females (F) and males (M), and then within sex classes of F-F, M-M, F-M, and M-F. Affiliation rates between and within sex classes were tested for significance using a two-tailed Mantel test (significance of $p < 0.025$ or > 0.975) (Mantel 1967, Schnell et al. 1985, Whitehead 2009).

To investigate the characteristics of the NWC humpback dolphin social network, we calculated the following network metrics for all dyads and for each sex class: strength, clustering coefficient, and affinity. Network strength refers to the sum of all GAIs of any individual with all other individuals and is a measure of gregariousness (Barrat et al. 2004). High strength indicates strong associations with other individuals (Whitehead 2009). The clustering coefficient indicates how well the associates (neighbours) of an individual are associated (Holme et al. 2007) and also the level of structure in a society (Croft et al. 2005). Affinity is a measure of the strength of an individuals' associates (Whitehead 2009), where high affinity is an indication of high associations with other individuals who have high strength. For each network metric, we compared the observed mean with the mean of random values (Lusseau et al. 2008) using 1,000 permutations.

To investigate whether there was any variation in affiliation patterns according to geographic location within the study site, we assigned individuals to a geographic class and tested if affiliation rates between and within classes were significant using a two-tailed Mantel test. To determine the geographic class of each individual, we considered the spatial distribution of sightings and the demarcation in benthic habitat type. Sighting distributions (of all 50 individuals sighted ≥ 5 times) were visually inspected in ArcMap, and using the 'Measure' tool, linear measurements were made (in km) between those dolphin school sightings with the greatest spatial gap (i.e. no sightings in-between). These measurements were then ranked from highest to lowest. We then overlayed these 'spatial gaps' with a spatial benthic habitat type layer (Fig. S3.2 in APPENDIX S3, Bancroft & Sheridan 2000), to determine if these spatial gaps coincided with any benthic habitat differentiation (as has been demonstrated in humpback dolphins; see Cagnazzi et al. 2011). A break in continuous shallow coral reef, delineated by a large (ca. 1 km) diameter area of sand was evident near Wobiri on the north-west side of NWC (Fig. 4.1), and we assigned an East-West border line at Wobiri Beach (Fig. 4.3a). Using the Intersect tool in ArcMap, we split the sightings then into 'East' and 'West', then assigned individuals as either East (where ≥ 90% of an individuals' sightings were to the east of the border line), West (where ≥ 90% of an individuals' sightings were to the west of the border line), or East-West (individuals with sightings on both sides of the border line; Fig. 4.3a).

We explored and compared residency clusters derived from the agglomerative hierarchical clustering analysis in Chapter 2/Hunt et al. 2017 with affiliations amongst all individuals. We cross-checked each of the 50 IDs against the long-term residents (LTR; Group A), part-time residents (PTR; Group B) and occasional residents (OCR; Group C) clusters identified, and then used a two-tailed Mantel test to test for assortative interactions by residency.

4.3.5 Social clustering

We used Newman's modularity (Q) method to assess social clustering within the population (i.e. clusters that have higher association indices between members of the same cluster than expected by chance; Newman 2004, Whitehead 2008a). The eigenvector-based method aims to maximise Q that best assigns clusters and to ascertain communities within a population (Newman 2006).

Modularity values > 0.3 indicate useful division of the population into social clusters (Newman 2004).

4.3.6 Temporal patterns of association

To investigate changes in affiliation rates over time amongst all individuals and by sex class, we estimated standardised lagged association rates (SLARs) and compared these with null association rates (the expected value if individuals were associating at random; Whitehead 1995). SLARs are estimates of the probability that should two individuals, *A* and *B*, associate, then a randomly chosen associate of *B* identified some time lag later will be *A* (Whitehead 1995, 2008a). Standard errors for each SLAR were obtained using the jackknife procedure (Efron & Stein 1981). SLARs were calculated, given that they are the preferred option when not all associations of an individual may be observed within a sampling period (Whitehead 1995, 2008a). All 84 identified individuals were included in the estimation of SLARs, as inclusion of infrequently-sighted individuals (i.e. less than the five sighting threshold used in this study) have no disproportional effect on the analysis of SLARs (Whitehead 2008a). The inclusion of all individuals resulted in an additional 18 females (total of 57), four males (total of 14) and 12 individuals of unknown sex (total of 13) being considered in SLARs.

We compared observed SLARs to expected SLARs from exponential mathematical models of varying temporal stability (Whitehead 2008a). To consider association rates within yearly survey periods (and, hence, exclude the ca. six-month time period between these yearly survey periods), we set a maximum time lag of 177 days for calculation of SLARs. This period was the longest possible time between the first association and last association of any pair of individuals in any yearly survey period. Applying this restriction allowed the models to consider overall association rates across the three years surveyed while removing consideration of association rates between yearly survey periods (aligning with considerations of lagged identification rate calculations from Chapter 2/Hunt et al. 2017). Model selection was based on the Quasi-Akaike Information Criterion (QAIC) value, with the lowest QAIC value representing the temporal stability model with the most support (Whitehead 2007). Models differing by 0 to 2 QAIC (ΔQAIC) from the model with the best fit were also considered supported (Burnham & Anderson 2002).

4.4 RESULTS

A total of 233 survey days (or part thereof) were completed between May to October 2013, April to October 2014 and May to October 2015. A total of 216 humpback dolphin schools were sighted. Out of the 86 distinctive adult individuals identified in Chapter 2/Hunt et al. (2017), 84 were considered for association analyses, given that two of these individuals transitioned to larger than juvenile size over the three-year study (and were, thus, excluded from analyses). Of these 84 adult individuals, 50 individuals, including 39 females, 10 males and one individual of unknown sex (see Table 4.1), were sighted ≥ five times (equating to 196 sightings) and subsequently included in association analyses. Total sightings per individual ranged from one to 30 (mean ± SD = 7.6 ± 6.0, median = 6.5).

4.4.1 Defining associations and estimating affiliation indices

The correlation coefficient of the true and estimated association matrices ($r = 0.35 \pm 0.02$ SE) indicated that the data set has moderate power to detect the true social system; and the coefficient of variation of the true association indices ($S = 1.16 \pm 0.02$ SE) indicated that the study population has a well-differentiated society (Table S4.2 & Fig. S4.2 in APPENDIX S4).

Home range overlap and temporal overlap were significantly correlated with association indices (MRQAP tests; Table 4.2) and were, therefore, included in GAI analyses. Gregariousness was not significant and was removed from GAI analyses (Table 4.2).

Table 4.2. Effectiveness of structural predictor variables in explaining association indices in Australian humpback dolphins around the North West Cape, Western Australia as indicated by partial correlation coefficients and results of multiple regression quadratic assignment (MRQAP) tests (10,000 permutations) conducted in SOCPROG 2.7 (Whitehead 2009).

Structural predictor variable	Partial correlation coefficient	MRQAP *p*-value
Gregariousness	0.0436	0.2480
Home range overlap	0.1846	< 0.001
Temporal overlap	0.7580	< 0.001

4.4.2 Analysis of affiliation patterns and assortative associations as a function of sex, geographic location and residency

The mean GAI amongst all individuals was 0.00 (± 0.02 SD), with a maximum 0.22 (± 0.08). For all tests of preferred/avoided affiliations, *p*-values stabilised at 1,000 permutations. There was a strong indication of non-random affiliations within the population (observed SD = 0.074, random SD = 0.067, $p < 0.001$; Table 4.3). Preferred and avoided affiliations were detected amongst females (F-F: observed SD = 0.073, random SD = 0.066, $p = 0.001$; Table 4.3), and between females and males (F-M: observed SD = 0.074, random SD = 0.072, $p = 0.009$; Table 4.3). Preferred/avoidance affiliations could not be tested amongst males (M-M) due to a paucity of associations within daily sampling periods, likely attributed to the low proportion of males in the study population (M:F = 1:4) (Table 4.3).

Table 4.3. Standard deviation (SD) of observed vs random mean generalised affiliation indices to test for preferred/avoided associations from permutation tests (n = 1,000) by sex class of Australian humpback dolphins around the North West Cape, Western Australia. F = female; M = male. M-M affiliations could not be tested due to the low number of association within daily sampling periods.

Sex class	Observed SD	Random SD	*p*-value
All individuals	0.074	0.067	< 0.001
F-F	0.073	0.066	0.001
F-M	0.074	0.072	0.009

The GAI links amongst individual humpback dolphins were mainly (80%) negative (Fig. 4.2a), indicating avoidance or 'loose associations' among most individuals. Deviance residuals indicated 24 preferred, 1,185 casual and 16 avoided pairs of affiliates. Of those preferred pairs, 19 were F-F (23 individuals), two were M-M (three individuals), and three were F-M (five individuals; 3 F, 2 M; Fig. 4.2b). Seven females had two or more affiliates, one with four preferred affiliates, and three females had both male and female affiliates (Fig. 4.2b). Of the avoided pairs, two were F-F (four individuals), 13 were F-M (17 individuals), and one was F-unknown (Fig. 4.2c). Two males had four avoided females each, and one individual female had six avoided affiliates (five male, one unknown sex) (Fig. 4.2c). There were no avoided male pairs (preferred/avoided affiliate pairs summarised in Table S4.3 in APPENDIX S4). These sex-specific preferred/avoided affiliations suggest segregation by sex class in the humpback dolphin social network (Fig. 4.2d).

Affiliations were significantly higher within than between sex classes (Mantel test, *t* = 3.33, matrix correlation = 0.31, *p* = 0.001; Table 4.4), indicating adult humpback dolphins preferentially associate with members of the same sex. The mean M-M GAI (0.04 ± 0.03 SD) was higher than the F-F GAI (0.00 ± 0.02 SD), and both were higher than F-M (-0.01 ± 0.04SD) and M-F (-0.01 ± 0.02) (Table 4.4).

The social network measure of strength (i.e. gregariousness) was significantly different from random across all individuals and by sex class (Table 4.5). Strength (sum of GAIs; see also Table 4.4) was higher amongst males than females (almost double; 0.35 c.f. 0.19) and noticeably higher from males to females than from females to males (0.54 c.f. -0.14; Table 4.5). Affinity (measure of strength of associates) was high for sex overall (13.76), with females displaying a substantially higher average affinity (17.60) than males (-1.22; Table 4.5). Clustering coefficient was not significantly different from random in any class (Table 4.5). In summary, network analysis indicates that females have strong associations with other females, and males have strong associations with both males and females.

Individuals within the geographically assigned East, West, and East-West classes affiliated with other individuals within their assigned class more often than individuals in other classes (Mantel test, *t* = 2.15, matrix correlation = 0.06, *p* = 0.03; Table S4.5 in APPENDIX S4). A negative mean GAI value of -0.01 between East and West suggests there may have been avoidance amongst individuals within these classes (Table S4.5 in APPENDIX S4). The spatial segregation of sightings within these East and West classes supports this (Fig. 4.3a), as does the lack of positive GAI links amongst these classes (Fig. 4.3b). Further, four individual females appeared to be acting as key central nodes within the social network (i.e. S067, S016, S021 and S049; Fig. 4.2a), displaying comparatively higher strength than the majority of individuals in the population (Table S4.4 in APPENDIX S4). These same four individuals appeared to provide a link between the East and West clusters, with three of them (S067, S016, and S049) belonging to the East-West cluster (see Fig. 4.2a in conjunction with Fig. 4.3b).

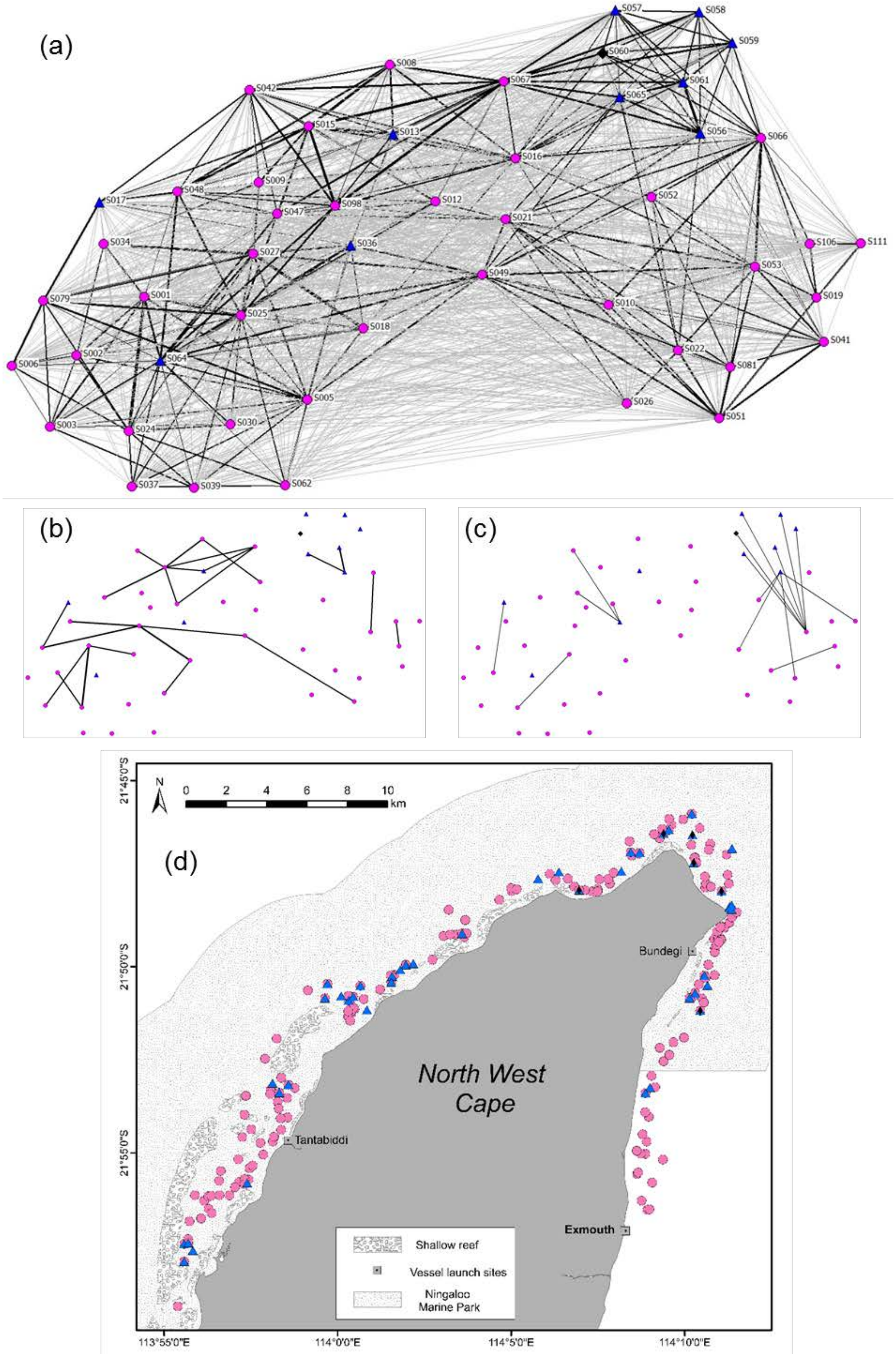


Fig. 4.2. Social networks of adult Australian humpback dolphins around the North West Cape, Western Australia. Each individual is represented by a node, and positive affiliations (edges) are represented by black lines, with thicker lines representing stronger affiliations. Negative affiliations are represented by grey lines. Node shape and colour denotes sex; pink circle = female, blue triangle = male, black diamond = unknown sex. a) complete network representing 50 individuals used in the social analysis; b) preferred affiliates within the network, based on deviance residuals (> 2); and c) avoided affiliates within the network, based on deviance residuals (< -2). For GAI link strength amongst preferred/avoided affiliates, see Table S4.3 in APPENDIX S4. d) Sighting summary of all 50 individuals by sex class (total sightings = 196). Node and shape colour sex categories as above.

Table 4.4. Summary of generalised affiliation indices (GAI, raw residuals used) by sex class of adult Australian humpback dolphins around the North West Cape, Western Australia. SD = standard deviation; Mean GAI = for each individual, the mean GAI with all other individuals (excluding with itself in all cases); Sum of GAIs = for each individual, the sum of all GAIs; Max. GAI = for each individual, the maximum GAI. Mantel tests for differences in associations between/within classes are indicated at the bottom of the table.

Class	Mean GAI	SD	Sum of GAIs	SD	Max. GAI	SD
F	0.00	0.02	0.05	0.82	0.22	0.08
M	0.00	0.02	-0.18	0.78	0.23	0.10
F-F	0.00	0.02	0.19	0.61	0.22	0.08
F-M	-0.01	0.04	-0.14	0.41	0.07	0.08
M-F	-0.01	0.02	-0.54	0.93	0.14	0.06
M-M	0.04	0.03	0.35	0.31	0.19	0.13
Within	0.01	0.02	0.22	0.56	0.22	0.09
Between	-0.01	0.04	-0.22	0.57	0.09	0.08
Overall	0.00	0.02	0.00	0.81	0.23	0.08

Test for differences in associations between/within classes:

Mantel test: t = 3.33; p = 0.001; matrix correlation = 0.13

Contrary to our expectations, although affiliations were stronger between than within residency clusters (*t*-value = -1.45; matrix correlation = -0.04; Table 4.6), this difference was not significant (Mantel test, p = 0.15; Table 4.6). Females accounted for 78% of all individuals (39 out of 50; Table 4.1) and comprised the majority of LTRs and PTRs (88% and 65%, respectively; Table S4.6 in APPENDIX S4). The majority of males (70%, n = 7) were considered PTRs (Table S4.6 in APPENDIX S4). Of the three male LTRs, two were preferred affiliates (S056 and S061; see Table S4.3 in APPENDIX S4).

Table 4.5. Social network metrics (strength, clustering coefficient and affinity) estimated for adult Australian humpback dolphins around the North West Cape, Western Australia. Network analysis statistics calculated using raw residuals of generalised affiliation indices (GAI), averaged by all individuals, and by sex class. Significant differences from mean random network values (expected values if individuals had no association preferences) were evaluated using 1,000 permutations. Significance ($p < 0.05$) is indicated by an asterisk (*). F = female, M = male. Individual social network metrics can be viewed in Table S4.4 in APPENDIX S4.

Category		Strength	Clustering coefficient	Affinity
Overall (all individuals)	Mean	0.01 ± 0.83*	-0.51 ± 1.72	0.06 ± 4.27
	Random	-0.01 ± 0.78	-1.28 ± 13.66	0.03 ± 11.76
Female (n = 39)	Mean	0.05 ± 0.82*	-1.03 ± 6.39	17.60 ± 107.98*
	Random	0.02 ± 0.78	0.11 ± 4.54	0.01 ± 2.08
Male (n = 10)	Mean	-0.18 ± 0.78*	-4.71 ± 6.07	-1.22 ± 1.43
	Random	-0.22 ± 0.74	0.64 ± 11.61	-1.19 ± 2.44
Within and between classes[a]	F-F	0.19 ± 0.61	-1.97 ± 15.46	-3.44 ± 16.35
	F-M	-0.14 ± 0.41	-	-
	M-F	0.54 ± 0.93	-	-
	M-M	0.35 ± 0.31	0.23 ± 0.29	0.44 ± 0.28
Sex overall	Mean	0.00 ± 0.81*	-1.79 ± 6.44	13.76 ± 96.39*
	Random	-0.03 ± 0.77	0.22 ± 8.41	-0.24 ± 2.29

[a] Network measure statistics for within and between class, and measures of clustering coefficient and affinity between classes, are not available (Whitehead 2009).

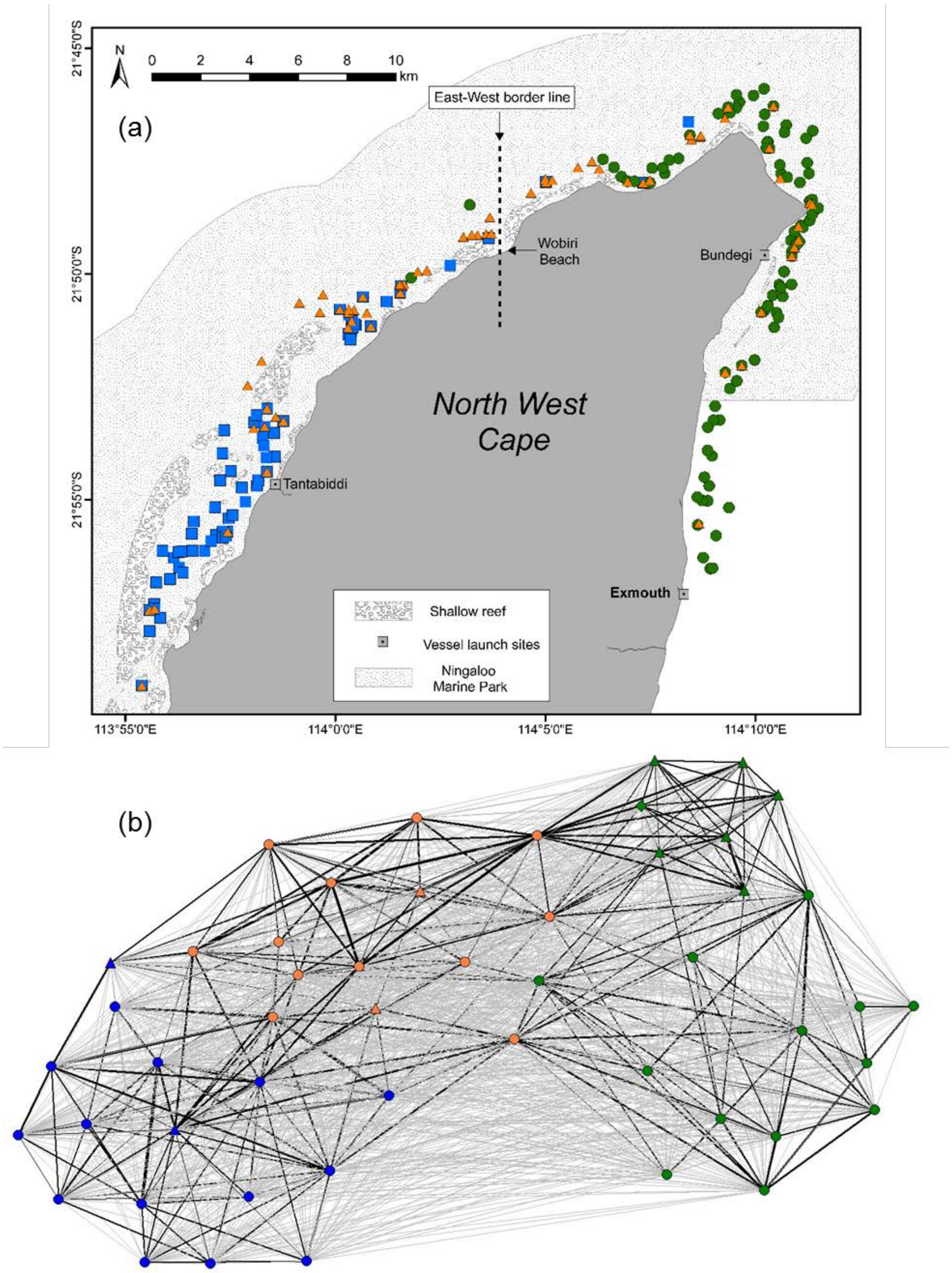


Fig. 4.3. a) Sightings used in social structure analysis of adult Australian humpback dolphins (*n* = 196, 50 IDs) around the North West Cape, Western Australia. Assigned geographic location classes delineated by East (green circles, 20 IDs), East-West (orange triangles, 14 IDs) and West (blue squares, 16 IDs). The assigned East-West borderline is represented by a single dashed line at Wobiri Beach. b) Social network diagram of 50 adult Australian humpback dolphins used in social structure analyses. Each individual is represented by a node, and positive affiliations (edges) are represented by black lines, with thicker lines representing stronger affiliations. Negative affiliations are represented by grey lines. Node shape denotes sex; circle = female, triangle = male, diamond = unknown sex. Node colour of individuals by geographic class is categorised as above.

Table 4.6. Summary of generalised affiliation indices by residency cluster class (as per Chapter 2/Hunt et al. 2017) of Australian humpback dolphins around the North West Cape, Western Australia. LTR = long-term residents, PTR = part-time residents, and OCR = occasional residents. See Table S4.6 in APPENDIX S4 for summary of residency clusters by sex class. Mantel tests for differences in associations between/within classes are indicated at the bottom of the table.

Class	Mean GAI	SD	Sum of GAIs	SD	Max. GAI	SD
LTR	0.00	0.01	-0.03	0.64	0.24	0.08
PTR	0.00	0.02	0.01	0.94	0.21	0.08
OCR	0.01	0.03	0.33	1.41	0.25	0.14
LTR-LTR	0.00	0.02	-0.07	0.38	0.17	0.11
LTR-PTR	0.00	0.01	0.04	0.27	0.20	0.09
LTR-OCR	0.00	0.04	0.00	0.12	0.06	0.08
PTR-LTR	0.00	0.02	0.05	0.57	0.19	0.08
PTR-PTR	0.00	0.02	-0.08	0.40	0.16	0.08
PTR-OCR	0.02	0.05	0.05	0.14	0.08	0.10
OCR-LTR	0.00	0.03	0.00	0.77	0.17	0.08
OCR-PTR	0.02	0.03	0.35	0.67	0.25	0.14
OCR-OCR	-0.01	0.00	-0.01	0.00	-0.01	0.00
Within	0.00	0.02	-0.07	0.38	0.16	0.10
Between	0.00	0.02	0.08	0.58	0.20	0.09
Overall	0.00	0.02	0.01	0.83	0.22	0.08

Test for differences in associations between/within classes:

Mantel test: t = -1.45; p = 0.15; matrix correlation = -0.04

4.4.3 Social clustering

A low modularity index (*Q* = 0.04) indicated a well-connected social network with no evident social clusters (Fig. 4.2a).

4.4.4 Temporary patterns of association

The SLARs for the entire dataset and by sex class remained higher than the null association rates for the whole study period (Fig. 4.4), indicating that associations were non-random over time. Overall and for males, the best fitting models (i.e. ΔQAIC 0-2) were those of 'preferred companions' (individuals with stable associations over time) and 'casual acquaintances' (individuals who associate for some time, disassociate, and may reassociate; Whitehead 2009) (Fig. 4.4a,c). The best fitting models for females indicated equally dynamic temporal association patterns, characterised by models of 'casual acquaintances', 'preferred companions' and 'two levels of casual acquaintances' (Fig. 4.4b). The 'two levels' model indicated fission/fusion of more permanent pairs of individuals into and out of groups on the short time scale, and then changes in these associations on the longer time scale through either shifts in companionship, mortality, emigration or a combination of either (Whitehead 2008a). Full model descriptions can be viewed in Table S4.7 in APPENDIX S4.

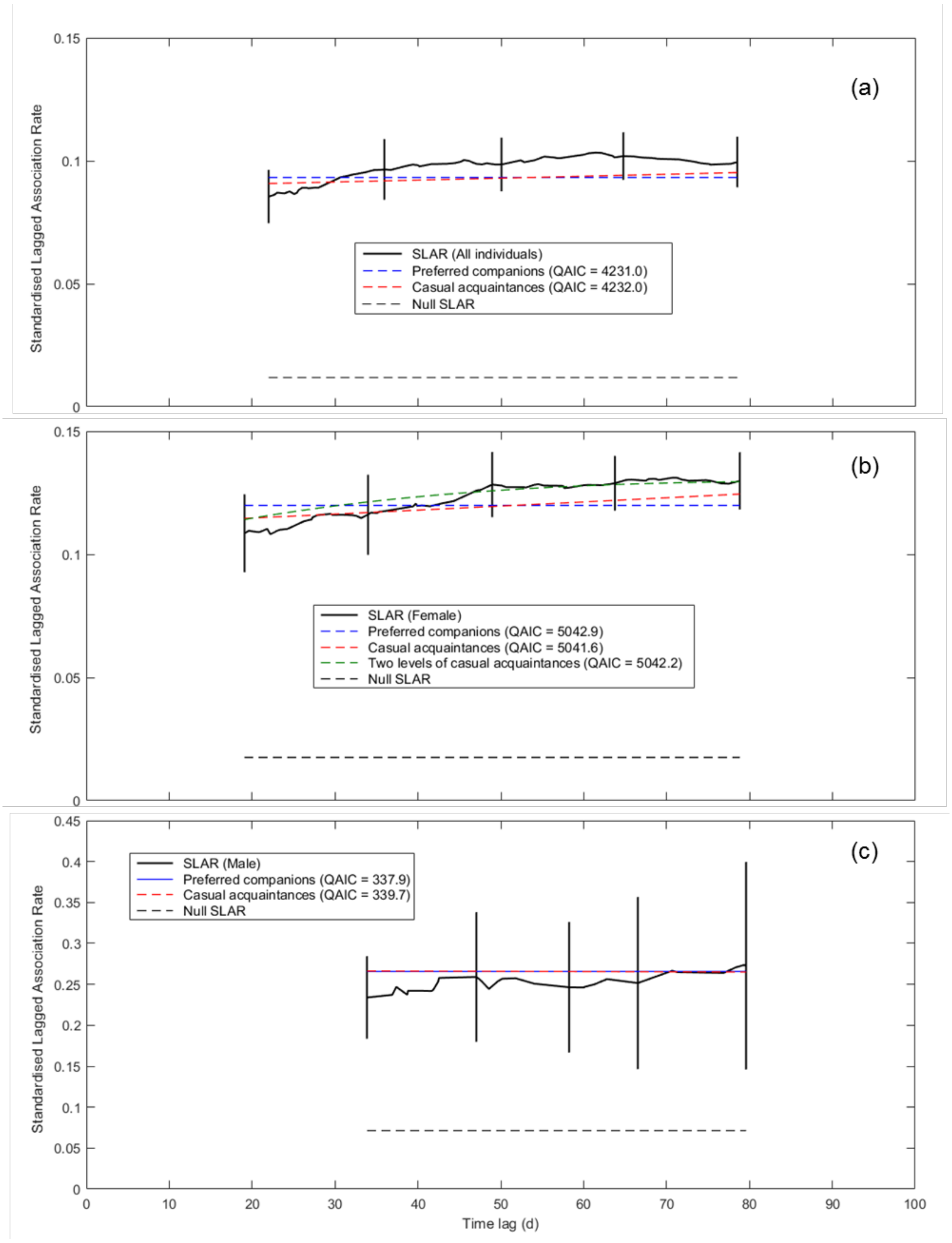


Fig. 4.4. Standardised lagged association rates (SLARs; solid black line) for: (a) the population; (b) female-female; and (c) male-male adult Australian humpback dolphins around the North West Cape, Western Australia. Models of best fit (ΔQAIC 0-2) are indicated by dashed coloured lines, and null association rates indicated by dashed black lines. Maximum time lag was set to 177 days (i.e. the longest period of time between the first association and last association of any pair of individuals in any yearly survey period) in order to consider overall association rates across the three years surveyed while removing consideration of association rates between yearly survey periods. Standard error bars were calculated using jackknife procedures. Population level, female, and male SLARs used moving averages of 10,000, 6,000 and 300, respectively; median time intervals were 78, 68 and 60 days, respectively. Note the different scale of the y-axis between (c) and both (a) and (b). Due to standardisation of lagged association rates, the absolute values of the y-axis cannot be directly compared between overall (a), female (b) and male (c) plots. See full model descriptions in Table S4.7 in APPENDIX S4.

4.5 DISCUSSION

Understanding social interactions among conspecifics is important in behavioural and evolutionary ecology, as well as conservation and management (Blumstein 2010, Snijders et al. 2017). Delphinids live in complex societies with variable grouping and fission-fusion dynamics, but we have much to learn about their social structure and the phenotypic, ecological, or behavioural factors driving such variation in most species. Here, we used photo-identification data, generalised affiliation indices, and social network techniques to investigate the dyadic relationships, assortative interactions and social clustering in the poorly known Australian humpback dolphin. Our results confirmed our expectations, that humpback dolphins live in a fission-fusion society, characterised by non-random dyadic relationships. Assortative interactions were identified both within and between sex classes and according to geographic location, but there was no evidence of distinct social communities or clusters. Models of temporal patterns of association demonstrated variable levels of stability, including stable (preferred companionships) and fluid (casual acquaintances) associations. Comparisons of observed social network metrics with their random counterparts revealed there was significant preference for associating with members of the same sex. Our hypothesis of assortative associations among individuals by residency patterns was not supported, highlighting the dynamic fission-fusion nature of associations amongst individuals. The strong same-sex preferred associations suggests sexual segregation among individual humpback dolphins; adding a level of social complexity not yet recognised for this species.

4.5.1 Structural predictors of association

Investigating associations among individuals without taking into consideration structural factors that might affect them (spatial-temporal overlap and gregariousness) can lead to biases in the estimation of true affiliations (Whitehead & James 2015). Few studies of delphinid sociality have considered any structural variables, so biases in reported associations are likely. The use of GAI on association data from humpback dolphins allowed for the removal of the effect of structural variables on true association patterns. Temporal overlap was identified as a significant structural factor, supporting the Markovian temporary emigration patterns previously documented in this population (Chapter 2/Hunt et al. 2017). Home range overlap was also a significant structural variable, highlighting the importance of taking into account space use patterns in analysis of animal social structure (e.g. Frère et al. 2010, Best et al. 2014). The incorporation of gregariousness as a structural factor aims to account for associations amongst individuals in large schools (Godde et al. 2013). Given the small school sizes observed throughout the survey period (mean ± SD = 4.6 ± 3.2; Chapter 2/Hunt et al. 2017), it is not surprising that gregariousness was not a significant structural predictor variable. Further structural non-affiliative factors that affect association, but are not represented by predictor variables, will remain and potentially bias association estimates (Whitehead & James 2015). We note that other variables not included in our analysis, such as kinship and age structure, may be structural determinants of associations and these will need to be taken into account in future studies. Nevertheless, our use of GAI and consideration of some structural variables has provided new insights into the strength and true affiliations among individual humpback dolphins.

4.5.2 A dynamic fission-fusion humpback dolphin society

Fission-fusion dolphin societies appear to be strongly driven by resource availability and predation risk (Connor et al. 1998, Gowans et al. 2007). The non-random structure of such societies indicates individuals will preferentially associate with others to reduce risk of predation and/or enhance foraging opportunities. The humpback dolphin fission-fusion dynamics observed at the NWC may be a result of the trade-off between these two factors. For example, Parra et al. (2011) suggested that the highly variable group sizes and degrees of fission-fusion in eastern Queensland Australian humpback dolphins may result from fluctuations in prey availability, whereby individuals aggregate when prey is abundant and disperse when it is scarce (to reduce competition). The authors also noted that predation risk was very low at their study site (Parra et al. 2011). This is not necessarily so around the NWC, where large tiger sharks, *Galeocerdo cuvier*, occur and dolphins bear evidence of predation attempts (Chapter 3/Hunt et al. in review). Variation in NWC humpback dolphin site fidelity, residency patterns (Chapter 2/Hunt et al. 2017) and areas of occurrence (Chapter 3/Hunt et al. in review) are likely to be influenced by both prey availability and predation risk, as is their sociality.

Our findings were consistent with the non-random patterns of association and short-term relationships identified in previous studies on the social structure of Indian Ocean humpback dolphins in Algoa Bay, South Africa (e.g. Karczmarski 1999), Indo-Pacific humpback dolphins in the South China Sea (e.g. Jefferson 2000, Jefferson & Karczmarski 2001, Chen et al. 2011, Dungan et al. 2012, Xu et al. 2012), and Australian humpback dolphins in eastern Queensland (e.g. Parra et al.

2011). Both Karczmarski (1999) and Dungan et al. (2012) suggested that the presence of calves influences social patterns in terms of group size, site fidelity and habitat preference. For example, groups containing calves were often larger, which seemed to encourage association amongst breeding females, and such associations regularly took place in near-shore waters, possibly to increase protection (Karczmarski 1999, Dungan et al. 2012). The high proportion of resident females, suspected year-round calving (see below), and preference for coastal shallow water habitat (Chapter 3/Hunt et al. in review) observed in humpback dolphins at the NWC support these observations. Additionally, the high affinity and multiple preferred affiliates amongst females is likely indicative of NWC humpback dolphin associations being driven by maternal needs (e.g. reproductive success, caring for offspring, knowledge transfer), as suggested by Gowans et al. (2007). Those authors also suggested *Sousa* social structure is likely driven by mating opportunities for males (Gowans et al. 2007), which may explain the preferences and avoidances observed within and between sexes in this study (see below). The primary drivers of the fission-fusion NWC humpback dolphin society are as yet unknown, but warrant further research.

4.5.3 Assortative interactions by sex

In mammals, assortative interactions by sex are largely driven by mating systems, where females are philopatric and males disperse to avoid inbreeding (Greenwood 1980). Whether or not this holds true for humpback dolphins has not previously been explored, but our findings of high female residency and most males being ‘part-time’ residents would, arguably, support this. Associations amongst females in the NWC population showed significant and high strength and affinity, and SLARs indicated three strong models of variable temporal stability patterns (i.e. both the short and long-term nature of associations) amongst individual females. It is likely that these dynamic, strong associations amongst female humpback dolphins are a function of kinship, as demonstrated in other delphinids (e.g. Möller et al. 2006, Frère et al. 2010, Zanardo et al. 2016, Diaz-Aguirre 2017, Reisinger et al. 2017). These female assortative interactions may also be important in protection from predators and consorting males (indeed, a number of adult females avoided associating with adult males in this study), and/or in the rearing of calves and transmission of learned behaviours (Connor et al. 2000, Möller et al. 2006, Gowans et al. 2007, Frère et al. 2010).

In terms of male associations, six of the 10 males identified in this study were directly affiliated, two pairs of which (three individuals: S056, S061 & S065) were deemed preferred affiliates. Gregariousness, clustering and affinity were markedly higher amongst M-M affiliates than F-F, despite the small M-M sample size. Further, a 'preferred companions' model in male SLARs is also indicative of strong and stable associations amongst males, and supports the preferred affiliate pairs and strong affiliations amongst other males. Recently, Allen et al. (2017) presented preliminary evidence of possible coalition formation among adult male Australian humpback dolphins. Males were also observed performing multi-modal sexual displays, involving sponge presentation and, on occasion, visual posturing referred to as the "banana pose" in proximity to females (Allen et al. 2017). In this study, all three male preferred affiliates were observed performing the banana pose in proximity to known females, and one was observed presenting a sponge to known females on a few occasions (Hunt, pers. obs.). These observations, in combination with our findings of strong and some long-term M-M social bonds, are notionally supportive of the preliminary findings in Allen et al. (2017).

The strength of these same-sex associations amongst the NWC humpback dolphins suggests some degree of sexual segregation, as is evident in Indo-Pacific bottlenose dolphins (e.g. Connor et al. 2000, Fury et al. 2013) and Amazon river dolphins, *Inia geoffrensis* (e.g. Martin & da Silva 2004). Sex segregation may be related to mating opportunities (Wearmouth & Sims 2008) and, for male humpback dolphins, it may function to facilitate access to, or coercion of, receptive females (as eluded to above). For female humpback dolphins, such segregation may be influenced by a combination of kinship, maternal needs, habitat preferences, and predator avoidance (as above).

Our ability to account for temporal and spatial overlap as a structural variable and, thus, to demonstrate avoided affiliates, provided insight into social avoidance (Strickland et al. 2017). We noted some F-M avoidance, M-F avoidance and F–F avoidance. While explanatory mechanisms behind F-M avoidance are intuitive (above), reasons for M-F or F-F avoidances are more challenging. They may be related to sex segregation (e.g. Wielgus & Bunnell 1994, also described above), dominance hierarchies (e.g. Carter et al. 2016), avoiding resource competition, avoiding conflict (Strickland et al. 2017), or simply avoiding by way of no home range overlap. If the social structure of this humpback dolphin population is linked to kinship, such avoidances may serve to minimise inbreeding (as in elephants; Archie et al. 2007).

4.5.4 Assortative interactions by geographic location

The assortative interactions amongst humpback dolphins based on geographic location suggests there may be underlying social units in the NWC population, which could be influenced by environmental factors (e.g. habitat). For example, humpback dolphins residing in the Great Sandy Strait of south-east Queensland are separated into two distinct social units with limited interactions (Cagnazzi et al. 2011). This separation was likely a result of habitat differences, as the region is characterised by two bodies of water (north and south) connected by two passages (Cagnazzi et al. 2011). Geographic separation of distinct social communities has also been documented in Indo-Pacific humpback dolphins in China (e.g. Dungan et al. 2012, Wang et al. 2015). Wiszniewski et al. (2009) demonstrated that Indo-Pacific bottlenose dolphins occupying an eastern Australian embayment were socially segregated into two distinct communities based on habitat preferences; one estuarine dominated, the other largely marine. On the NWC, individuals in the West class were predominantly sighted in lagoon waters between shallow fringing reef and land, whereas those in the East class were outside shallow reef habitat. Individual preferences for these two different habitat types may explain the assortative interactions among individual humpback dolphins by geographic location at the NWC.

Four females (S067, S016, S021, S049) were key central nodes in the structure of the humpback dolphin social network documented here. Three of these individuals were from the East-West class (Fig 4.3b) and may act as a “bridge” between east and west. The removal of them from analyses would, arguably, delineate two separate communities in the study population, show stronger evidence of geographic separation, and provide insight into the underlying roles of certain individuals on the social structure of the population. These individuals may be key to maintaining community connectivity and social unit stability in the NWC population (e.g. Williams & Lusseau 2006).

4.5.5 Limitations and future studies

We acknowledge that sex determination through modelling is not without uncertainty, and that molecular or visual confirmation would be ideal. Nevertheless, the logistic regression analysis used to predict the sex of known individual Australian humpback dolphins proved 97% accurate (Brown et al. 2016a). Furthermore, 67% (n = 26) of the females in the NWC population were confirmed via molecular analysis, visual confirmation, or repeated sightings with a dependent calf or juvenile. Thus, we can be confident of most, if not all, sex determinations reported here. For males that do not exhibit LOP (i.e. below the logistic regression threshold), the model would deem them female. The study population may therefore include males incorrectly assigned to being female. An alternative explanation for the relative lack of adult males is that they may range substantially further than females (as is in some Indo-Pacific bottlenose dolphin populations; Connor et al. 2000, Sprogis et al. 2016b). They would therefore have been photographically recaptured less often and so under-represented in our sampling regime.

Kinship and age structure can influence association patterns in dolphin societies (Möller 2012), so inclusion of these as either structural predictor variables or as an affiliation variable in future studies will be important to further assess social structure. Behavioural traits may also be influencing association patterns (Croft et al. 2009) and, thus, the collection of behavioural data from dedicated focal follows is needed for incorporation into future sociality assessments. Lastly, prey availability (and associated foraging behaviour) and predation risk remain largely unquantified and are important in understanding the potential drivers of fission-fusion dynamics.

4.5.6 Implications for conservation and management

Understanding social relationships is a key consideration in effective conservation and management of animal populations because it provides insights into ecological processes (e.g. mating systems, reproductive fitness, cooperative behaviour) and how they may be influenced by external stimuli (Berger-Tal et al. 2011, Greggor et al. 2016, Snijders et al. 2017). Rapid environmental change, be it human-induced or otherwise, can disrupt social bonds, interfering with demographically important social processes (Snijders et al. 2017). Certain adult females in the NWC humpback dolphin social network appear to occupy central nodes and may play pivotal roles in the maintenance of connectivity amongst individuals or, indeed, the East and West classes. Disruption to, or removal of, such key individuals may have a disproportionate influence on social stability (Blumstein 2010). McComb et al. (2001) demonstrated that female matriarchs in African elephants possess knowledge that influences group productivity, so reproductive success would be negatively impacted by their removal. Similarly, Williams and Lusseau (2006) simulated targeted removal of female killer whales from a population with natal group philopatry, resulting in detrimental effects on social unit stability. Whether or not the NWC humpback dolphin social network is robust to disturbance from anthropogenic disturbance (e.g. increasing tourism activity) remains to be studied.

We documented a high proportion of adult female humpback dolphins around the NWC, 92% of these females displaying high levels of residency. More than half (56%) of these females were regularly observed with a dependent calf or juvenile. Calves (including newborns) were sighted across both seasons in all three years of surveys. The numerical dominance, high site fidelity, apparent year-round nursing and density of females around the NWC highlight the conservation importance of this area for humpback dolphins. The influence of increasing human activities in the NMP (Rob & Barnes 2016), including vessel traffic (e.g. Smallwood et al. 2011; Chapter 3/Hunt et al. in review) and recreational fishing (e.g. Mitchell et al. 2018), on the humpback dolphin population's social structure warrants close scrutiny.

Our results highlight the dynamic and complex fission-fusion characteristics of a resident population of Australian humpback dolphins, pointing to more social complexity in this species than previously recognised. This knowledge provides the necessary baseline information upon which to build ongoing studies of humpback dolphin sociality, and to assess the impacts of environmental and/or anthropogenic disturbances on their social structure.

CHAPTER 5: GENERAL DISCUSSION AND RECOMMENDATIONS

The paucity of information on Australian humpback dolphins (*Sousa sahulensis*) along Western Australia's (WA) coastline has hindered adequate environmental impact assessments, as well as assessment of their conservation status (Allen et al. 2012, Bejder et al. 2012, Hanf et al. 2016). Generally small population sizes, slow life-history characteristics and shallow water, coastal distribution heighten their vulnerability to disturbance from anthropogenic activity in the growing Pilbara region (Chapter 1; Hanf et al. 2016). In this thesis, I used systematic boat-based surveys and photo-identification methods in the field and a suite of analytical tools to estimate population demographics (abundance, apparent survival, temporary emigration, site fidelity and residence patterns; Chapter 2/Hunt et al. 2017), distribution and habitat use (Chapter 3/Hunt et al. in review), and social structure (Chapter 4/Hunt et al. in review) of Australian humpback dolphins ("humpback dolphins" hereafter) around the North West Cape (NWC), in the northern section of the Ningaloo Marine Park (NMP). This final chapter summarises the main findings (Chapters 2-4) and highlights the importance of the NWC for Australian humpback dolphins. I then review the implications of these findings in the context of anthropogenic activity in the region, and provide recommendations for conservation, management and future research directions for this species.

This thesis represents the first comprehensive assessment of the population demographics (Chapter 2), habitat use (Chapter 3) and social structure (Chapter 4) of humpback dolphins inhabiting the waters around the NWC in WA, including the first reported abundance estimate for this species along the ca. 1,000 km Pilbara coastline, and the first within a marine park in WA. The novel methodological approaches used in this thesis to investigate humpback dolphin ecology have provided insight into this population, along with a strong methodological framework that can be applied to humpback dolphin populations elsewhere and, indeed, to other populations and species of individually marked animals. Most importantly, the results provide a solid baseline upon which ongoing research can build, and informed management decisions toward the conservation of Australian humpback dolphins can be made.

5.1 The NWC is important to Australian humpback dolphins

The near-shore waters around the NWC study area (ca. 130 km^2) are used by ca. 130 individual humpback dolphins and, at around one dolphin per km^2, this represents the highest density recorded for this species to date (Chapter 2). A great proportion of these individuals has high levels of site fidelity and residency in the study area (Chapter 2), and utilise shallow (< 15 m), coastal waters (Chapter 3). These findings demonstrate that the NWC is an important habitat for humpback dolphins. Markovian temporary emigration strongly suggested seasonal movement in and out of the study area (Chapter 2), supported by some seasonal difference in dolphin occurrence throughout the study site (Chapter 3). Such movements may be driven by pulses in anthropogenic activity and/or prey availability (Chapter 3) and indicate that the home ranges of humpback dolphins extends outside the NWC study area (Chapters 2-4). The notion of seasonal movements was further supported by findings of significant temporal overlap in assessment of social structure (Chapter 4). The social structure of humpback dolphins around the NWC was characterised by a dynamic fission-fusion society, with assortative interactions suggesting a degree of sexual segregation, stronger male-male bonds than other categories, high levels of female residency and the avoidance of adult males by adult females (Chapter 4).

The demography, habitat use and social structure findings (Chapters 2-4) corroborate and extend those of earlier research on humpback dolphins (primarily) in eastern and northern Australia, while also filling some of the gaps in knowledge we have for this poorly known species (see below).

5.1.1 Demography (Chapter 2)

The capture-recapture abundance estimates reported here, both seasonally (ca. 60-100 individuals) and overall (ca. 130 individuals), are comparable to those reported in eastern Queensland (Corkeron et al. 1997, Parra et al. 2006a, Cagnazzi 2011, Cagnazzi et al. 2011) and in the Northern Territory (Palmer et al. 2015, Brooks et al. 2017), but notably higher than those reported for other areas in WA (Brown et al. 2016b). For Indian Ocean humpback dolphins (*Sousa plumbea*), abundance estimates have all been less than 500 individuals, and are usually fewer than 200 (reviewed in Braulik et al. 2015). For Indo-Pacific humpback dolphins (*Sousa chinensis*), abundance estimates are typically less than a few hundred individuals, but can range up to ca. 2600 individuals in the Pearly River Estuary (China) population, which is considered ‘exceptional’ in terms of size (reviewed in Jefferson & Smith 2016). Generally speaking, *Sousa* spp. occur in small population sizes, however quantitative studies are limited throughout most of their range. The density of 0.98 individuals/km² reported here, however, is around five times greater than the average reported for all Australian humpback dolphin studies combined (0.1-0.19 individuals/km²;

Parra & Cagnazzi 2016) and more than 1.5 times greater than the highest density previously reported (0.64 individuals/km^2; Palmer et al. 2015). The NWC humpback dolphin density is also higher than the majority of Australian snubfin dolphin densities reported, with the exception of that in Roebuck Bay, WA (1.33 individuals/km^2; Brown et al. 2016b). Such density highlights the importance of the NWC for this species.

5.1.2 Habitat use (Chapter 3)

The humpback dolphin distribution and habitat use findings corroborate this species' preference for shallow waters (< 15 m) close to the coast, as reported in eastern Queensland (Parra et al. 2006b, Cagnazzi 2011, 2013). The use of an ensemble species distribution modelling (EM) approach proved effective in overcoming the predictive uncertainties from single SDMs (species distribution models), highlighting its utility for future studies assessing cetacean distribution and habitat use (concurring with Zanardo et al. 2017). Additionally, the assessment of high areas of dolphin occurrence in relation to sanctuary zones has provided important management considerations for future marine spatial planning reviews (see below).

5.1.3 Social structure (Chapter 4)

The fission-fusion social dynamics identified for the NWC humpback dolphin population align with those reported for humpback dolphins in eastern Queensland (Parra et al. 2011), and also for populations of the genus *Sousa* in other parts of the world (e.g. Karczmarski 1999, Jefferson 2000, Jefferson & Karczmarski 2001, Chen et al. 2011, Xu et al. 2012). The assortative interactions by sex (same-sex preferred affiliations, avoidances and sexual segregation) and geographical location suggest a level of social complexity that was not previously known for Australian humpback dolphins (Cagnazzi et al. 2011, Parra et al. 2011), and that seems comparable to some populations of bottlenose dolphins *Tursiops* spp. (Owen et al. 2002, Wiszniewski et al. 2009, Allen et al. 2017).

5.2 Potential anthropogenic impacts on humpback dolphins in the NWC region

Coastal development can result in habitat degradation and loss, displacement, noise pollution and increased vessel traffic; the sudden and cumulative disturbance from which can, and already has in some cases, negatively impact coastal marine mammal populations (e.g. Culloch et al. 2016, reviewed in Hawkins et al. 2017), particularly the genus *Sousa* (Wang et al. 2007, Jefferson et al.

2009, Piwetz et al. 2015). Given the coastal distribution of Australian humpback dolphins, the cumulative impacts of coastal development and associated human activities (e.g. seismic surveys, land reclamation, dredging, blasting, pile driving, increased shipping, fisheries interactions, influx of environmental contaminants) are recognised as serious threats to their persistence (Cagnazzi et al. 2013a, Parra & Cagnazzi 2016, Weijs et al. 2016). The NMP within the NWC region is a multi-use marine park, with various zoning schemes, including sanctuary zones, where extractive activities (e.g. fishing) are not permitted (CALM & MPRA 2005). The primary potential impacts on humpback dolphins from anthropogenic activities in the NWC region can be divided, at least loosely, into two broad categories: 1) increased vessel traffic and recreational fishing due to increasing tourism within the NMP and adjacent Cape Range National Park (CRNP), and 2) increased development pressures in adjacent, non-protected areas (e.g. Exmouth Gulf).

5.2.1 Increasing tourism

The Ningaloo Coast World Heritage Area, which encompasses the NMP and the CRNP, currently experiences greater than 500,000 visits annually (estimated, see Chapter 1 for further details), and there is evidence to suggest an increasing tourism trend (Rob & Barnes 2016). Increased visitation to the area is likely to result in a concomitant rise in vessel use (both commercial and recreational) and recreational fishing pressure, which is already quite high within the northern NMP (Mitchell et al. 2018). Van Parijs and Corkeron (2001) showed significantly increased rates of whistling by Australian humpback dolphin groups with mother/calf pairs in the presence of vessel traffic, suggesting that noise from vessel traffic may disrupt group cohesion and necessitate the re-establishment of vocal contact between mother/calf pairs. Given prior suggestions that this Genus uses passive listening to locate sound-producing prey in some areas (Parra & Ross 2009), anthropogenic noise may mask their ability to efficiently locate prey (Liu et al. 2017). Increased acoustic disturbance from vessel traffic may be stressors in areas important for *Sousa* spp. mother/calf pairs (Hung 2008), and fast-moving vessels appear to illicit immediate fleeing and diving behavioural responses, with evidence of the avoidance of some areas with high vessel traffic (Karczmarski et al. 1997, Ng & Leung 2003, Hashim & Jaaman 2011, Sims et al. 2012).

For coastal delphinids elsewhere, changes in residency patterns and energy budgets, as well as declines in the relative abundance, have been detected in association with increased vessel activity (e.g. Lusseau 2005, Bejder et al. 2006, Williams et al. 2006). Prolonged vessel disturbance can cause repeated disruption to foraging, socialising or resting behaviour and can, ultimately, have adverse impacts on reproductive success, distribution and ranging patterns, access to preferred habitat, and individual health and fitness (Bejder & Samuels 2003). Chapter 3 illustrates the importance of shallow, coastal waters around the NWC to humpback dolphins, highlighting their vulnerability to potential disturbance from recreational and commercial vessel traffic in these areas of high overlap. The majority (> 90%) of areas of high probability of humpback dolphin occurrence were outside sanctuary zones, where recreational fishing is permitted. With evidence of fine-scale habitat use being driven by fish density over vessel density (Pine et al. 2017), changes in prey availability (from increased recreational fishing) in important habitat for NWC humpback dolphins is of concern. Future marine management plans and spatial planning reviews should consider these areas of high dolphin occurrence when delineating sanctuary zone boundaries (see 5.3.4 below) and affording greater protection from increasing recreational fishing.

5.2.2 Increasing development pressures in adjacent areas

The Pilbara coast is one of the fastest growing regions in WA, and coastal development associated with the extraction and export of oil, gas and mineral resources will likely continue, with further exploration planned for the coastal areas around Exmouth and Onslow (Fig. 1.2 in Chapter 1). In Exmouth Gulf, for example, a proposal is currently under consideration to build a pipeline bundle fabrication facility ca. 30 km south of Exmouth, the purpose of which will be to manufacture and then tow pipelines for the development of offshore gas fields (see EPBC referral 2017-8079; available at http://epbcnotices.environment.gov.au/referralslist/). Non-government organisations and local community groups have expressed concerns that the approval of such a development will signal the opening of the Exmouth Gulf to industrialisation (e.g. CCG 2017, Zaunmayr 2017b). The Exmouth Gulf currently remains relatively undeveloped and of high ecological value, supporting a myriad of protected marine fauna, including sea snakes (Hydrophiinae), turtles (Chelonidae), dugongs (*Dugong dugon*), migrating humpback whales (*Megaptera novaeangliae*), Indo-Pacific bottlenose, Australian snubfin (likely vagrant) and, of-course, Australian humpback dolphins (CSIRO 2007, Allen et al. 2012).

Unfortunately, coastal development projects to date in the Pilbara have proceeded without adequate baseline ecological information on humpback dolphins, and without a precautionary approach in associated EIAs (Bejder et al. 2012, Hanf et al. 2016). This thesis provides an appropriate methodological framework for use in future EIAs and, along with the adoption of appropriate assessment, monitoring, and adaptive management frameworks (Hawkins et al.

2017), future development in the NWC region can give appropriate consideration to potential cumulative impacts on humpback dolphins and other coastal delphinids.

5.3 Recommendations for the conservation and management of humpback dolphins

5.3.1 Addressing research priorities and informing conservation status

The NWC was identified by the Australian Government as a key priority area for research into humpback dolphin ecology because of its accessibility and preliminary evidence of a sizeable dolphin population within an MPA adjacent to major development prospects (DoE 2015). The results in the data chapters (Chapters 2-4) of this thesis can feed directly into the research objectives outlined in the Coordinated National Research Framework (CNRF; Fig. 1.3 in Chapter 1), as the overall purpose of this framework is to improve the scientific basis for the conservation and management of Australia's tropical inshore dolphins (DoE 2015). Specifically, the results of this thesis should serve as a platform for long-term monitoring aimed at determining population trends, mitigating impacts from threats, and aiding decisions in adaptive management and conservation of Australian humpback dolphins (relating to High Priority Research Objective #2). The distribution models and areas of high probability of dolphin occurrence identified in Chapter 3 can feed directly into threat risk assessments and marine spatial conservation prioritisation (relating to High Priority Research Objective #3). The identification of humpback dolphin seasonal movements in and out of the study area (Chapters 2-4) and evidence of sexual segregation (Chapter 4) have provided insight into dispersal and movement patterns and identified home ranges as an important aspect to investigate to gain further understanding into population structure in the region (relating to Medium Priority Research Objective #4). Accordingly, the relevant data from this thesis has been uploaded to a national database to assist in fulfilling High Priority Research Objective #1 regarding national distribution data. This thesis also addresses high priority inshore dolphin research priorities at the state level (DPaW 2014b) by answering fundamental research questions around population demographics (Chapter 2), and distribution and habitat use (Chapter 3).

5.3.2 The Blueprint for Marine Science Initiative

The Blueprint for Marine Science Initiative (Blueprint for Marine Science 2015, 2016) is, broadly speaking, an initiative of multiple stakeholders to develop a structured framework of marine science programs such that a balance can be achieved in sustainable development of WA’s oceans while supporting the growth of the ‘Blue Economy’. The development of such an initiative highlights there is mandate for continued development of WA’s coastline (and offshore) to drive the state’s economy. While such a coordinated approach is a positive step, it acknowledges the impacts of anthropogenic activity on ecological values. With this Initiative, there is an opportunity to establish research programs that examine potential (and cumulative) anthropogenic impacts on humpback dolphins. As highlighted in Chapter 2 (and above), the methods presented provide a methodological framework that should be used by those conducting future EIAs, and the results provide a strong platform for the design and implementation of Before-After-Control-Impact studies. Specifically, the NWC study area can serve as a quasi-control site, and there is a need to survey adjacent areas to better understand humpback dolphin populations that do not occur in protected areas and may be subject to the cumulative pressures associated with future coastal development. Lastly, the Initiative can link in with the research objectives outlined in state government prioritisation frameworks (DPaW 2014b), and in the federal CNRF (DoE 2015). Specifically, ‘High Priority Research Objective #3: *Threat risk assessment: Identify, map and assess threats to tropical inshore dolphins, understand related impacts, and mitigate risks’.* The NWC humpback dolphin population represents an ideal candidate to feed in to this assessment and threat matrix, given substantial baseline ecological information is available, as well as knowledge of the potential threats in the immediate and adjacent regions.

5.3.3 Humpback dolphins as independent key performance indicators (KPIs)

In the majority of marine park management plans throughout WA, dolphins are considered ecological values as ‘Marine mammals’ or ‘Whales and dolphins’. Humpback dolphins are currently considered under this ‘Whales and dolphins’ category in the *Management Plan for the Ningaloo Marine Park and Muiron Islands Marine Management Area 2005-2015* (the Plan; CALM & MPRA 2005), but the only information provided in the Plan about this species is that they are *“regularly seen in reserve waters”*, and *“regularly sighted around Tantabiddi Lagoon.”* The Plan’s current strategies are primarily whale-focused, but they do identify boating activities as an ‘existing and potential use and/or pressure’ for whales and dolphins.

It is a legislative requirement that the Plan for NMP is reviewed “*as soon as possible*” (Chapter 3). This pending review represents an opportunity to use the knowledge gained throughout the course of this thesis and implement specific management measures for humpback dolphins. I recommend that the review of the Plan identifies ‘dolphins’ as a high priority, independent ecological value, as in the recently (2016) declared ‘Lalang-garram/Horizontal Falls and North Lalang-garram marine parks’ in the Kimberley region of WA, where both Australian humpback and snubfin dolphins have been specifically identified (DPaW 2016). Given the importance of the NMP/NWC habitat for humpback dolphins (Chapters 2-4), I propose listing them separately as a key performance indicator (KPI) within the Plan. This will afford recognition as the highest conservation priority and, as such, specific humpback dolphin management strategies, with targeted research objectives, can be developed. Having humpback dolphins as a KPI means that their strategies must be addressed and their overall condition, pressure(s) and responses are regularly assessed, reported on, and managed accordingly. In the NMP, the concept of humpback dolphins as ‘ecosystem indicators’ is warranted; the temporal patterns (seasonal movement) and spatial patterns observed in this thesis study appear to show some fine scale response to ‘unmeasured’ ecological patterns (e.g. prey/predator presence). As such, continued monitoring of these animals within the NMP will provide strong insight into the dynamics of the NMP ecosystem. Listing humpback dolphins as a KPI mandates management agencies to include these ecological assets into their research and monitoring works programs, just as dugongs are considered a KPI in the Shark Bay Marine Park Management Plan (CALM 1996). The benefit of such a classification in the Plan provides the opportunity to continue with long-term studies by ratifying research objectives so that this information can be used to inform humpback dolphin management, not only within the marine park, but at the regional, state and national level. It will also be important for management strategies in the Plan to align with national (i.e. CNRF; DoE 2015) and state (DPaW 2014b) research priorities. Future research areas are outlined below (5.4).

5.3.4 Marine parks for humpback dolphin conservation: The NWC as an IMMA (Important Marine Mammal Area)

Marine protected areas (MPAs) are recognised as a tool for the conservation and management of cetacean populations (Hoyt 2011, di Sciara et al. 2016), with proven efficacy in some circumstances (e.g. Slooten 2013). The recent designation of Important Marine Mammal Areas (IMMAs) by the IUCN Marine Mammal Protected Areas Task Force is a means by which *“to increase protection of marine mammals within the overarching approach of systematic marine spatial planning”* (di Sciara et al. 2016). IMMAs are a science-based tool for place-based conservation, defined as *“discrete portions of habitat, important to one or more marine mammal species, which have the potential to be delineated and managed for conservation”* (di Sciara et al.

2016). I have demonstrated the importance of the northern NMP to humpback dolphins and, given the marine park management framework is already in place, areas can be delineated and managed accordingly, and consideration should be given to proclaiming the coastal waters of the NWC an IMMA (Chapter 3). Assigning an IMMA would raise the profile of this species for conservation purposes both inside and outside the marine park and, further, contribute to the conservation of associated coastal species and ecosystems. This would represent the first IMMA in Australia, recognising the importance of the NWC region for this endemic, protected species, as well as those other marine mammals that reside or migrate through, including, but not limited to, humpback whales, Indo-Pacific bottlenose dolphins, and dugongs. Designation of an IMMA for the NWC region also provides an opportunity to align IMMA management and research objectives with those at the state and national level for humpback dolphins (described above). Further, there can be direct links with the Plan and any forthcoming reviews, and aligning the management strategies and targets of the humpback dolphin KPIs with those of the IMMA, so that the benefits of such conservation measures reach beyond the spatial boundaries of the marine park. IMMA boundaries and pending marine spatial planning reviews could be linked with future humpback dolphin research to ascertain other areas of high probability of occurrence (see 5.4.2 below).

Given the evidence of increasing human use within the NMP and the conservation value this marine park can provide for future management of humpback dolphins, I recommend that future marine spatial planning reviews consider increasing the size of current sanctuary zones (or establishes new ones) to encompass areas of high humpback dolphin occurrence (Chapter 3). The marine park's management framework is in place, but its efficacy in humpback dolphin (and other marine mammal) conservation is as yet unproven. The findings presented in this thesis should be used to enhance existing protections, using the MPA framework to establish ongoing research to assess impacts from human activities and ensure effective management of this species, and other marine mammals.

5.4 Future research recommendations for humpback dolphins

Here, based on the results of this study, I outline a number of recommendations for future research directions in order to: 1) increase our ecological understanding of Australian humpback dolphins, and 2) assess the potential impacts from human use on this endemic species both within and in the greater NWC region. These research objectives should also be incorporated into humpback dolphin management strategies in future marine park management plan reviews.

5.4.1 Better understanding of population demographics

Continued capture-recapture studies with greater effort are important to increase dolphin detection probabilities and alleviate uncertainty around abundance, migration and survival parameters (Chapter 2). To avoid Maximum Likelihood Estimate issues with population model fitting, such as parameter singularities (Chapter 2), it would be useful to explore the thesis dataset using recently developed individual-heterogeneity Bayesian models (Rankin et al. 2016). Future capture-recapture model analyses would also benefit by taking into account differences in individual site-fidelity (as per the cluster analysis; Chapter 2). In addition to surveying adjacent areas, it will also be important to survey during the summer (November to April) period to address the hypothesis of year-round residency (Chapter 2) and calving (Chapter 4), as well provide insight into seasonal (i.e. 'Summer-Autumn') habitat use (discussed in Chapter 3) for this humpback dolphin population.

Given that the NWC only represents a fraction of the home range of humpback dolphins (Chapter 2), future studies should consider simultaneous surveys inside and outside the NWC study area, with multi-state capture-recapture models (Brownie et al. 1993, Cheney et al. 2013) to enable estimates of movement probabilities between areas, and better definition of sex-specific home ranging patterns (as hypothesised in Chapter 4), and of population boundaries. Further biopsy sampling within and outside the NWC region will enable the assessment of population genetic structure and delineation of specific management units based on the level of population structure and migration rates between these units (e.g. Bilgmann et al. 2014). Available genetic data suggests that NWC humpback dolphins showed significant levels of population structure with limited gene flow from samples obtained ca. 300 km to the north-east in the Dampier Archipelago (Brown et al. 2014).

5.4.2 Better understanding of distribution and habitat use

To assist in pinpointing the potential biotic factors that may be influencing distribution and habitat use, future studies should explore humpback dolphin habitat use using available finer-scale spatial resolution benthic habitat data (e.g. Kobryn et al. 2013; see also the Pilbara Marine Conservation

Partnership, and Ningaloo Outlook Program: available at https://research.csiro.au). These datasets do not encompass the entire study area and, hence, were not used in this thesis, but they could be complemented with new, ground-truth benthic habitat data to delve deeper into habitat use at a 'fine scale' (e.g. 100 m compared to 500 m grid cells). Finer spatial scale SDMs may also assist in determining boundaries for future marine spatial planning and zoning reviews.

Prey availability, as well as predator presence, are important factors likely to influence dolphin distribution and habitat use (e.g. Heithaus & Dill 2002). Thus, it will be important to quantify and consider these in future studies to further investigate potential drivers of humpback dolphin distribution and habitat use. The occurrence of predators and prey sources could be investigated in both high and low areas of occurrence using baited-remote underwater videos (BRUVs; see methodology review in Whitmarsh et al. 2017), in conjunction with echo sounder surveys. Targeted behavioural focal follows would also need to be incorporated to identify a) potential areas of foraging behaviour, and b) identification of prey consumed. Such studies will help test the hypothesis that consistent prey availability may be influencing regular use of NMP by humpback dolphins, compared to the adjacent (unprotected) Exmouth Gulf (Chapter 2).

Humpback dolphin distribution in the NWC region may also be influenced by resource partitioning with sympatric Indo-Pacific bottlenose dolphins (as shown between humpack and snubfin dolphins; see Parra 2006). Bottlenose dolphins occur in large numbers (relative to humpback dolphins) throughout the NWC study site, and form mixed-species associations with humpback dolphins (Hunt, unpub. data), so their occurrence alone may be influencing humpback dolphin habitat use. Using the methods outlined in Parra (2006) as a starting point, potential interspecific differences could be investigated by comparing space use patterns, behaviour and habitat preferences through use of a combination of GIS tools, such as kernel methods and ensemble modelling.

Although behavioural data was collected in the field, the paucity of data limited analysis and inclusion in this thesis. More behavioural data is needed through focal follows, which would enable the inclusion of behaviour in SDMs in future, as well as the use of kernel density estimates to gain a better understanding of the potential ecological function of areas of high use (e.g. Zanardo et al. 2017). This behavioural data might also assist in explaining the social association patterns observed (Chapter 4), which may in fact be influencing humpback dolphin distribution and habitat use.

Anthropogenic activity may also be influencing humpback dolphin occurrence (see 5.2.1 above; Chapter 3) so future studies would benefit from quantifying vessel traffic density, and investigating associated underwater noise. Combining vessel density and acoustic data with behavioural response data might provide insight into the potential impacts from vessel traffic and whether it influences dolphin behaviour, habitat use and distribution.

Large-scale variation in oceanographic features such as sea surface temperature, SST (e.g. the Ningaloo Niño; Feng et al. 2015b) may also influence dolphin distribution (e.g. Sprogis et al. 2017). Variability in SST was evident in the Autumn-Winter SST layer (Fig. S3.4 in APPENDIX S3). Obtaining mean values of SST across years for modelling of humpback dolphin distribution was deemed suitable given low variation (Chapter 3). Future studies could look at modelling individual years (and by individual season), and investigate whether SST has an influence (directly or indirectly) on humpback dolphin distribution. This is worth examining, given the SST variability shown during El Nino and La Nina years and the influence this has on the Leeuwin Current along WA’s coast (Feng et al. 2013, Feng et al. 2015a), and marine megafauna at Ningaloo Reef (e.g. Anderson et al. 2014). The current Plan does not explicitly consider climate change (Davies et al. 2016). I therefore recommend that future Plan reviews incorporate this factor into management strategies of all ecological values as there are likely to be broader ecosystem and species implications of coral reef degradation within NMP. Our understanding of climate change impacts on Ningaloo Reef health is developing (e.g. Johansson et al. 2010, Hinrichs et al. 2013, Fulton et al. 2014), however, the resulting influence on humpback dolphin distribution is currently unknown.

The species distribution model developed in this study (Chapter 3) could be used to predict humpback dolphin distribution throughout the entire NMP. The results of this modelling could be used to: 1) assess model transferability (extrapolative accuracy) to new areas across large spatial scales (Heikkinen et al. 2012, Torres et al. 2015); 2) guide future survey efforts (e.g. Peterman et al. 2013); and 3) identify areas of suitable habitat for humpback dolphins that might be under threat from overlapping human activity (e.g. Coral Bay; see Smallwood et al. 2011)

Understanding humpback dolphin space use at the broader regional level is important to inform future marine spatial planning. For example, around 200 km to the north-east of the NWC lies the Montebello Islands Marine Park (MIMP; CALM & MPRA 2007). A minimum of 28 individually distinctive humpback dolphins has been identified in the MIMP between February and July 2017, including resights (Raudino et al. 2018). A comparative study between northern NMP and MIMP would represent a valid way to explore potential dolphin movements between the NWC and MIMP; and assess demography, habitat use and social structure of island-associated humpback dolphins exposed to minimal anthropogenic activity. To date, however, there have been no matches of individuals from the NWC and MIMP (Raudino et al. 2018). The MIMP could serve as a quasi-control site (as suggested for the NWC; Chapter 2, 5.3.2 above) for those studies of humpback dolphins in non-protected areas of the Pilbara that are exposed to anthropogenic activity (e.g. Onslow, Dampier Archipelago). Further, collection of genetic samples at the MIMP will also assist in understanding population genetic structure, gene flow and the designation of management units.

5.4.3 Better understanding of social structure

Collection of genetic material from more individuals through biopsy sampling will assist in a) confirming sex and, thus, assortative interactions by sex amongst individuals in the population, and b) determine whether kinship influences these associations. Behavioural studies using focal follows are needed to examine and compare male behaviour and access to females. This behavioural data, combined with kinship and paternity analyses, will help elucidate the potential presence of alliances and coalitions among adult male humpback dolphins. Further behavioural data will assist in understanding potential sexual segregation in this population and observed ‘social avoidances’ amongst individuals, as well as providing insight into how sociality is influenced by resource availability and predation risk.

5.5 Conclusion

My assessment of humpback dolphins around the NWC, combining aspects of population demographics (Chapter 2/Hunt et al. 2017), habitat use (Chapter 3/Hunt et al. in review), and social structure (Chapter 4/Hunt et al. in review), has provided a robust understanding of the ecology of this population. Results from each of these data chapters reinforce that the NWC represents an important habitat of high conservation value for Vulnerable humpback dolphins. As such, the NWC represents an ideal study site for ongoing research and monitoring to gain a deeper understanding of this species’ ecological requirements and to better inform their conservation and management in Australian waters.

With a regulatory management framework already in place within the NMP, strategic research objectives identified at the state and national level, and significant baseline information available, there is a unique and important opportunity here to implement conservation measures that will benefit the conservation of this endemic, Vulnerable species.

SUPPLEMENTARY INFORMATION

APPENDIX S1 – CHAPTER 1

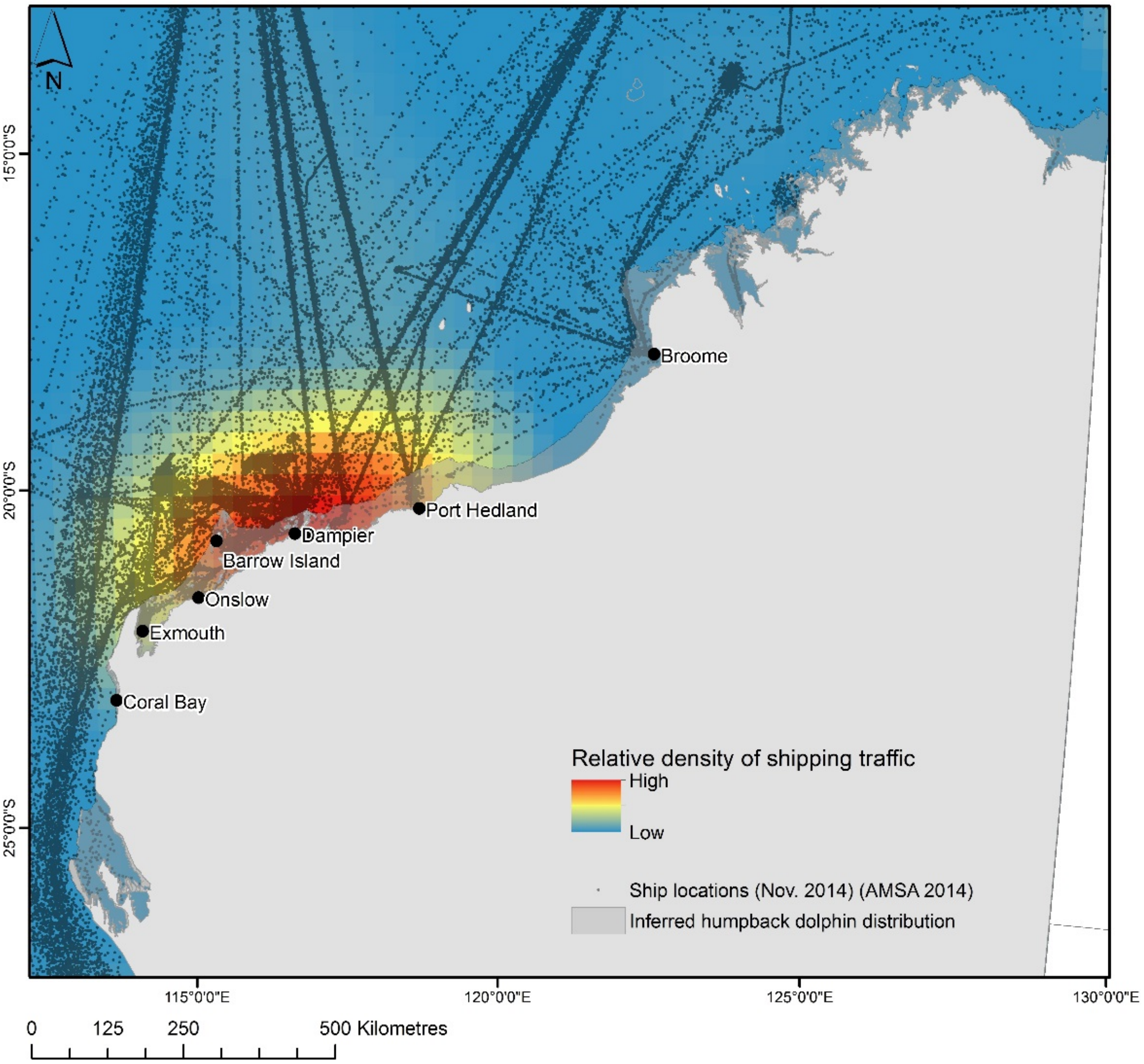


Fig. S1.1. Current level of shipping and its overlap with inferred humpback dolphin distribution along the northern coastline of Western Australia (AMSA 2014). Point ship locations are thinned data from the satellite Automated Identification System (AIS). The relative density gridded data was created using the kernel density tool with default settings in ArcMap 10.3 (ESRI). Figure taken from Hanf et al. (2016), reuse is permitted in a thesis under Elsevier License Number 3916151272291.

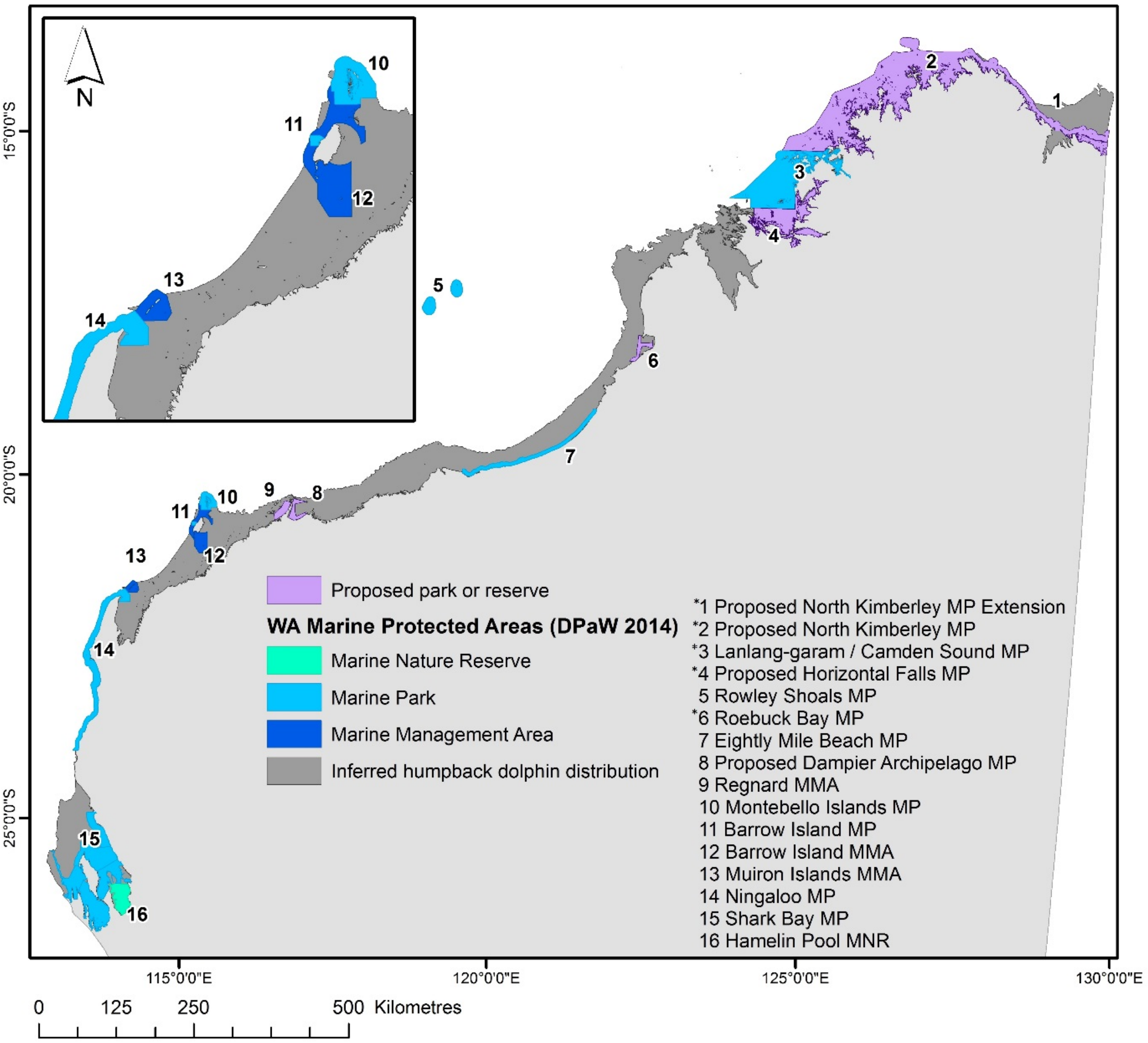


Fig. S1.2. Marine Protected Areas (MPAs) (DPaW 2014c) along northern Western Australia in relation to inferred humpback dolphin distribution. Figure taken from Hanf et al. (2016), reuse is permitted in a thesis under Elsevier License Number 3916151272291. NB. ‘*’ indicates marine parks (1, 2, 3, 4 & 6) that are no longer ‘proposed’ and have been formally gazetted since the publication of Hanf et al. (2016) in January 2016.

APPENDIX S2 – CHAPTER 2

S2.1 Photo-identification protocol

Individual humpback dolphins were primarily identified based on the unique natural marks on their dorsal fins (Würsig & Jefferson 1990), which included nicks, notches, and scoops on the leading and trailing edges of the dorsal fin, and loss of pigmentation (LOP) in the upper region of the dorsal fin and/or saddle patch (see Brown et al. 2016a for LOP definitions). Secondary features such as scarring, small patches of LOP and peduncle nicks/notches were also used for individual identification. All photographs taken were examined and subject to a modified quality (Q) and distinctiveness (D) grading protocol (derived from Urian et al. 1999, 2015) to minimise misidentification and heterogeneity in capture probabilities. All photographs (JPEG format) were examined and classified into three grades (excellent, good, and poor) according to four image quality parameters: (1) clarity – refers to the sharpness/level of focus of an image, (2) contrast – refers to the range of tones in the image, where too much contrast causes detail of small features to wash out to white and too little contrast the dorsal fin is lost into the background and features lack definition, (3) angle – refers to the angle of the dolphin's dorsal fin relative to the camera, and (4) partial – refers to how much of the dorsal fin is visible in the image, includes where water droplets may be present on the fin and obstructing features. Each of these image quality parameters received a score between 2 and 10 (where 10 is excellent and 2 is poor). These scores were then summed and divided by four to achieve an overall image quality (Q) score out of 10. Photographs of excellent grade were those with a Q value 8 to 10, those with a good grade were Q5 to 7, and a poor grade was Q < 5.

Once a Q value had been assigned to an image, distinctiveness was assessed for each individual photo based on the relative distinctive features displayed on the dorsal fin. A distinctiveness score (D1, D2, D3 or Clean) was assigned to each individual photo, independent of image quality, where; D1 = highly distinctive features (singular or multiple), includes individuals with missing tops, extended tips, large notches or multiple notches, and/or extensive LOP; D2 = medium distinctive features – single feature (e.g. notch), or multiple smaller less distinctive nicks and notches, fins with substantial scarring, and/or some LOP evident; and D3 = no distinctive features - fins basically clean except for minor scarring or small waves, or very small nicks. Images that were considered 'Clean' did not display any distinctive features, except for very minor scars that were sufficient enough to delineate different individuals within a sighting and ascertain total dolphin school sizes.

Only excellent and good quality ($Q \geq 5$) photographs displaying distinctive individuals (D1 and D2) were used to identify individuals and develop an identification catalogue for the analysis of abundance, site fidelity and residency patterns.

All individual images of dorsal fins were processed, matched to the catalogue and managed in the photo-identification data management software ‘Discovery’ (Gailey & Karczmarksi 2012). Before matching or adding new individuals to the identification catalogue, photographs were cross-checked by a minimum of two experienced research assistants against all images in the catalogue. After a match was confirmed (or a new individual identification number assigned), individual capture data was entered into the Discovery database before being verified by the research project leader (i.e. Tim Hunt, or someone designated on his behalf). Juveniles of sufficient distinctiveness were included in capture histories for analysis, however, calves were excluded from all analyses because they typically do not possess sufficient markings to ensure their future recognition without error.

S2.2 Proportion of marked individuals in the population

The proportion of marked (i.e. distinct) individuals in the population ($\hat{\theta}$) was estimated as the average number of marked individuals (D1 & D2) found in each sighting where photographic coverage was ≥ 50% (determined by total number of animals photographically identified per sighting over the best school size estimated in the field, excluding calves) (modified from Nicholson et al. 2012).

To estimate the total population size, we adjusted the model estimates to take into account the proportion of marked individuals in the population (Wilson et al. 1999, Nicholson et al. 2012) as follows:

$$\hat{N}_{total} = \frac{\hat{N}_m}{\hat{\theta}},$$

where $\hat{N}_{total}$ is the estimated total population size, $\hat{N}_m$ is the estimated marked population size and $\hat{\theta}$ is the estimated proportion of marked individuals in the population. Standard errors of total population sizes were calculated as per (Williams et al. 2002), where n is the total number of photographs from which $\hat{\theta}$ was derived:

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

Lower and upper log-normal 95% confidence intervals were calculated as

$\hat{N}_{total}^{Lower} = \frac{\hat{N}_{total}}{C}$, $\hat{N}_{total}^{Upper} = \hat{N}_{total} \times C$ (Burnham et al. 1987) where:

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

S2.3 Validation of model assumptions and goodness-of-fit results

PCRD models assume: (1) the population is closed within P-periods, (2) all individuals (marked and unmarked) have equal probability of being captured within a sampling period, (3) all individuals have equal probability of survival, (4) marks are unique, permanent and identified correctly, (5) each individual's probability of capture is independent of all others, (6) the study area remains constant, and (7) the sampling interval for a particular s-period is instantaneous (i.e. that is sampling periods are short and birth, death, immigration and emigration do not occur during the recapture process) (Pollock 1982, Pollock et al. 1990, Williams et al. 2002).

POPAN models assume: (1) all individuals (marked and unmarked) have equal probability of being captured within a sampling period, (2) all individuals have equal probability of survival, (3) marks are unique, permanent and identified correctly, (4) sampling is instantaneous, and (5) the study area remains constant (Pollock et al. 1990, Williams et al. 2002).

Australian humpback dolphins do not associate at random (Parra et al. 2011), thus, the assumption of independent individual capture probability may have been violated, given that close associates of an individual are more likely to be captured over other individuals. However, associations are dynamic and change often with time (Parra et al. 2011). We therefore deemed violation of this assumption to cause minor bias in our estimates. Secondary sampling periods were kept as short as possible (3 to 31 days); and thus we considered biases due to births, deaths and migration to be negligible given these dolphins' lifespan (decades).

To test the assumption that the population is closed within each P-period, we used the Otis et al. (1978) closure test for capture-recapture data implemented in the CloseTest software (Stanley & Richards 2005, Stanley & Richards 2011). Further, we used U-CARE to carry out TEST 2.CT for heterogeneity in capture probabilities, including testing for a trap response, and used TEST 3.SR to test for a transience effect (i.e. dolphins sighted only once during the study period more often than expected). We also used TEST 3.SM to examine any difference 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).

S2.4 Results

Table S2.1. Reduced set of Pollock’s Closed Robust Design models fitted to the capture histories of Australian humpback dolphins to estimate population size (N), apparent survival rate (Φ), emigration (γ'', γ') and capture probability (p). The notation ‘•’ indicates that a given parameter was kept constant, ‘*t*’ indicates that a given parameter was allowed to vary with time, and ‘*season*’ indicates that emigration parameters were allowed to vary by seasons Autumn-Winter (April to July; P1, P3 & P5) and Winter-Spring (August to October; P2, P4, & P6). Capture probability was allowed to vary with time among and within primary sampling periods (*t,s*). Recapture probability (c) was set equal to p and therefore is not included in the model description. The top three ranked models are shown in **bold.**

Model	Rank	AICc	Δ AICc	AICc weights	Cumulative AICc weight (%)	Number of parameters
Φ(•) γ"(season) ≠ γ'(•) p(t,s)	**1**	**585.3**	**0.0**	**0.331**	**33.12%**	**47**
Φ(•) γ"(season) ≠ γ'(season) p(t,s)	**2**	**585.4**	**0.1**	**0.318**	**64.92%**	**48**
Φ(•) γ"(season) = γ'(season) p(t,s)	**3**	**586.9**	**1.5**	**0.154**	**80.30%**	**46**
Φ(t) γ"(season) = γ'(season) p(t,s)	4	589.3	4.0	0.046	84.87%	50
Φ(•) γ"(t) ≠ γ'(•) p(t,s)	5	589.9	4.6	0.033	88.19%	50
Φ(t) γ"(•) = γ'(•) p(t,s)	6	590.0	4.7	0.032	91.41%	49
Φ(•) γ"(•) ≠ γ'(•) p(t,s)	7	591.3	6.0	0.016	93.06%	46
Φ(t) γ"(season) ≠ γ'(•) p(t,s)	8	591.8	6.5	0.013	94.34%	51
Φ(t) γ"0 = γ'0 p(t,s)	9	592.0	6.6	0.012	95.54%	48
Φ(t) γ"(•) ≠ γ'(•) p(t,s)	10	592.5	7.2	0.009	96.46%	50
Φ(•) γ"(•) = γ'(•) p(t,s)	11	592.6	7.2	0.009	97.35%	45
Φ(t) γ"(season) ≠ γ'(season) p(t,s)	12	593.3	8.0	0.006	97.96%	52
Φ(•) γ"(t) = γ'(t) p(t,s)	13	593.7	8.4	0.005	98.46%	49
Φ(t) γ"(•) ≠ γ'(season) p(t,s)	14	593.8	8.5	0.005	98.93%	51
Φ(•) γ"(•) ≠ γ'(season) p(t,s)	15	593.9	8.6	0.005	99.38%	47
Φ(t) γ"(t) = γ'(t) p(t,s)	16	594.6	9.3	0.003	99.70%	52
Φ(t) γ"(•) ≠ γ'(t) p(t,s)	17	596.1	10.8	0.002	99.86%	52
Φ(t) γ"(t) ≠ γ'(•) p(t,s)	18	597.1	11.8	0.001	99.95%	53
Φ(•) γ"0 = γ'0 p(t,s)	19	600.4	15.1	<0.001	99.96%	44
Φ(•) γ"(t) ≠ γ'(t) p(t,s)	20	600.6	15.3	<0.001	99.98%	53
Φ(t) γ"(t) ≠ γ'(t) p(t,s)	21	601.2	15.8	<0.001	99.99%	55
Φ(•) γ"(•) ≠ γ'(t) p(t,s)	22	601.7	16.4	<0.001	100.00%	49

Table S2.2. Weighted-average estimates of capture probabilities (p) for all 22 Robust Design models (for model descriptions see Table S2). P-period = primary sampling period, s-period = secondary sampling period, LCI = 95% Lower Confidence Interval limit, UCI = 95% Upper Confidence Interval limit, p_P = effective detection probability per P-period: $p_P = 1 - (1-p_{s1})(1-p_{s2})...(1-p_K)$, where s1, s2,... sK, are the s-period capture probabilities in each P-period.

Parameter	P-period	s-period	Estimate	LCI	UCI	p_P
p	1	1	0.11	0.05	0.25	0.55
p	1	2	0.10	0.04	0.22	
p	1	3	0.32	0.17	0.53	
p	1	4	0.16	0.07	0.32	
p	2	5	0.18	0.09	0.31	0.66
p	2	6	0.25	0.14	0.39	
p	2	7	0.09	0.04	0.20	
p	2	8	0.33	0.21	0.49	
p	2	9	0.11	0.05	0.22	
p	3	10	0.08	0.04	0.18	0.71
p	3	11	0.07	0.03	0.16	
p	3	12	0.01	0.00	0.09	
p	3	13	0.18	0.11	0.29	
p	3	14	0.29	0.19	0.42	
p	3	15	0.07	0.03	0.16	
p	3	16	0.22	0.14	0.34	
p	3	17	0.18	0.11	0.29	
p	4	18	0.13	0.06	0.25	0.86
p	4	19	0.22	0.13	0.35	
p	4	20	0.40	0.27	0.55	
p	4	21	0.20	0.11	0.33	
p	4	22	0.07	0.03	0.18	
p	4	23	0.16	0.09	0.29	
p	4	24	0.31	0.20	0.45	
p	4	25	0.20	0.11	0.33	
p	5	26	0.24	0.16	0.36	0.50
p	5	27	0.21	0.13	0.32	
p	5	28	0.02	0.01	0.09	
p	5	29	0.11	0.06	0.20	
p	5	30	0.05	0.02	0.12	
p	6	31	0.11	0.05	0.22	0.71
p	6	32	0.07	0.03	0.18	
p	6	33	0.04	0.01	0.13	
p	6	34	0.39	0.25	0.55	
p	6	35	0.07	0.03	0.18	
p	6	36	0.25	0.14	0.39	
p	6	37	0.16	0.08	0.29	

Table S2.3. Real parameter estimates of apparent survival (Φ), capture probability (p), temporary emigration (γ'', γ'), and abundance (N) for the Robust Design model $\Phi(\bullet)\ \gamma''(season) \neq \gamma'(\bullet)\ p(t,s)$ (Rank 1). N_m = estimate of number of marked animals in the population. P-period = primary sampling period, s-period = secondary sampling period, SE = standard error, LCI = 95% Lower Confidence Interval limit, UCI = 95% Upper Confidence Interval limit.

Parameter	P-period	s-period	Estimate	SE	LCI	UCI
Φ	ALL	-	0.99	0.07	0.00	1.00
γ''	P2, P4, & P6	-	0.31	0.07	0.20	0.45
γ''	P3 & P5	-	<0.001	<0.001	<0.001	<0.001
γ'	Constant	-	0.80	0.11	0.50	0.94
p	1	1	0.11	0.05	0.05	0.25
p	1	2	0.10	0.04	0.04	0.22
p	1	3	0.32	0.10	0.17	0.53
p	1	4	0.16	0.06	0.07	0.32
p	2	5	0.17	0.05	0.09	0.30
p	2	6	0.24	0.06	0.14	0.38
p	2	7	0.09	0.04	0.04	0.20
p	2	8	0.33	0.07	0.21	0.48
p	2	9	0.10	0.04	0.05	0.22
p	3	10	0.08	0.03	0.04	0.18
p	3	11	0.07	0.03	0.03	0.16
p	3	12	0.01	0.01	0.00	0.09
p	3	13	0.18	0.05	0.11	0.29
p	3	14	0.29	0.06	0.20	0.42
p	3	15	0.07	0.03	0.03	0.16
p	3	16	0.22	0.05	0.14	0.34
p	3	17	0.18	0.05	0.11	0.29
p	4	18	0.12	0.04	0.06	0.24
p	4	19	0.21	0.06	0.12	0.34
p	4	20	0.39	0.07	0.26	0.53
p	4	21	0.20	0.05	0.11	0.32
p	4	22	0.07	0.03	0.03	0.18
p	4	23	0.16	0.05	0.08	0.28
p	4	24	0.30	0.06	0.19	0.44
p	4	25	0.20	0.05	0.11	0.32
p	5	26	0.25	0.05	0.16	0.36
p	5	27	0.21	0.05	0.13	0.32
p	5	28	0.02	0.02	0.01	0.09
p	5	29	0.11	0.04	0.06	0.21
p	5	30	0.05	0.02	0.02	0.13
p	6	31	0.10	0.04	0.04	0.21
p	6	32	0.07	0.03	0.02	0.17
p	6	33	0.03	0.02	0.01	0.13
p	6	34	0.37	0.07	0.24	0.52
p	6	35	0.07	0.03	0.02	0.17
p	6	36	0.23	0.06	0.14	0.37
p	6	37	0.15	0.05	0.08	0.27
N_m	1	-	61.63	14.61	44.44	107.12
N_m	2	-	57.46	8.26	46.76	81.20
N_m	3	-	72.39	7.26	62.36	92.12
N_m	4	-	54.66	3.91	49.98	66.68
N_m	5	-	83.29	12.97	64.77	117.55
N_m	6	-	56.14	7.44	46.59	77.69

Table S2.4. Real parameter estimates of apparent survival (Φ), capture probability (p), temporary emigration (γ'', γ'), and abundance (N) for the Robust Design model $\Phi(\bullet)\ \gamma''(season) \neq \gamma'(season)\ p(t,s)$ (Rank 2). N_m = estimate of number of marked animals in the population. P-period = primary sampling period, s-period = secondary sampling period, SE = standard error, LCI = 95% Lower Confidence Interval limit, UCI = 95% Upper Confidence Interval limit.

Parameter	P-period	s-period	Estimate	SE	LCI	UCI
Φ	ALL	-	1.00	0.07	0.00	1.00
γ''	P2, P4, & P6	-	0.35	0.06	0.23	0.48
γ''	P3 & P5	-	<0.001	<0.001	<0.001	<0.001
γ'	P2, P4, & P6	-	0.56	0.19	0.21	0.85
γ'	P3 & P5	-	1.00	0.18	0.00	1.00
p	1	1	0.11	0.05	0.05	0.25
p	1	2	0.10	0.04	0.04	0.22
p	1	3	0.32	0.10	0.17	0.53
p	1	4	0.16	0.06	0.07	0.32
p	2	5	0.18	0.06	0.10	0.32
p	2	6	0.25	0.07	0.15	0.40
p	2	7	0.09	0.04	0.04	0.20
p	2	8	0.34	0.08	0.21	0.50
p	2	9	0.11	0.04	0.05	0.23
p	3	10	0.08	0.03	0.04	0.17
p	3	11	0.07	0.03	0.03	0.16
p	3	12	0.01	0.01	0.00	0.09
p	3	13	0.18	0.05	0.10	0.29
p	3	14	0.29	0.06	0.19	0.41
p	3	15	0.07	0.03	0.03	0.16
p	3	16	0.22	0.05	0.14	0.33
p	3	17	0.18	0.05	0.10	0.29
p	4	18	0.13	0.05	0.06	0.25
p	4	19	0.23	0.06	0.13	0.36
p	4	20	0.41	0.07	0.28	0.56
p	4	21	0.21	0.06	0.12	0.34
p	4	22	0.08	0.04	0.03	0.18
p	4	23	0.17	0.05	0.09	0.30
p	4	24	0.32	0.07	0.20	0.46
p	4	25	0.21	0.06	0.12	0.34
p	5	26	0.23	0.05	0.15	0.35
p	5	27	0.20	0.05	0.12	0.31
p	5	28	0.02	0.02	0.01	0.09
p	5	29	0.11	0.03	0.05	0.20
p	5	30	0.05	0.02	0.02	0.12
p	6	31	0.11	0.04	0.05	0.22
p	6	32	0.07	0.03	0.03	0.18
p	6	33	0.04	0.02	0.01	0.13
p	6	34	0.39	0.08	0.25	0.55
p	6	35	0.07	0.03	0.03	0.18
p	6	36	0.25	0.06	0.14	0.39
p	6	37	0.16	0.05	0.08	0.29
N_m	1	-	61.63	14.61	44.44	107.12
N_m	2	-	55.96	7.90	45.88	78.94
N_m	3	-	73.42	7.54	62.96	93.87
N_m	4	-	53.51	3.53	49.41	64.59
N_m	5	-	87.35	14.34	66.90	125.30
N_m	6	-	54.23	6.86	45.56	74.36

Table S2.5. Real parameter estimates of apparent survival (*Φ*), capture probability (*p*), temporary emigration (γ'', γ'), and abundance (*N*) for the Robust Design model *Φ(•)* γ''*(season)* = γ'*(season) p(t,s)* (Rank 3). N_m = estimate of number of marked animals in the population. P-period = primary sampling period, s-period = secondary sampling period, SE = standard error, LCI = 95% Lower Confidence Interval limit, UCI = 95% Upper Confidence Interval limit.

Parameter	P-period	s-period	Estimate	SE	LCI	UCI
Φ	ALL	-	0.85	0.05	0.73	0.92
$\gamma''= \gamma'$	P2, P4, & P6	-	0.31	0.06	0.20	0.45
$\gamma''= \gamma'$	P3 & P5	-	<0.001	<0.001	<0.001	<0.001
p	1	1	0.11	0.05	0.05	0.25
p	1	2	0.10	0.04	0.04	0.22
p	1	3	0.32	0.10	0.17	0.53
p	1	4	0.16	0.06	0.07	0.32
p	2	5	0.18	0.06	0.09	0.31
p	2	6	0.25	0.07	0.14	0.40
p	2	7	0.09	0.04	0.04	0.20
p	2	8	0.34	0.08	0.21	0.50
p	2	9	0.11	0.04	0.05	0.23
p	3	10	0.08	0.03	0.04	0.17
p	3	11	0.07	0.03	0.03	0.16
p	3	12	0.01	0.01	0.00	0.09
p	3	13	0.18	0.05	0.10	0.29
p	3	14	0.29	0.06	0.19	0.41
p	3	15	0.07	0.03	0.03	0.16
p	3	16	0.22	0.05	0.14	0.33
p	3	17	0.18	0.05	0.10	0.29
p	4	18	0.13	0.05	0.06	0.26
p	4	19	0.23	0.06	0.13	0.36
p	4	20	0.42	0.07	0.29	0.56
p	4	21	0.21	0.06	0.12	0.34
p	4	22	0.08	0.04	0.03	0.19
p	4	23	0.17	0.05	0.09	0.30
p	4	24	0.32	0.07	0.21	0.47
p	4	25	0.21	0.06	0.12	0.34
p	5	26	0.24	0.05	0.16	0.36
p	5	27	0.21	0.05	0.13	0.31
p	5	28	0.02	0.02	0.01	0.09
p	5	29	0.11	0.04	0.06	0.20
p	5	30	0.05	0.02	0.02	0.12
p	6	31	0.11	0.04	0.05	0.22
p	6	32	0.07	0.04	0.03	0.18
p	6	33	0.04	0.03	0.01	0.13
p	6	34	0.39	0.08	0.26	0.55
p	6	35	0.07	0.04	0.03	0.18
p	6	36	0.25	0.06	0.15	0.39
p	6	37	0.16	0.05	0.08	0.29
N_m	1	-	61.63	14.61	44.44	107.12
N_m	2	-	56.31	8.11	45.99	79.96
N_m	3	-	73.29	7.36	63.02	93.13
N_m	4	-	53.30	3.44	49.31	64.15
N_m	5	-	85.18	13.52	65.85	120.87
N_m	6	-	53.89	6.74	45.38	73.71

Table S2.6. POPAN open models fitted to the capture histories of Australian humpback dolphins to estimate super population size, apparent survival (*Φ*), capture probability (*p*) and probability of entry into the study area (*pent*). Each model incorporates either constant (•) or time-varying (*t*) parameters.

Model	Rank	AICc	Δ AICc	AICc weights	Cumulative AICc weights (%)	Number of parameters
Φ(t) p(•) pent(t)	1	485.3	0.0	0.439	43.9%	11
Φ(t) p(t) pent(t)	2	485.5	0.2	0.401	84.0%	14
Φ(•) p(t) pent(t)	3	488.5	3.2	0.090	93.0%	12
Φ(•) p(•) pent(t)	4	489.0	3.7	0.070	100%	8
Φ(t) p(t) pent(•)	5	48376.7	47891.4	0.000	100%	10
Φ(•) p(•) pent(•)	6	48410.6	47925.2	0.000	100%	3

Table S2.7. Results from goodness-of-fit tests run in Program RELEASE and U-CARE for the six primary sampling periods of Australian humpback dolphin surveys conducted during 2013-2015 (April to October) around the North West Cape, Western Australia. Global test results (Test 2 + Test 3) and corresponding ĉ values are also included. χ2 = chi-squared statistic, df = degrees of freedom, N/A = statistic not available for this test.

Program	Parameters	TEST 3.SR	TEST 3.SM	TEST 2.CT[a]	Global test	$\hat{c}$
RELEASE	χ^2	2.06	6.80	0.39	9.24	0.99
	df	4	3	3	10	
	p-value	0.72	0.08	0.94	0.51	
U-CARE	Statistic	1.01	N/A	-0.58	N/A	1.33
	χ^2	2.57	7.78	1.11	16.00	
	df	4	3	3	12	
	p-value	0.31	0.05	0.57	0.19	

[a] This test is referred to as TEST 2.C in RELEASE.

Table S2.8. Models fitted to observed LIR data of Australian humpback dolphins on the North West Cape, Western Australia. For description of model equations see Whitehead (2001). The models that best fitted the data according to Akaike's Information Criterion, corrected for small sample size and overdispersion (QAICc) are shown in bold. ΔQAIC indicates how well the data support the less favoured model (Burnham & Anderson 2002).

Model equation	Model explanation	QAIC	ΔQAIC	Model parameter explanation[d]
a2*exp(-a1*td)	**Emigration/mortality[a]**	**2437.8**	**0.0**	**a1=emigration rate; 1/a2=N**
(1/a1)*exp(-td/a2)	**Emigration/mortality[a]**	**2437.8**	**0.0**	**a1=N; a2=mean residence time**
a3*exp(-a1*td)+a4*exp(-a2*td)	Emigration + reimmigration + mortality	2440.0	2.2	a1=N; a2=mean time in study area; a3=mean time out of study area; a4=mortality rate
a2+a3*exp(-a1*td)	Closed: emigration + reimmigration[b]	2441.0	3.2	a1=emigration rate; a2/(a2+a3)=proportion of population in study area at any time
a1	Closed (no movement)[c]	2441.4	3.6	a1=N
1/a1	Closed (no movement)[c]	2441.4	3.6	1/a1=N
(exp(-a4*td)/a1).*((1/a3)+(1/a2)*exp(-(1/a3+1/a2)*td))/(1/a3+1/a2)	Emigration + reimmigration + mortality	2441.8	4.0	a1=N; a2=mean time in study area; a3=mean time out of study area; a4=mortality rate

[a,c] Both model equations are considered the same but are parameterized differently, and yielded identical QAIC values.

[b] The corresponding emigration + reimmigration model [(1/a1)*((1/a3)+(1/a2)*exp(-(1/a3+1/a2)*td))/(1/a3+1/a2)] from (Whitehead 2001, 2009) is not reported. This model includes the best fitting model plus one parameter, and given QAIC=-2LogLikelihood/ĉ + 2K (where K is the number of parameters), it is therefore constrained to have ΔQAIC within 2 of the best fitting model (because Log-Likelihood cannot decrease). It is therefore not a representative model of proper fit to the data and is not reported (Hal Whitehead, pers. comm. 17 January 2016).

[d] For each model with a 'td' parameter, this refers to 'time lag'. Parameters a1, a2, a3 and a4 differ slightly amongst models and are therefore explained in the table. 'N' refers to the population size (at any one time) in the study area (Whitehead 2009).

APPENDIX S3 – CHAPTER 3

Table S3.1. Descriptive summary of ecogeographic predictor variables used in ensemble species distribution modelling of Australian humpback dolphins in northern Ningaloo Marine Park. All predictor variable raster layers were derived in ArcMap 10.3.1 (ESRI, Redlands, California), and all layers (except habitat type, and depth) used tools in the Spatial Analyst extension*. All predictor variables, excluding SST, were considered fixed (i.e. did not vary temporally).

Predictor variable	Variable type	Variable abbreviation	Description
Benthic habitat type	Biotic (fixed)	Habitat	Broad scale habitat types (from Bancroft and Sheridan (2000) within the study area include: coral reef communities (intertidal or shallow/limestone) [CRCI]; coral reef communities (subtidal) [CRCS]; sand [S], subtidal reef (low relief - lagoonal) [SRL]; subtidal reef (low relief - seaward) [SRS]; shoreline reef [SHR]; macroalgae (limestone reef) [MA]; salt marsh [SM]; mangrove [MN], mudflat [MU]; and deep water mixed filter feeding and soft bottom communities [DWM]. These habitat maps were obtained using remote sensing imagery (25 m pixels) from Landsat aerial photography maps (sampled 1994) and habitat point data validated in the field (sampled 1999). See Table S3.2 and Fig. S3.2 for definitions. Habitat type for each grid cell was defined based on the predominant habitat type (i.e. > 50% of grid cell area, or closest largest) when intersected with the Bancroft and Sheridan (2000) habitat layer. Predominant habitat types within the study area were CRCS (~40%), SRS (~20%), SRL (~15%), CRCI (~10%), and S (~10%). The remaining habitat area (~5%) was made up of MA and SHR. SM, MN, MU, and DWM were not considered in analyses.
Water depth	Abiotic (fixed)	Depth	Bathymetric data was obtained from hyperspectral image mapping (3.5 m pixel resolution) collected in April 2006 (see Kobryn et al. 2011, Kobryn et al. 2013). Due to the hyperspectral data collection process, accuracy of depth measurements beyond 20 m was questionable. To account for this variability, and validate depths < 20 m, we overlayed the hyperspectral depth layer with *in situ* measurements of depth (*n* = 1467; from TES, ES and dolphin sightings; Fig. S3.1) and bathymetric grids obtained from Geoscience Australia (2008, 2009). Where hyperspectral depth discrepancies were > 5 m (i.e. in the > 20 m readings), depth values were manually altered to reflect the larger depth value. See Fig. S3.3.

			Given tidal range in the study area is up to 2.5 m, correction of depth data in relation to tidal state was not deemed necessary given: a) 500 m grid cells average depth measurements over a spatial scale where depth variation can be > 2.5 m, and b) humpback dolphins grow up to 2.7 m in length (Jefferson et al. 2015) so a (maximum) 2.5 m difference in water depth is likely to be negligible in terms of modelling species distribution.
Slope	Abiotic (fixed)	Slope	Derived from the depth layer* (see MacLeod 2013). See Fig. S3.3.
Seabed complexity	Abiotic (fixed)	Complexity	Derived from calculating the standard deviation of the slope layer* (see MacLeod 2013). See Fig. S3.3.
Sea surface temperature	Abiotic (temporal)	SST	SST was interpolated for both the Autumn-Winter (AW) and Winter-Spring (WS) seasons using the Original Kriging method (spherical semivariogram model with a 500 m output cell size and a 12 point variable search radius)*. The interpolated layer was derived from *in situ* measurements of SST (n = 405 for AW, and 521 for WS) at TES, ES and dolphin sightings (Fig. S3.1). The output variance of prediction raster was also calculated for each interpolated layer. Low values (0.7-3.4) indicated a high degree of confidence in the predicted values. See Fig. S3.4.
Distance to coast	Abiotic (fixed)	Dist_coast	Grid cells are assigned a distance to coast value using Euclidean distance*. See Fig. S3.3.
Distance to reef crest	Abiotic (fixed)	Dist_reef	Reef crest refers to coral reef habitat (including coral bommies) that are either exposed or very shallow (< 1 m) at low tide, and as such can create a physical barrier to dolphin movement. This digital layer was modified from Smallwood et al. (2012) and the Bancroft and Sheridan (2000) ‘Coral reef communities (intertidal or shallow/limestone)’ layer, as well as nautical charts and author’s knowledge of the study area. The purpose of this layer is to determine if offshore reef has an influence on dolphin distribution. Layer therefore does not include exposed or shallow reef adjacent to the shoreline, as the shoreline itself creates a physical barrier to dolphin movement, depending on the tidal level. Reef crest was intersected with each grid cell, and defined when reef crest encompassed > 50% of total grid cell area. Each non-reef crest grid cell was assigned a value based on Cost distance* from the mid-point of the cell to the nearest reef crest cell. See Fig. S3.3.
Distance to sanctuary zone	Anthropogenic (fixed)	Dist_sz	A total of six sanctuary zones (no fishing zones) are within the boundaries of the study area. Given fish assemblages at sanctuary zones in NMP have higher biomass and abundance than at sites where fishing is permitted (Fitzpatrick et al. 2015), and it’s

			hypothesised that consistent prey availability may be influencing regular use of NMP by humpback dolphins (Chapter 2/Hunt et al. 2017), we are considering the presence of the sanctuary zone and distance from it, together. We are making the assumption that highest density of fish is within the sanctuary zone, and that this reduces as a gradient the further you move away from it. Given humpback dolphins are considered opportunistic feeders (Parra & Jedensjö 2014), and the foraging observations observed in the study area (Hunt, unpub. data), we argue that there is a lack of evidence to suggest that sanctuary zones do not support relevant prey taxa for this species. Exploring this variable as a potential predictor of dolphin distribution is therefore justified. Sanctuary zones were intersected with each grid cell, and defined when the sanctuary zone encompassed > 50% of the grid cell area. Each grid cell outside a sanctuary zone was assigned a value based on Cost distance* from the mid-point of the cell to the perimeter of the sanctuary zone. A map of the sanctuary zones within the study area can be viewed in Fig. S3.2, see also DPaW DoF (2014). The distance to sanctuary zone gridded layer can be viewed in Fig. S3.3.
Distance to passage	Anthropogenic (fixed)	Dist_passage	North Passage, False Passage, and South Passage are areas of deeper water between reef crest that vessels use to transit through when leaving or returning to Tantabiddi boat ramp (Fig. 3.1). This variable was considered a proxy for human activity given commercial nature-based tourism (e.g. whaleshark swim-with and humpback whale swim-with tour operations) and recreational fishing vessels use these passages regularly during the tourism season (i.e. March to October) to get seaward side of the fringing reef and out to deeper waters. Points were created at the centre of each passage, and using Cost distance*, calculated the shortest distance from the mid-point of each grid cell to the nearest passage. See Fig. S3.3.
Distance to boat ramp	Anthropogenic (fixed)	Dist_ramp	Tantabiddi and Bundegi boat ramps (Fig. 3.1) are frequently used by vessels during the tourism season. This anthropogenic variable was also considered a proxy for human activity (i.e. vessel movement). Points were created at each of the two boat ramps, and using Cost distance*, calculated the shortest distance from the mid-point of each grid cell to the nearest boat ramp. See Fig. S3.3.

Table S3.2. Benthic habitat category definitions from Bancroft and Sheridan (2000) used in ensemble species distribution modelling (SDM) of Australian humpback dolphin in northern Ningaloo Marine Park. Categories above the bold double black line were included in SDMs. LAT/HAT = Lowest/Highest Astronomical Tide.

Habitat code	Habitat category	Definition (from Bancroft and Sheridan 2000)
CRCI	Coral reef communities (intertidal or shallow/limestone)	Located in the intertidal or shallow regions (< 1 m LAT) on a limestone substrate. This habitat includes the reef crest, reef flats and shallow back reef zones. Live coral cover varies greatly and some areas have a high proportion of coral rubble. Macroalgae, sand or pavement also may be present. Hard corals (e.g. *Acropora* spp.), soft corals (e.g. *Sinularia* spp.) are typical of the fauna present in these habitats. Parts of this habitat typically support a high diversity and abundance of fish and invertebrate fauna.
CRCS	Coral reef communities (subtidal)	High live coral cover with macroalgal turf and coralline algae covering areas of reef not occupied by living corals. Sand patches, bare pavement and rubble may also be present. This habitat is used to describe the upper seaward slope, sheltered back reef, deep lagoonal reef and bommie clusters. Areas of high coral cover are generally restricted to water depth less than 15 m. Offshore, these habitats are dominated by faster growing coral species such as *Acropora* (hard, branching) and *Montipora*. In the lagoons, coral communities consist of a mixture of *Acropora* and a diverse range of massive species (in particular family *Faviidae.*
S	Sand	Habitat is defined as subtidal habitats that have predominately white carbonate sands as a substrate, however the sand may overlay reef platform or have patches of other habitats present. Sand habitats are typically bare, and may have seasonal vegetation or permanent patches of seagrass or macroalgae. Invertebrate fauna may also be present.
SRL	Subtidal reef (low relief - lagoonal)	Describes subtidal areas of limestone substratum that may incorporate sand patches, rubble and scattered isolated corals. This habitat typically is pavement, which may have low relief (< 1 m high) and occurs within the sheltered shallow waters (< 10 depth) of the lagoons of the Ningaloo Marine Park. This habitat may support a diverse array of algae and sessile invertebrates including sponges, sea-whips and sea-pens, and may also support some macroalgae (e.g. *Turbinaria* sp., *Sargassum* sp., *Halimeda* sp.), or seagrass (e.g. *Halophila* sp.) in patchy mobile sands. Dugongs (*Dugong dugon*) are often seen feeding in this habitat within Ningaloo Marine Park.
SRS	Subtidal reef (low relief - seaward)	Habitat describes subtidal areas of limestone substratum that may be predominantly covered by sand. This habitat is typically pavement, which may have low relief (< 1 m high) and occurs in the more exposed deeper waters (> 15 m depth) seaward of the barrier reef system. This habitat is typical bare or overlaid with large sand patches, however macroalgal turf and sessile invertebrates may also be present.
SHR	Shoreline reef	The shoreline reef habitat is typically located in the lower intertidal or nearshore subtidal zones (< 1 m below LAT) and occurs as low relief reef platforms of sedimentary (limestone or sandstone) substratum that are contiguous with the shoreline. In the Ningaloo Marine Park,

		shoreline reef habitat typically supports turf algae and invertebrates such as molluscs (*Tridacna* spp. clams, *Cypraea* sp. cowries), hermit crabs (*Dardanus* sp.) and isolated soft and hard coral communities.
MA	Macroalgae (limestone reef)	Areas of subtidal limestone substratum of low or high relief. In the Ningaloo Marine Park and the proposed southern extension, this habitat is found in shallower waters (< 10 m depth) and may also incorporate mobile sand patches, and scattered isolated hard and soft corals. This habitat is generally covered in large fleshy macroalgae (e.g. *Sargassum* spp.) or macroalgal turf (red, green and brown algae). A wide range of invertebrate life such as sponges, ascidians and soft corals, are associated with this habitat.
DWM	Deep water mixed filter feeding and soft bottom communities/ Pelagic	This category is specific to those areas that are greater than 50m in depth. The focus in this classification is not on substrates but rather on the macrobiology of the water column, hence pelagic environments may have various substrates. Pelagic fish and invertebrates, and larval stages of various phyla dominate the macrobiology of this habitat. In the Ningaloo Marine Park, whale sharks (*Rhincodon typus*) and manta rays (*Manta birostris*) are known to feed in the surface waters of this habitat.
SM	Salt marsh	Areas of low relief located in the upper intertidal and supratidal (immediately above HAT) zones of low energy coastlines. The substrata consist of muddy or silty terrigenous sediment. Salt marsh habitats often occur landward of mangroves, tidal creeks and estuaries, and typically supports vegetation, but can also occur as unvegetated coastal saline flats. In the Ningaloo Marine Park burrowing crabs (*Uca* sp.) and ghost crabs (*Ocypode* sp.) are found in this habitat.
MU	Mudflat	Located in the lower intertidal zone and generally consists of terrigenous mud or silt sediments. Mudflats occur in areas of low energy and high deposition such as the areas seaward of mangroves. In the Ningaloo Marine Park, mudflat habitats are typically bare of vegetation, but support gastropods (e.g. *Cerinthium* sp.), crabs and invertebrate infauna.
MN	Mangrove	Areas of mangrove forest greater than 0.05 ha and typically is located in the upper intertidal zone. The substratum of this habitat typically comprises of mud and silt, however some mangrove species do occur on intertidal rocky shores. There are two mangrove species, *Avicennia marina* and *Rhizophora stylosa*, which occur in the Ningaloo Marine Park. Mangrove roots provide a substratum for many gastropods (e.g. *Natica, Cerithium, Strombus*) and other invertebrates, such as the mangrove crab (*Scylla serrata*) are often present.

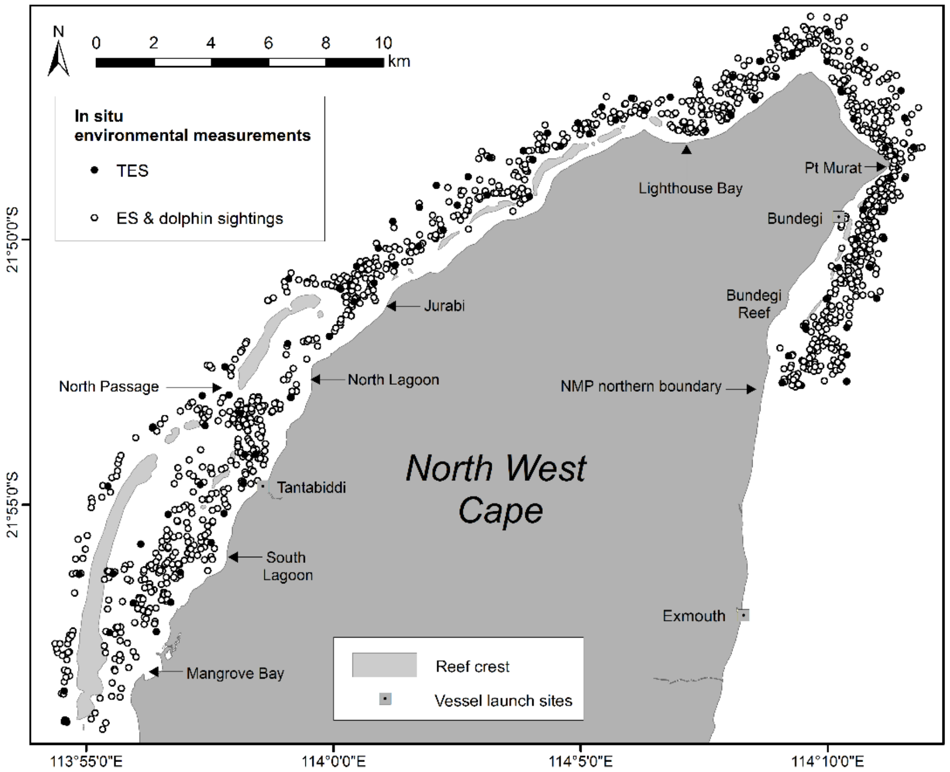


Fig. S3.1. Locations of *in situ* environmental measurements (depth, SST, salinity, turbidity, and pH) collected during boat-based surveys of Australian humpback dolphins in northern Ningaloo Marine Park (NMP) from May 2013 to October 2015. TES (transect environmental station) = 87 fixed locations (black dots) where a mean TES value of each variable was obtained (*n* per TES range 2-30, total *n* = 1582); ES (environmental station) and dolphin sighting data points (white dots, *n* = 1380, includes Indo-Pacific bottlenose dolphin sightings) are variable. Digital environmental layers of water depth (Fig. S3.3a) and SST (Fig. S3.4) were used in ensemble species distribution modelling, but turbidity, salinity, and pH digital layers were omitted from modelling due to low spatial variation and low confidence in predicted values across the study area (data not shown). See Table S3.1 for description of depth and SST layer creation.

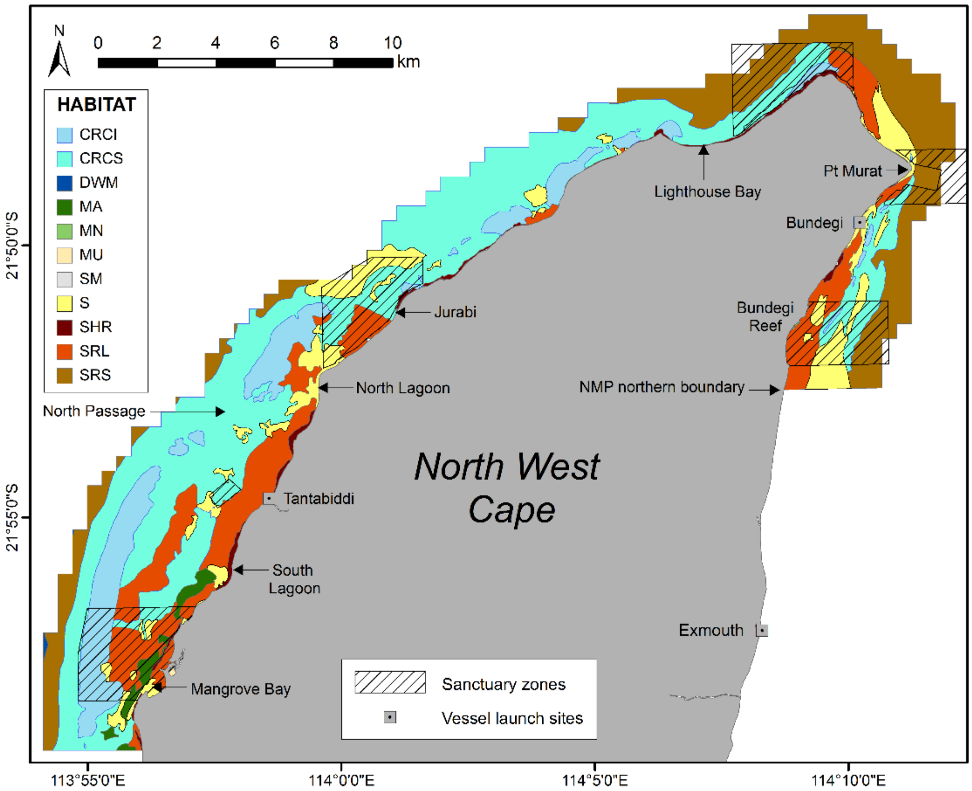


Fig. S3.2. Benthic habitat type (Bancroft and Sheridan 2000) and sanctuary zones of northern Ningaloo Marine Park used in ensemble species distribution modelling of Australian humpback dolphins. CRCI = coral reef communities (intertidal or shallow/limestone); CRCS = coral reef communities (subtidal); S = sand, SRL = subtidal reef (low relief - lagoonal); SRS = subtidal reef (low relief - seaward); SHR = shoreline reef; MA = macroalgae (limestone reef); SM = salt marsh; MN = mangrove, MU = mudflat; and deep DWM = water mixed filter feeding and soft bottom communities. See Table S3.2 for habitat category definitions.

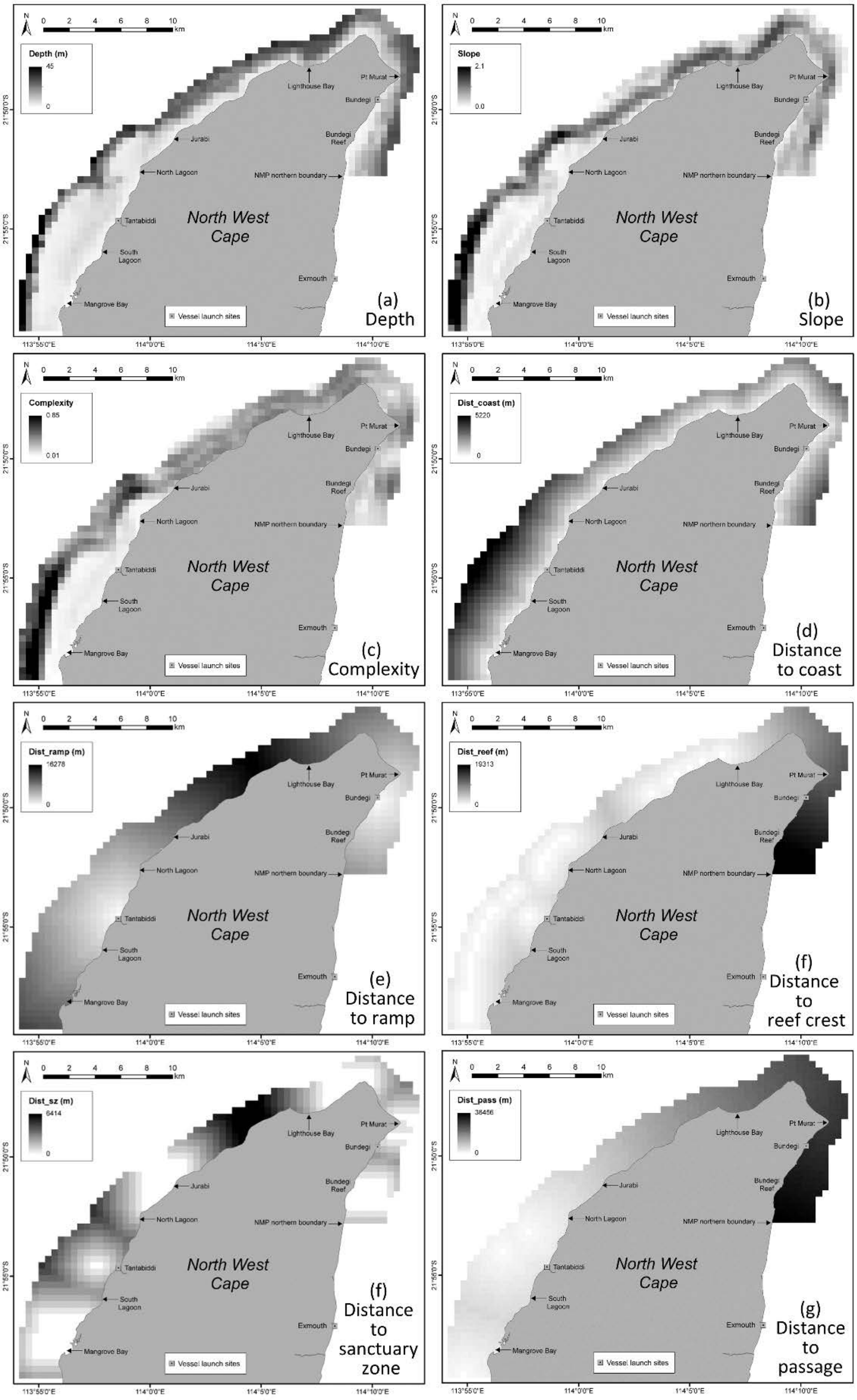


Fig. S3.3. Biotic, abiotic and anthropogenic environmental predictor variables used in ensemble species distribution modelling of Australian humpback dolphins in northern Ningaloo Marine Park (NMP) from May 2013 to October 2015. Layers: (a) depth; (b) slope; (c) seabed complexity; (d) distance to coast; (e) distance to ramp; (f) distance to reef crest; (g) distance to sanctuary zone; (h) distance to passage. Variables sampled at 500 x 500 m grid cell resolution. Raster layers derived in ArcMap 10.3.1 (ESRI). For variable definitions see Table S3.1.

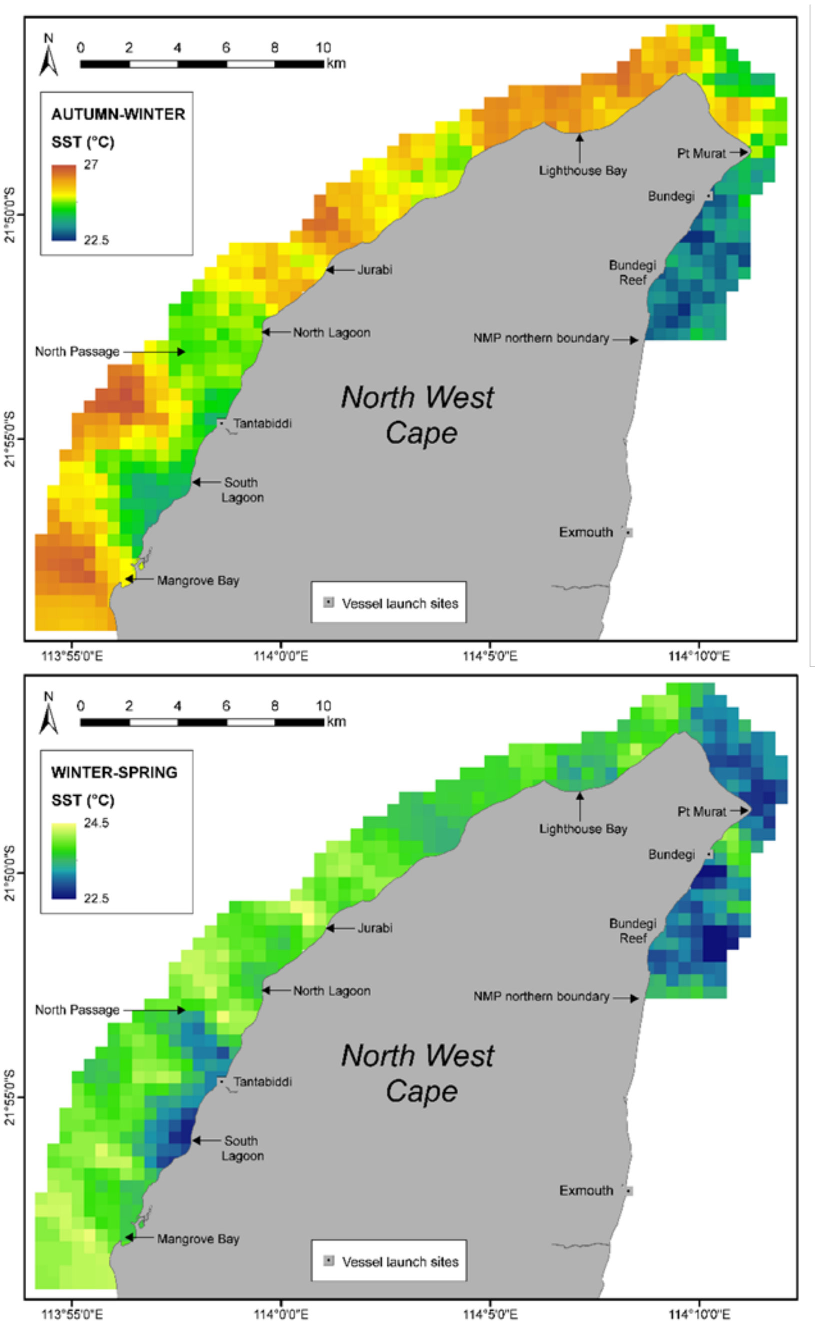
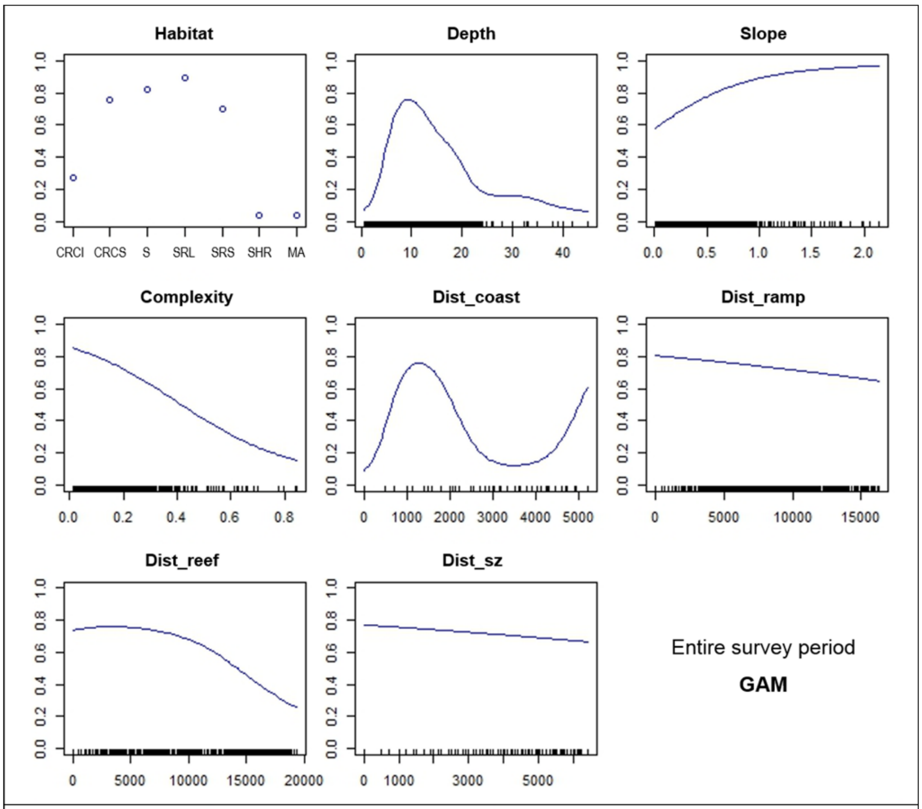


Fig. S3.4. Sea surface temperature (SST) maps of northern Ningaloo Marine Park (NMP) for the Autumn-Winter season (top; April-July) and Winter-Spring season (bottom; August-October) used in ensemble species distribution modelling of Australian humpback dolphins. Layer derived from measurements of data collected *in situ* (see Fig. S3.1) and using the original kriging interpolation in the Spatial Extension of ArcMap 10.3.1 (ESRI). For layer description see Table S3.1.


Habitat
Depth
Slope
Complexity
Dist_coast
Dist_ramp
Dist_reef
Dist_sz
0.0
0.2
0.4
0.6
0.8
1.0
CRCI
CRCS
S
SRL
SRS
SHR
MA
0
10
20
30
40
0.0
0.5
1.0
1.5
2.0
0.0
0.2
0.4
0.6
0.8
0
1000
2000
3000
4000
5000
0
5000
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15000
0
5000
10000
15000
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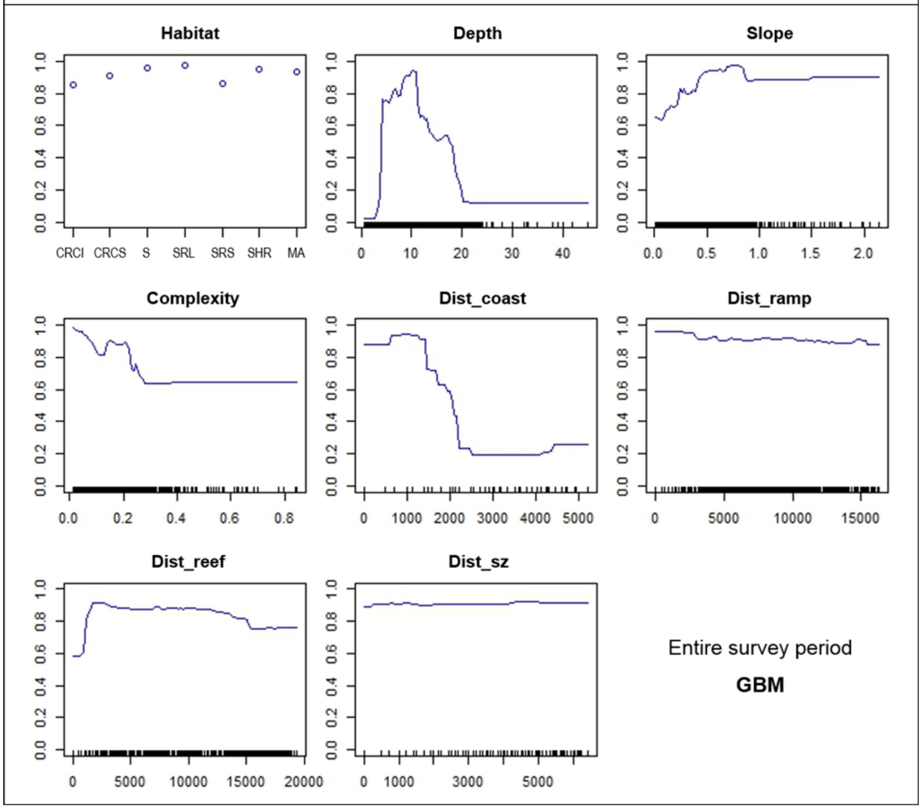
1000
3000
5000
Entire survey period
GAM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Slope
Complexity
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Dist_reef
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0.8
1.0
CRCI
CRCS
S
SRL
SRS
SHR
MA
0
10
20
30
40
0.0
0.5
1.0
1.5
2.0
0.0
0.2
0.4
0.6
0.8
0
1000
2000
3000
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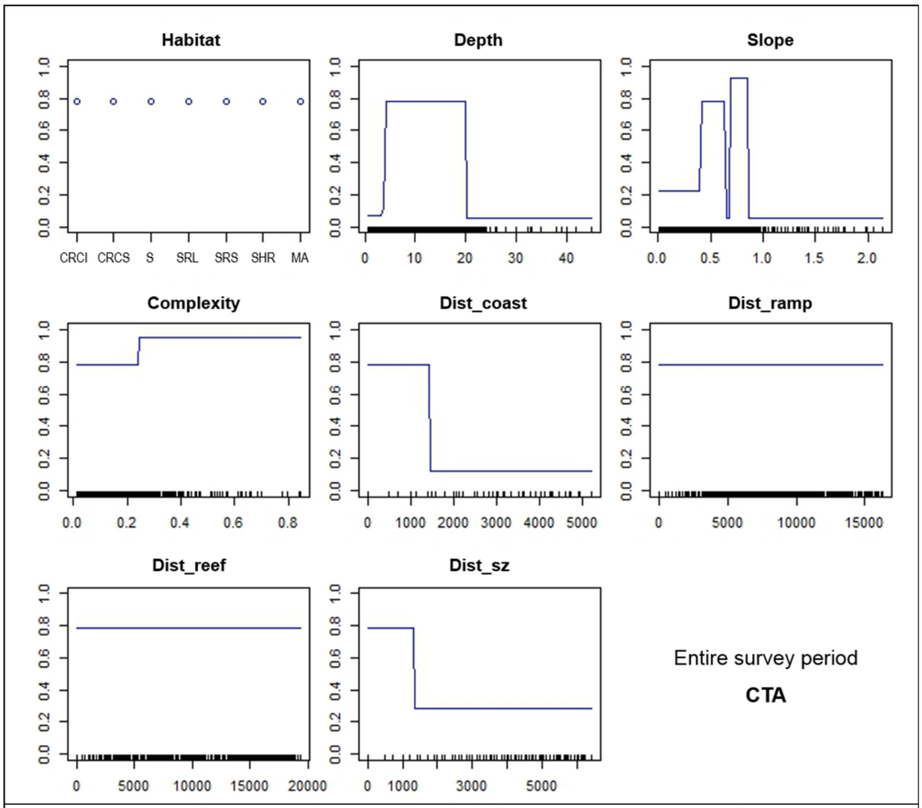
5000
10000
15000
0
5000
10000
15000
20000
0
1000
3000
5000
Entire survey period
GBM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Slope
Complexity
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Dist_sz
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0.2
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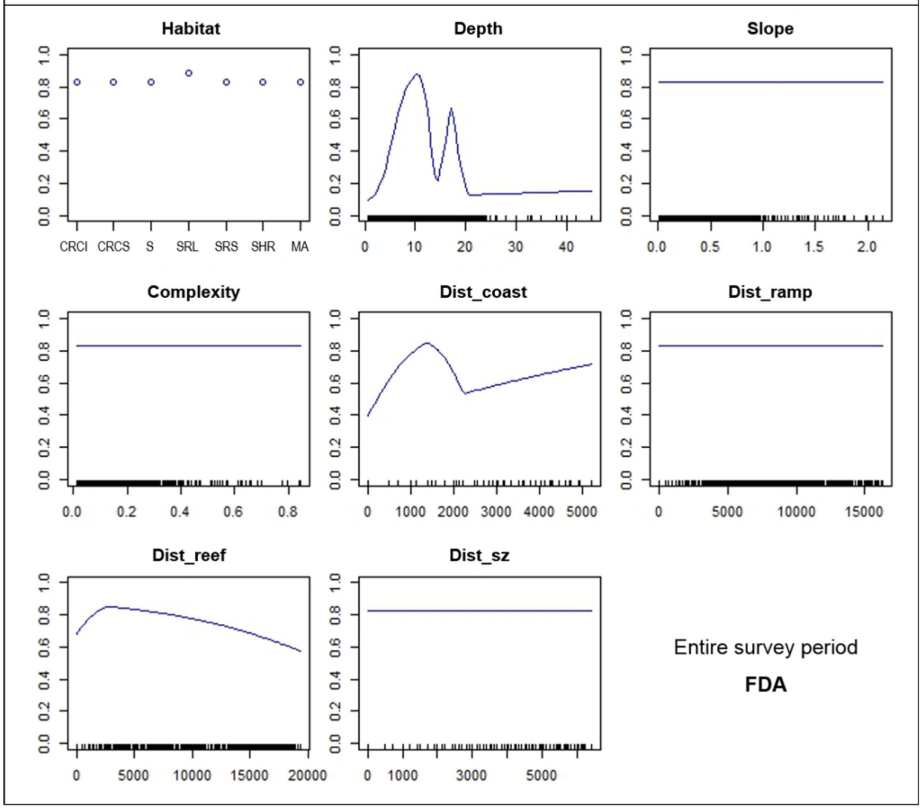
0.8
1.0
CRCI CRCS S SRL SRS SHR MA
0 10 20 30 40
0.0 0.5 1.0 1.5 2.0
0.0 0.2 0.4 0.6 0.8
0 1000 2000 3000 4000 5000
0 5000 10000 15000
0 5000 10000 15000 20000
0 1000 3000 5000
Entire survey period
CTA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Slope
Complexity
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Dist_sz
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0.2
0.4
0.6
0.8
1.0
CRCI CRCS S SRL SRS SHR MA
0 10 20 30 40
0.0 0.5 1.0 1.5 2.0
0.0 0.2 0.4 0.6 0.8
0 1000 2000 3000 4000 5000
0 5000 10000 15000
0 5000 10000 15000 20000
0 1000 3000 5000
Entire survey period
FDA

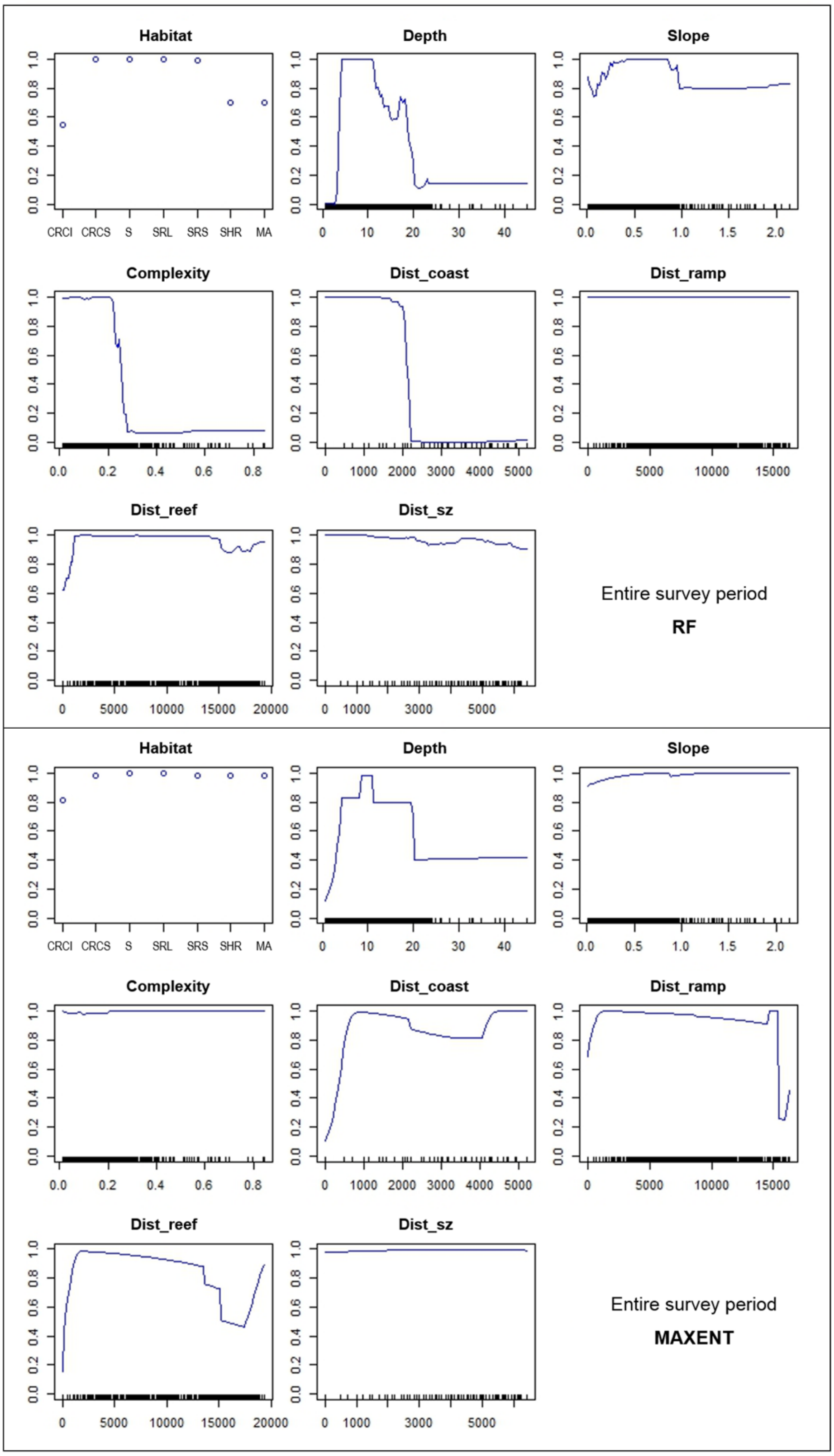
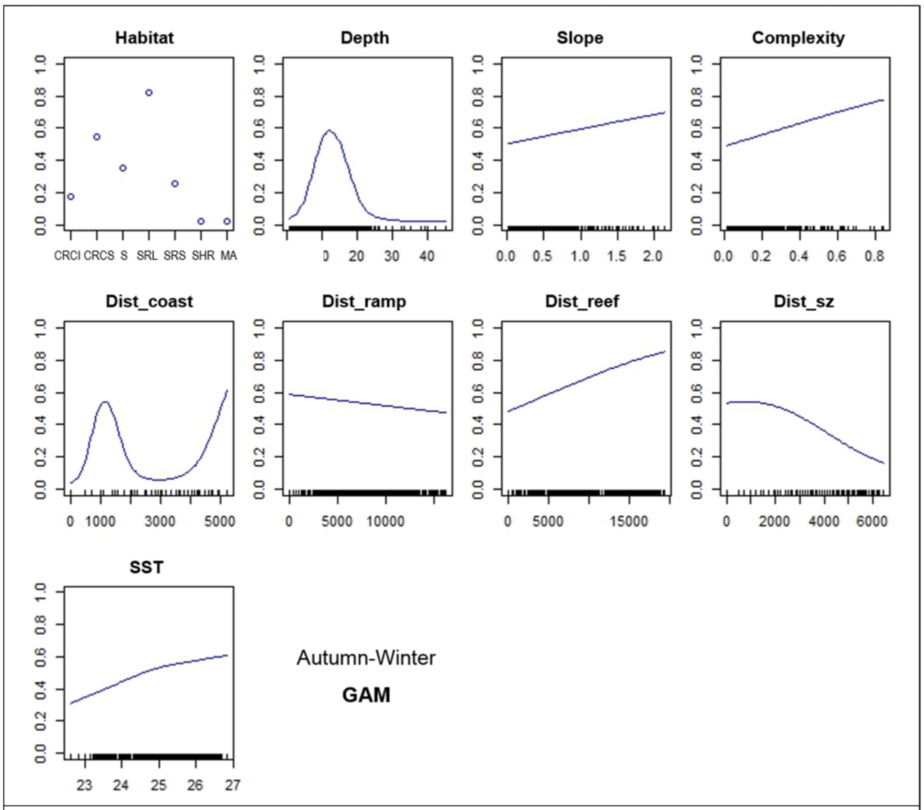
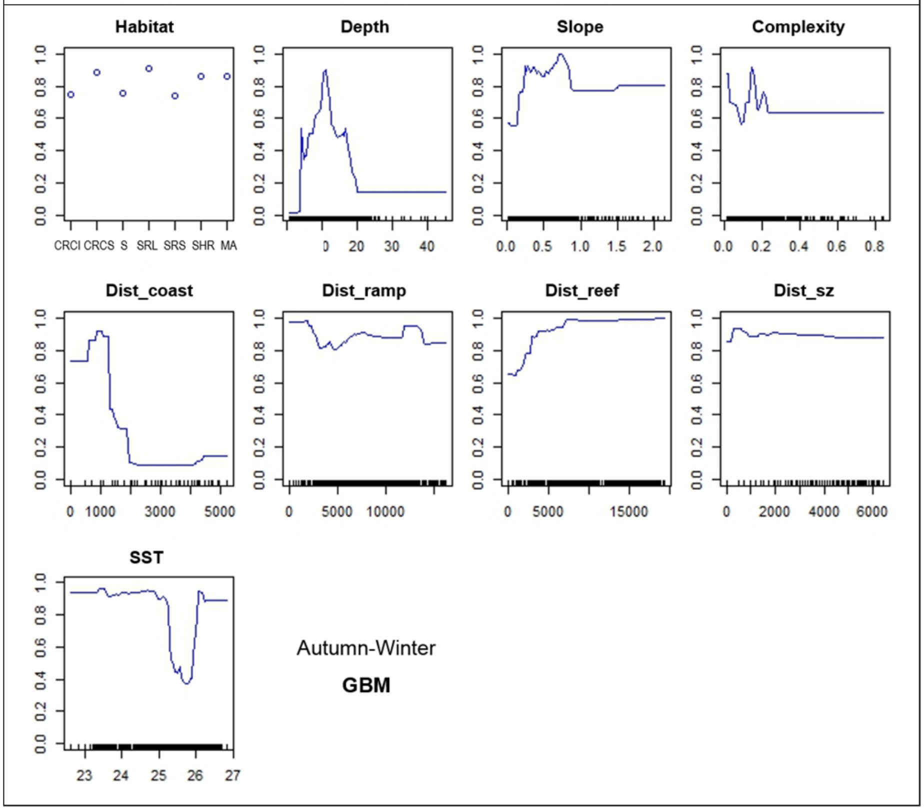
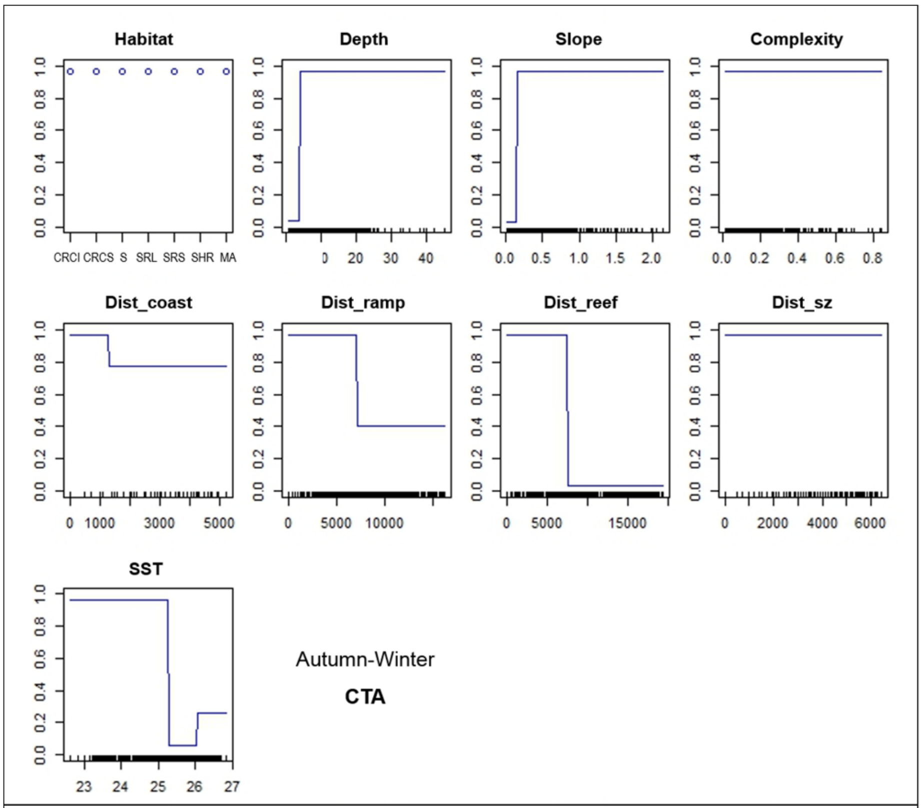


Fig. S3.5. Response curves of presence of Australian humpback dolphins in relation to the environmental predictor variables obtained for species distribution models run for the entire survey period (May 2013 - October 2015) in northern Ningaloo Marine Park. Panes from top to bottom show the curves for each modelling algorithm; GAM = generalised additive model, GBM = generalised boosted model, CTA = classification tree analysis, FDA = flexible discriminant analysis, RF = random forest, and MAXENT = maximum entropy). Each blue line represents the median of the 10 cross-validation runs. For habitat code definitions see Table S3.2 and Fig. S3.2.

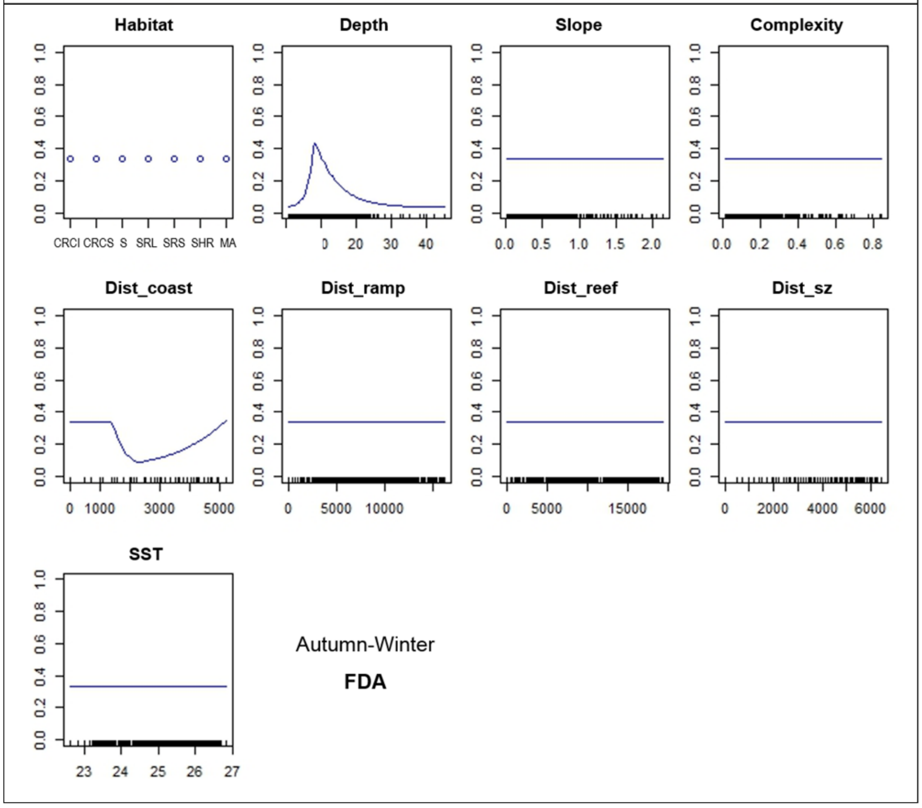

Habitat
Depth
Slope
Complexity
Dist_coast
Dist_ramp
Dist_reef
Dist_sz
SST
0.0 0.2 0.4 0.6 0.8 1.0
CRCI CRCS S SRL SRS SHR MA
0 20 30 40
0.0 0.5 1.0 1.5 2.0
0.0 0.2 0.4 0.6 0.8
0 1000 3000 5000
0 5000 10000
0 5000 15000
0 2000 4000 6000
23 24 25 26 27
Autumn-Winter
GAM


Habitat
Depth
Slope
Complexity
Dist_coast
Dist_ramp
Dist_reef
Dist_sz
SST
0.0 0.2 0.4 0.6 0.8 1.0
CRCI CRCS S SRL SRS SHR MA
0 20 30 40
0.0 0.5 1.0 1.5 2.0
0.0 0.2 0.4 0.6 0.8
0 1000 3000 5000
0 5000 10000
0 5000 15000
0 2000 4000 6000
23 24 25 26 27
Autumn-Winter
GBM



Autumn-Winter

CTA



Autumn-Winter

FDA

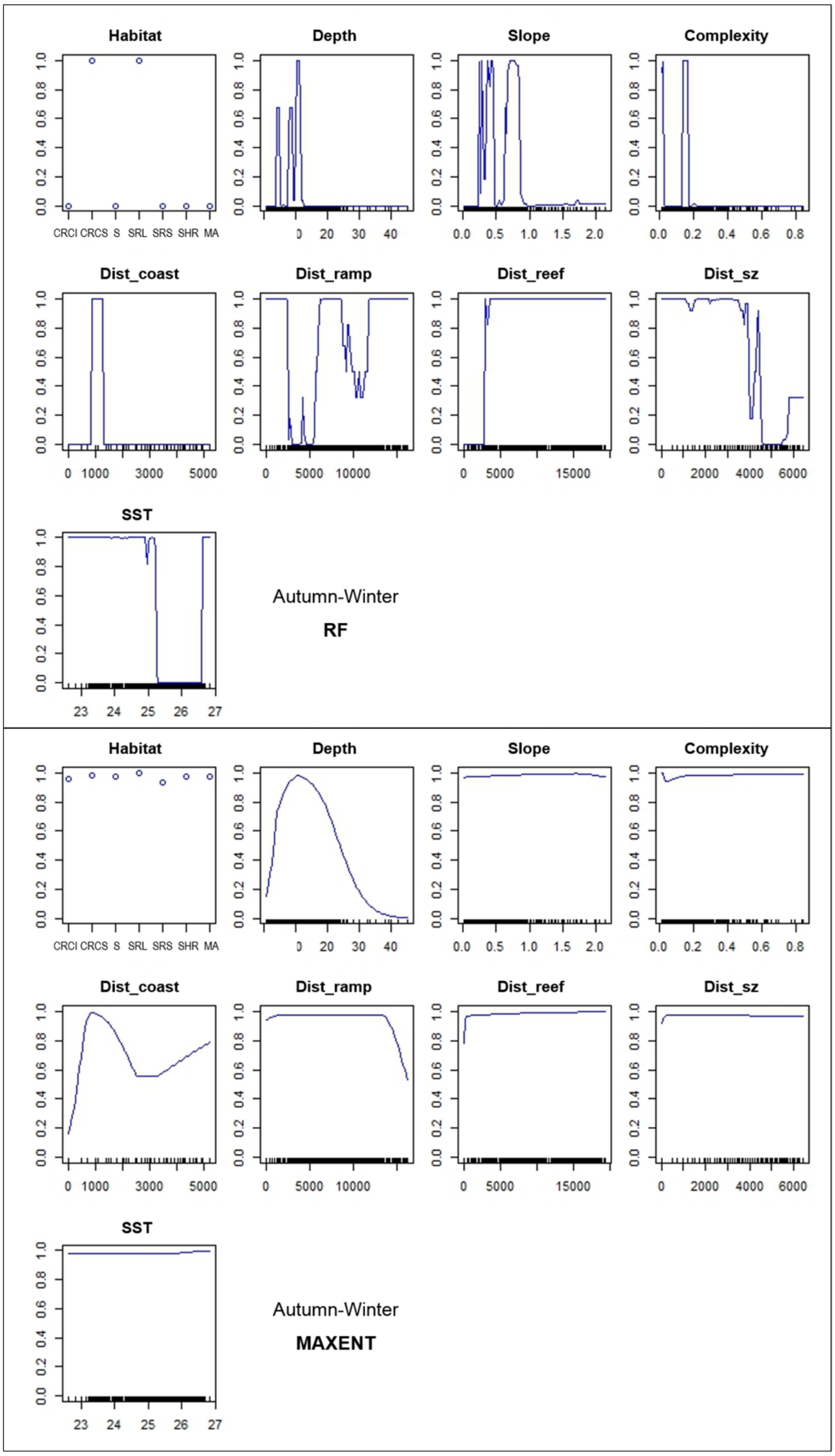
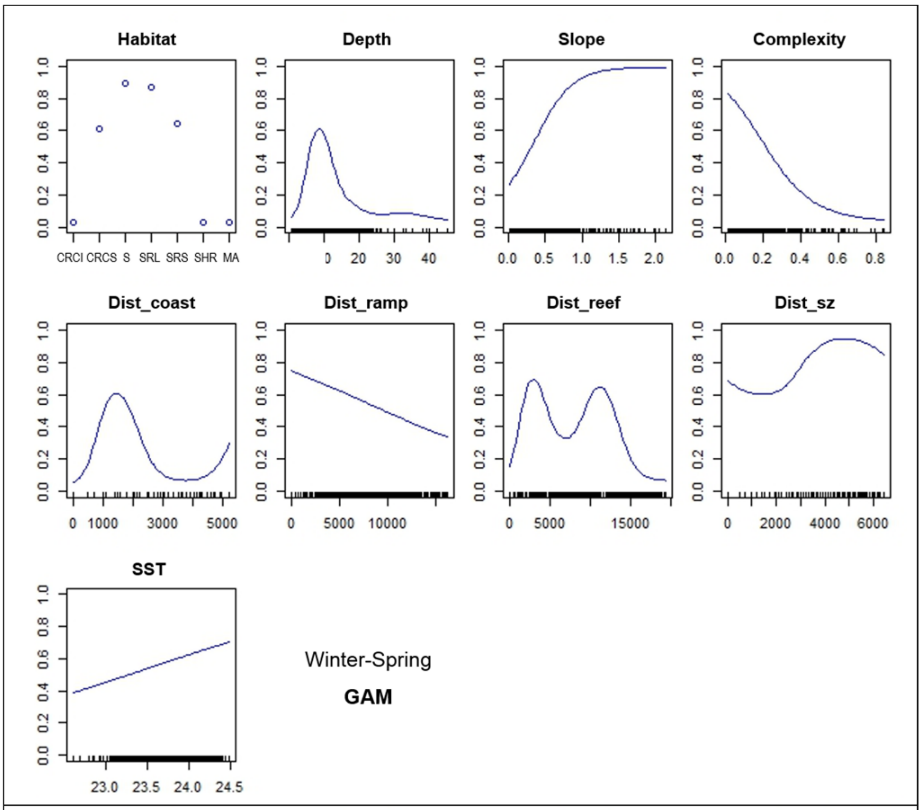
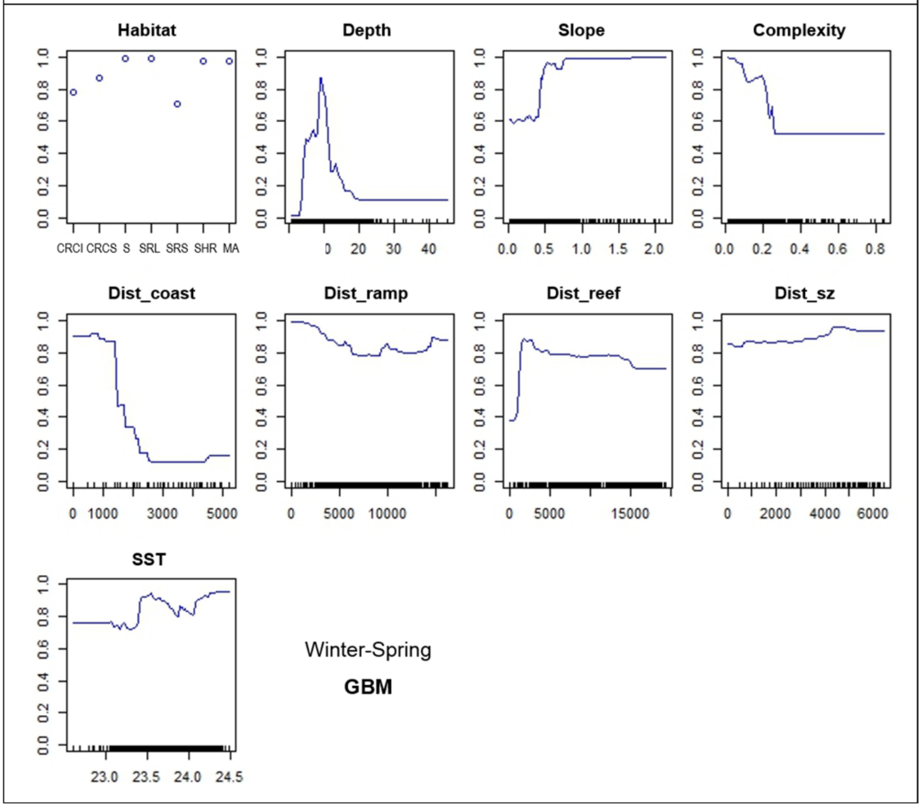
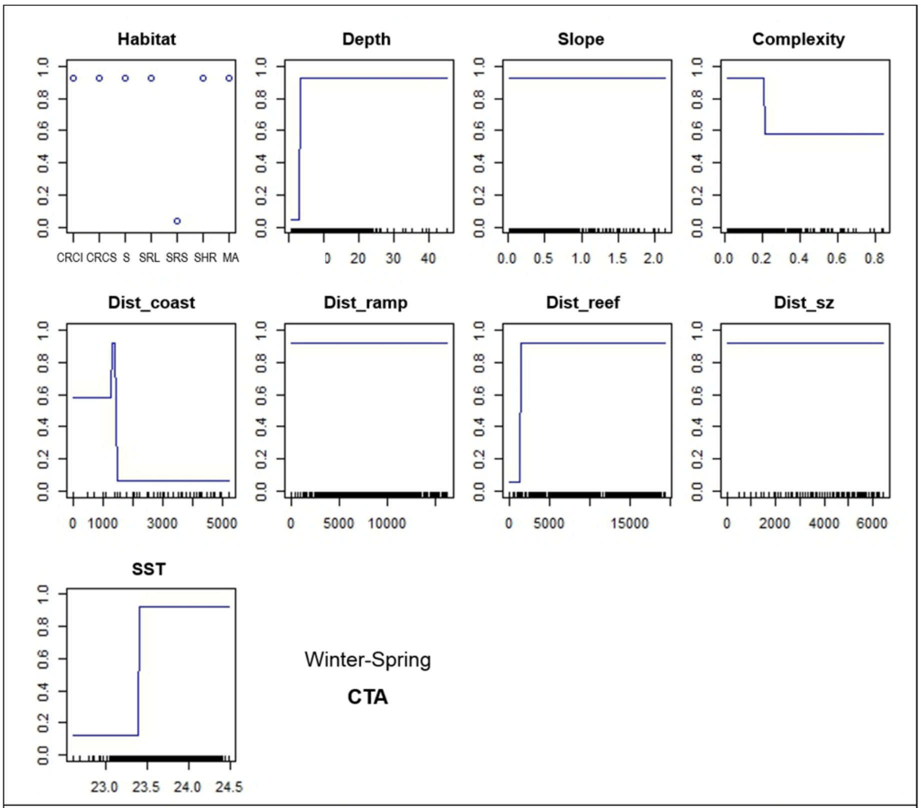
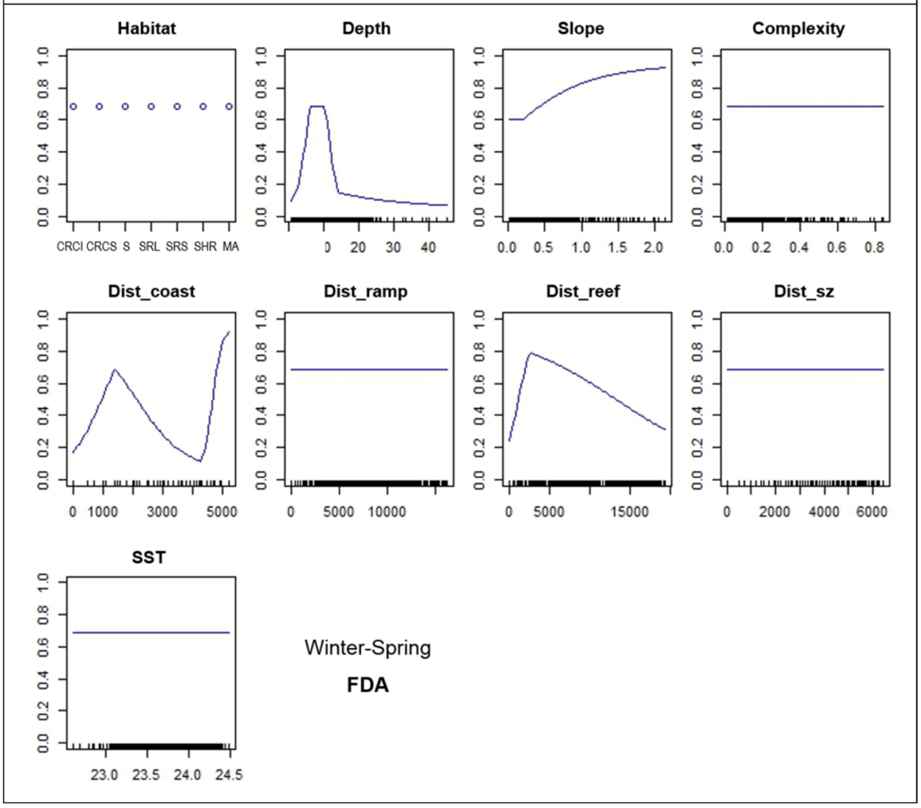


Fig. S3.6. Response curves of presence of Australian humpback dolphins in relation to the environmental predictor variables obtained for species distribution models run for the Autumn-Winter season (April-July) in northern Ningaloo Marine Park. Panes from top to bottom show the curves for each modelling algorithm; GAM = generalised additive model, GBM = generalised boosted model, CTA = classification tree analysis, FDA = flexible discriminant analysis, RF = random forest, and MAXENT = maximum entropy). Each blue line represents the median of the 10 cross-validation runs. For habitat code definitions see Table S3.2 and Fig. S3.2.


Habitat
Depth
Slope
Complexity
Dist_coast
Dist_ramp
Dist_reef
Dist_sz
SST
0.0 0.2 0.4 0.6 0.8 1.0
CRCI CRCS S SRL SRS SHR MA
0 20 30 40
0.0 0.5 1.0 1.5 2.0
0.0 0.2 0.4 0.6 0.8
0 1000 3000 5000
0 5000 10000
0 5000 15000
0 2000 4000 6000
23.0 23.5 24.0 24.5
Winter-Spring
GAM


Habitat
Depth
Slope
Complexity
Dist_coast
Dist_ramp
Dist_reef
Dist_sz
SST
0.0 0.2 0.4 0.6 0.8 1.0
CRCI CRCS S SRL SRS SHR MA
0 20 30 40
0.0 0.5 1.0 1.5 2.0
0.0 0.2 0.4 0.6 0.8
0 1000 3000 5000
0 5000 10000
0 5000 15000
0 2000 4000 6000
23.0 23.5 24.0 24.5
Winter-Spring
GBM


Habitat
Depth
Slope
Complexity
Dist_coast
Dist_ramp
Dist_reef
Dist_sz
SST
0.0
0.2
0.4
0.6
0.8
1.0
CRCI CRCS S SRL SRS SHR MA
0 20 30 40
0.0 0.5 1.0 1.5 2.0
0.0 0.2 0.4 0.6 0.8
0 1000 3000 5000
0 5000 10000
0 5000 15000
0 2000 4000 6000
23.0 23.5 24.0 24.5
Winter-Spring
CTA


Habitat
Depth
Slope
Complexity
Dist_coast
Dist_ramp
Dist_reef
Dist_sz
SST
0.0
0.2
0.4
0.6
0.8
1.0
CRCI CRCS S SRL SRS SHR MA
0 20 30 40
0.0 0.5 1.0 1.5 2.0
0.0 0.2 0.4 0.6 0.8
0 1000 3000 5000
0 5000 10000
0 5000 15000
0 2000 4000 6000
23.0 23.5 24.0 24.5
Winter-Spring
FDA

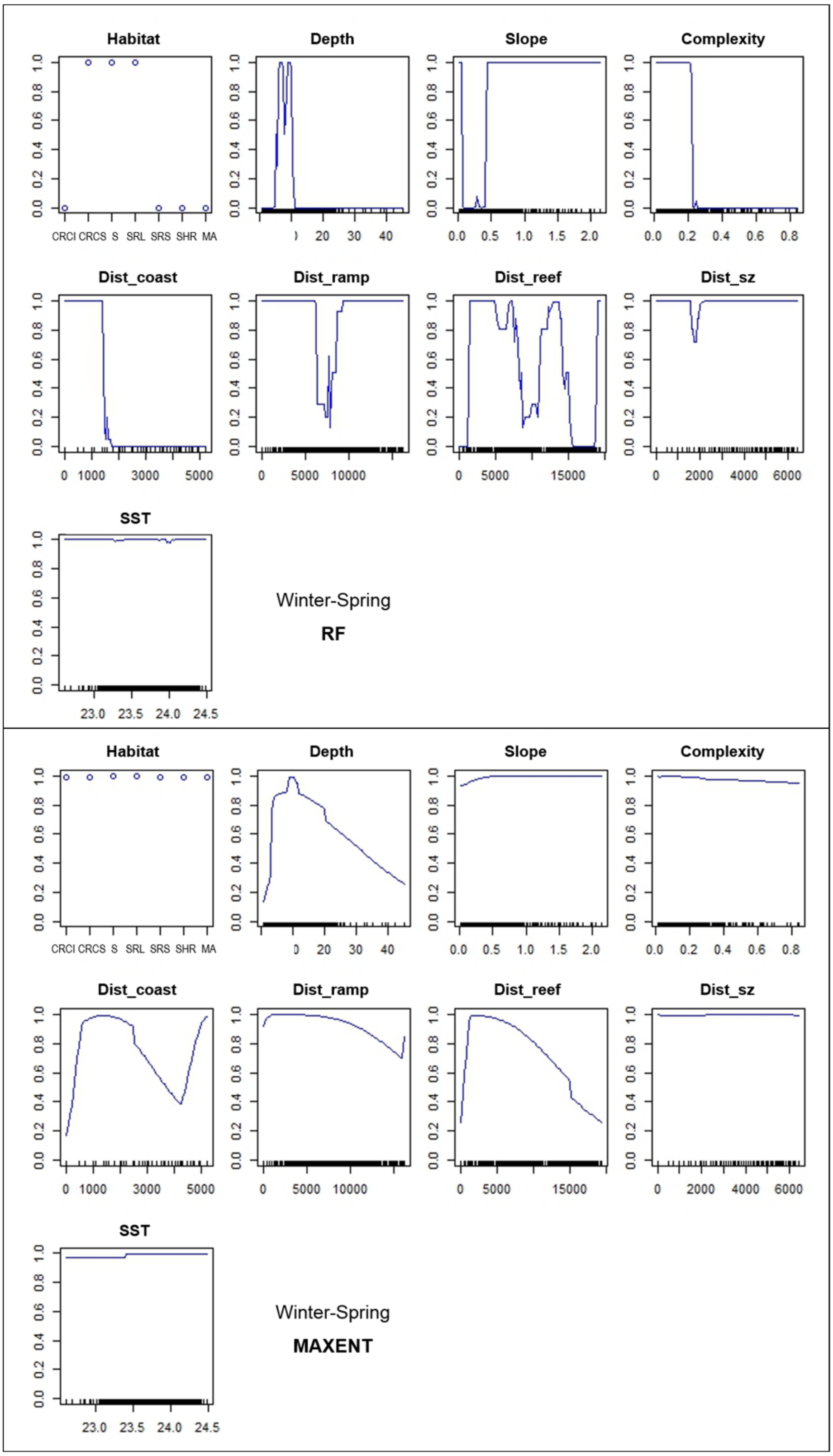


Fig. S3.7. Response curves of presence of Australian humpback dolphins in relation to the environmental predictor variables obtained for species distribution models run for the Winter-Spring season (August to October) in northern Ningaloo Marine Park. Panes from top to bottom show the curves for each modelling algorithm; GAM = generalised additive model, GBM = generalised boosted model, CTA = classification tree analysis, FDA = flexible discriminant analysis, RF = random forest, and MAXENT = maximum entropy). Each blue line represents the median of the 10 cross-validation runs. For habitat code definitions see Table S3.2 and Fig. S3.2.

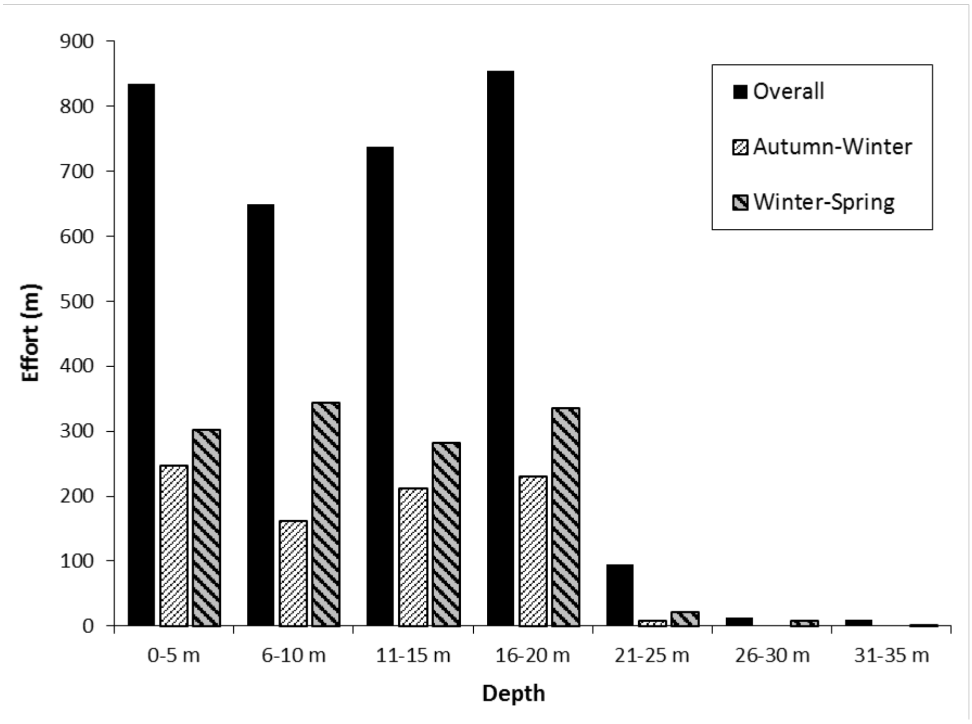


Fig. S3.8. Comparison of survey effort as a function of water depth for boat-based surveys of Australian humpback dolphins in northern Ningaloo Marine Park (NMP) for the overall survey period (May 2013-October 2015), and seasons Autumn-Winter (April-July) and Winter-Spring (August-October). Effort represented as metres of survey track lines per 500 x 500 m grid cell.

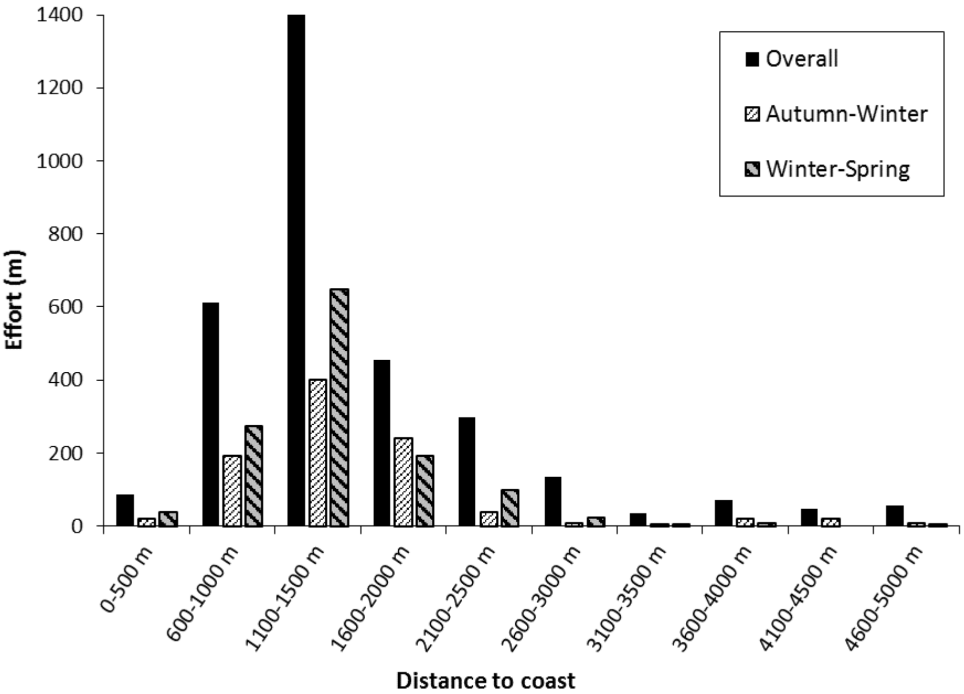


Fig. S3.9. Comparison of survey effort as a function of distance to coast for boat-based surveys of Australian humpback dolphins in northern Ningaloo Marine Park (NMP) for the overall survey period (May 2013-October 2015), and seasons Autumn-Winter (April-July) and Winter-Spring (August-October). Effort represented as metres of survey track lines per 500 x 500 m grid cell.

APPENDIX S4 – CHAPTER 4

S4.1 Use of dorsal fin characteristics in sex determination (Brown et al. 2016a)

The following outlines application of the methodology presented in Brown et al. (2016a) to determine the sex of individual Australian humpback dolphins based on dorsal fin characteristics. Specifically, quantitative measures of percentage of loss of pigment on the upper half of the dorsal fin (upper LOP), and qualitative measures of the level of spotting on dorsal fins were used as they are the best model parameters for logistic regression analyses to predict sex of sampled adults (97% accuracy).

S4.1.1 Selection of images

Identified individuals that had previously had sex determined based on either molecular analysis, visual confirmation or regular association with a dependent calf/juvenile (see Table 4.1 for definitions) were removed from consideration given these methods are robust and established in dolphin sex determination. (NB. A post-hoc image analysis was conducted on some of these sex determined individuals to assess the validity and applicability of the Brown et al. (2016a) method on the study population; see S4.1.6 below). Images of remaining distinctive individuals of unknown sex captured were then further filtered to include only those $Q \geq 7$, and then assessed based on sufficient angle (i.e. image completely perpendicular to the photographer), proportion of body visible above the water, resolution, lighting and focus for any LOP to be delineated, and colouration (i.e. spotting) to be scored. For all individuals, the single best quality suitable image (left and/or right side) was selected for analysis. Irrespective of total sightings an individual was captured, a total of 38 individuals were included for quantitative and qualitative image analysis. All image processing and analysis was performed using Adobe Photoshop (version 7.0, Adobe Systems Inc.).

S4.1.2 Quantitative assessment of upper LOP

To obtain an accurate measurement of the proportion of upper LOP, the posterior and anterior insertion points were delineated for each dorsal fin, and images were rotated and cropped, as per Fig. S4.1A and S4.1B). The outline of the dorsal fin was then selected from the background to count the number of pixels occupied by the dorsal fin, and areas of upper LOP were then traced in bright red, allowing them to be readily selected and their pixel coverage counted (Fig. S4.1C).

Dividing the number of pixels occupied by upper LOP by the number occupied by the dorsal fin gave the proportion of upper LOP. LOP along the trailing edge in the bottom half of the frame was ignored in the calculation of % upper LOP. Those individuals with no visible upper LOP were assigned a zero % value for this parameter. Examples of individual dorsal fins with varying levels of upper LOP use in analysis can be viewed in Table S4.1.1.

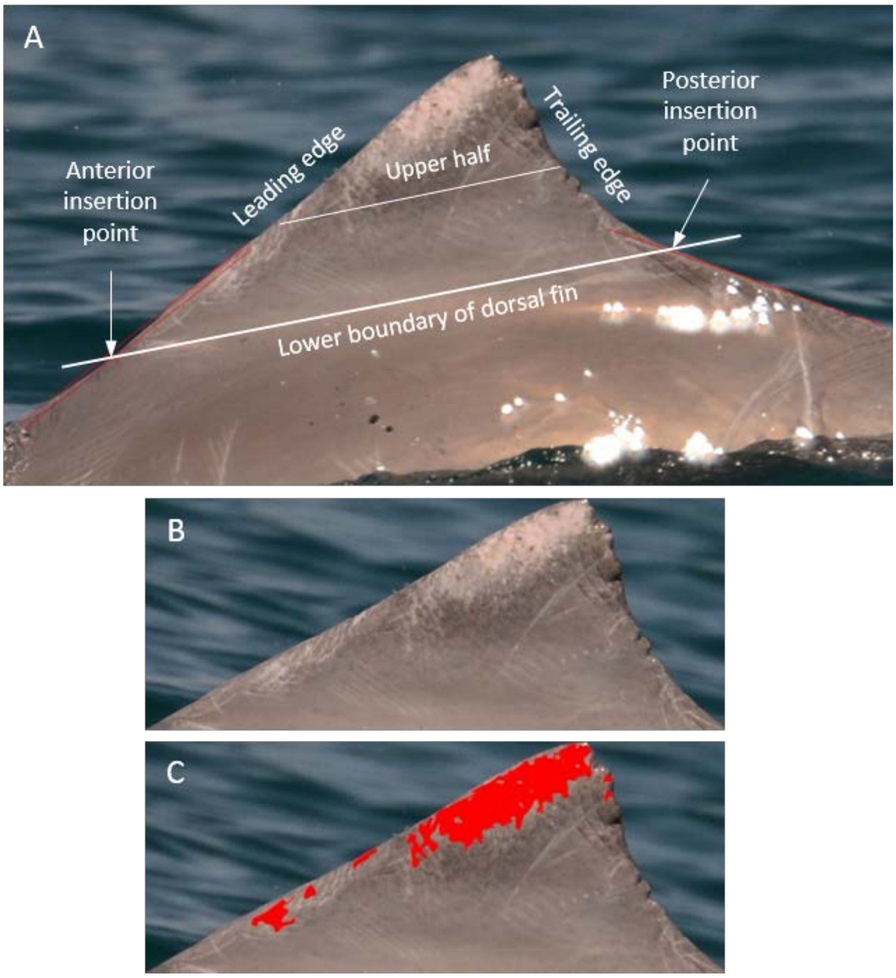


Fig. S4.1. (A) Reference lines (red and white) used to delineate the anterior and posterior insertion points of an Australian humpback dolphin dorsal fin, and consequently the lower boundary of the dorsal fin. Upper half, and trailing and leading edge of dorsal fin also indicated. B) Rotated and cropped dorsal fin image. (C) Dorsal fin image with upper loss of pigmentation (LOP) traced and selected. Individual shown (ID S013) had a proportion of upper LOP of 12.3%. For examples of other individuals with varying levels of upper LOP see Table S4.1.1. Figure modified/reproduced from Brown et al 2016a.

S4.1.3 Qualitative assessment of dorsal fin spotting

Spotting in humpback dolphins refers to even spotting across the dorsal fin (where LOP is absent), ranging from low-density small spots (either light or dark in colour) to a completely mottled appearance (see Table S4.1.2 for category definitions and reference images). Of the 38 individuals included in image analysis, a total of 53 images were used for qualitative spotting scoring as some individuals had images of comparable quality for left and right sides. Each image was renamed and sorted according to a unique, randomly generated number before being scored independently by five different scorers. Two of the scorers had extensive experience in photo-identification of humpback dolphins, one of which was familiar with the individuals in the analyses. Two of the scorers had extensive experience in photo-identification of small cetaceans, but not specifically with humpback dolphins, and were unfamiliar with the individuals included in the analyses. One scorer had little to no experience in photo-identification. Scorers were provided with instructions, including a description of the dorsal fin spotting characteristics, the three associated categories (i.e. none, faint or heavy spotting) and reference examples of each category (see Table S4.1.2 for examples). If scorers could not reliably score an image, either due to insufficient image quality or an obstructive modification/injury to the animal, they were instructed to score it as ‘unknown’. No information on the individual dolphins was provided to the scorers, and left and right side images were not consecutively ordered. The mode score across all five scorers was taken as the assigned category for that image. Where an individual had a left and right image scored, one of which was indicated as heavy spotting, the individual was assigned an overall heavy spotting score. For the purposes of including the spotting parameter (*b*) in the discriminant function to predict individual sex, those individuals that had spotting scored as none or faint were then pooled into a single category, allowing for two categories of spotting to be used in the discriminant function equation; none/faint, or heavy.

S4.1.4 Predicting sex using a discriminant function

The discriminant function from the logistic regression analyses outlined in Brown et al. (2016a), which can be used to predict the probability that a particular individual is male, is:

$$\pi_i = \frac{e^{\left[-4.420+0.501(a_i)+b_i\right]}}{1+e^{\left[-4.420+0.501(a_i)+b_i\right]}}$$

where π_i is the probability that the individual is a male, *a* is % upper LOP and *b* is the spotting parameter (NB. not to be confused with the spotting category indicated in Table S4.1.2 from which the spotting parameter is derived). For none/faint spotting, $b = 0$, while $b = -9.550$ for heavy spotting. Where $\pi_i > 0.5$, the individual is predicted to be male, while < 0.5 is female.

S4.1.5 Results of predicting sex using a discriminant function

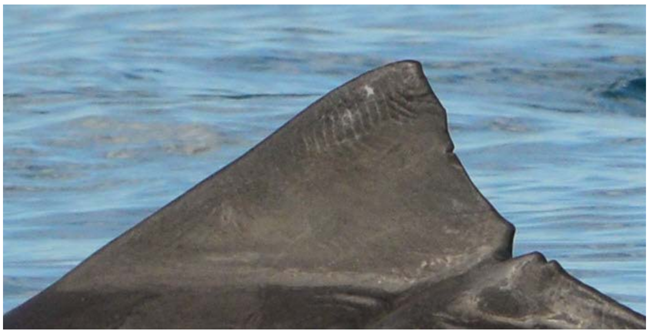
Of the 38 individuals included for logistic regression analyses, probabilities that an individual is male (i.e. π_i) ranged from 0.000 to 0.997, where nine individuals were predicted male (*M*), and 29 were predicted female (*F*). Those individuals sighted five or more times were then filtered out, resulting in a total of 18 individuals (*M* = 5, *F* = 13) included as part of the 49 sexed individuals to be used in social structure analyses (Table 4.1).

S4.1.6 Applicability of Brown et al. (2016a) method to the study population

The probability value for the incorrectly assigned individuals (i.e. 3%, three individuals) was not reported in Brown et al. (2016a), but we considered this high degree of accuracy to result in no more than negligible errors when applied to this study. While 97% might not realistically be expected in all applications, the discriminant function was developed using individuals from a number of different sites, including the NWC (33 of 87 individuals used in model), so there is good justification for it to be representative/appropriate for this site and population. To reduce error in applying this method to the NWC study population, the protocols for assessment and calculation of upper LOP were followed meticulously and were done in conjunction with Dr Alex Brown to ensure the published work was being appropriately replicated.

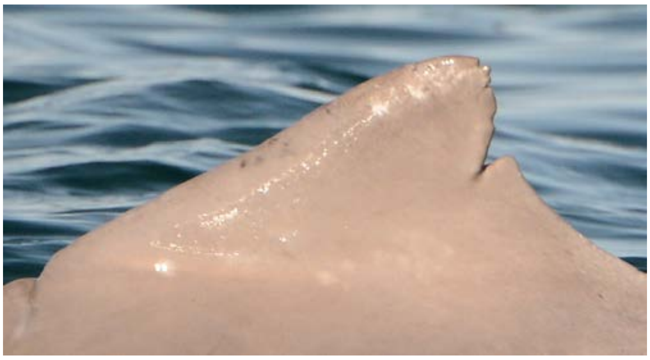
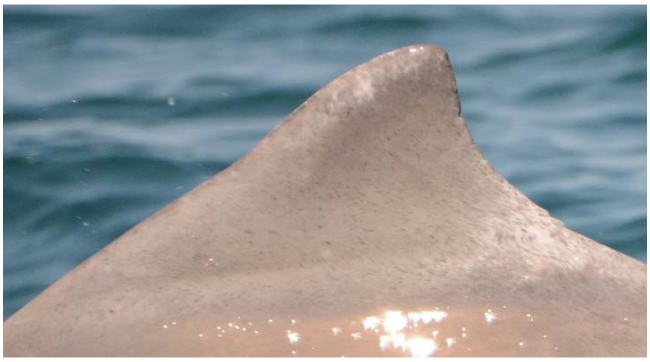
To further justify applicability of this image analysis method to this study population, a post hoc image analysis of females sexed by method of either molecular analysis, visual confirmation or regular association with a dependent calf/juvenile was undertaken by the lead author. Of the 26 females sexed by these methods and used in social structure analyses (see Table 4.1), a total of 25 were assessed for upper LOP and level of spotting (NB. one individual had to be removed from consideration due to a significant proportion of the upper half of the dorsal fin missing). Of these 25 individuals, 100% were predicted female using the discriminant function.

Table S4.1.1. Description and examples of images used in the quantitative assessment of dorsal fin upper loss of pigmentation (LOP) in Australian humpback dolphins around the North West Cape, Western Australia. Descriptions as per Brown et al. 2016a.

Upper LOP definition:	loss of pigmentation focussed on the upper half of the dorsal fin (but including the entire leading edge of the fin); ranges in density from sparse spots of white to a continuous region of white/pink covering over a third of the dorsal fin; may extend partially or completely down the leading edge of the dorsal fin. Does not include white marks clearly attributable to a tooth-rake. Proportions in scores relate to % of total dorsal fin.
Individual ID and % upper LOP	Example image
ID S106 = 0.25%	
ID S130 = 4.97%	
ID S059 = 9.19%	
ID S036 = 13.51%	

ID S096 = 20.67%

Table S4.1.2. Descriptions of categories used in the qualitative assessment of dorsal fin spotting in Australian humpback dolphins around the North West Cape, Western Australia. Category definitions as per Brown et al. 2016a.

Spotting definition:	even spotting across the dorsal fin (where LOP absent); ranges from low-density small spots (either light or dark in colour) to a completely mottled appearance where the fin is distinctly lighter in colour than the adjoining body.	
Category	Description	Example image
1	*Unspotted:* uniform grey colour across dorsal fin; no spotting.	
2	*Faintly spotted:* low-density light or dark small spots	
3	*Heavily spotted:* higher density light or dark spots of larger size; mottled appearance NB. Individual not from study population (from Brown et al. 2016a, used as reference example only)	

S4.2 Results

Table S4.2. Social differentiation summary of Australian humpback dolphins around the North West Cape, Western Australia, where; *S* = social differentiation (the coefficient of variation of the true association indices; a measure of social complexity amongst individuals in a population); *r* = Pearson's correlation coefficient (correlation between true and estimated association indices; a measure of the quality and power of the data to detect true social complexity); SE = standard error. Outputs based on 1000 replications in SOCPROG 2.7, using likelihood method based on half-weight index. Mean associations per dyad, and per individual also shown. This table to be viewed in conjunction with Fig. S4.2.

No. of sightings ≥	No. of IDs	*S* (± SE)	*r* (± SE)	Mean associations per dyad	Mean associations per individual
1	84	1.00 (0.03)	0.30 (0.02)	0.32	26.31
2	68	1.07 (0.03)	0.32 (0.02)	0.46	30.94
3	61	1.11 (0.02)	0.33 (0.02)	0.54	32.16
4	56	1.13 (0.02)	0.34 (0.02)	0.62	33.96
5	50	1.16 (0.02)	0.35 (0.02)	0.72	35.44
6	47	1.18 (0.02)	0.35 (0.03)	0.79	36.38
7	42	1.18 (0.03)	0.36 (0.03)	0.87	35.52
8	37	1.21 (0.02)	0.36 (0.03)	0.98	35.35
9	33	1.22 (0.02)	0.36 (0.03)	1.13	36.30
10	30	1.22 (0.02)	0.36 (0.03)	1.26	36.53

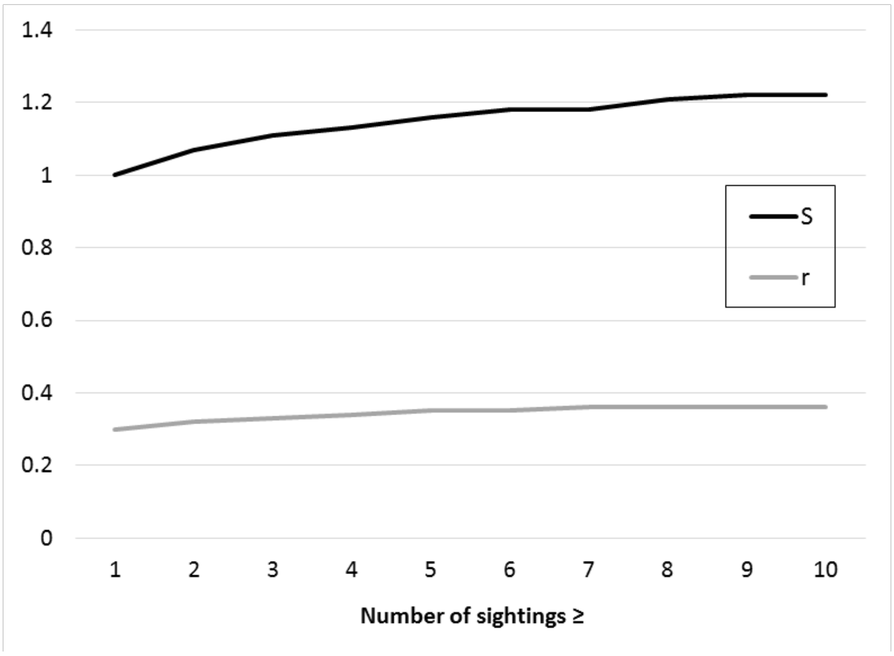


Fig. S4.2. Social differentiation summary for different numbers of sightings of Australian humpback dolphins around the North West Cape, Western Australia, where; S (black line)= social differentiation (the coefficient of variation of the true association indices; a measure of social complexity amongst individuals in a population), and r (grey line) = Pearson's correlation coefficient (correlation between true and estimated association indices; a measure of the quality and power of the data to detect true social complexity). Outputs based on 1000 replications in SOCPROG 2.7, using likelihood method based on half-weight indices. This figure to be viewed in conjunction with Table S4.2.

Table S4.3. Summary of preferred (n=24) and avoided (n=16) affiliate pairs of Australian humpback dolphins around the North West Cape, Western Australia. Affiliation index (AI) represents GAI deviance residuals, where > 2 indicates preferred affiliates, and < -2 indicates avoided affiliates. Pink cells = individual females, blue cells = individual males, and grey cell = an individual of unknown sex. For visual representation of preferred and avoided affiliates in the social network diagram see Fig. 4.2.

Pair category	*Preferred affiliates*[a]			*Avoided affiliates*[b]		
	From	To	AI	From	To	AI
Female	S027	S018	3.84	S019	S022	-2.58
	S027	S079	3.01	S024	S025	-2.32
	S027	S034	2.64			
	S027	S049	2.09			
	S001	S024	3.7			
	S001	S003	2.25			
	S001	S025	2.18			
	S008	S015	2.67			
	S008	S016	2.01			
	S067	S098	2.56			
	S067	S015	2.32			
	S015	S048	2.63			
	S015	S098	2.32			
	S015	S042	2.06			
	S053	S066	2.39			
	S005	S018	2.24			
	S019	S106	2.21			
	S002	S024	2.09			
	S049	S051	2.06			
Male	S056	S061	2.97			
	S056	S065	2.04			
Female-male & Male-female	S015	S013	2.55	S002	S017	-2.22
	S067	S013	2.51	S053	S057	-2.9
	S079	S017	2.02	S053	S058	-2.9
				S053	S059	-2.9
				S053	S061	-2.08
				S053	S065	-2.12
				S053	S060	-2.9
				S056	S081	-2.82
				S056	S111	-2.14
				S056	S052	-2.12
				S056	S010	-2.04
				S036	S009	-3.04
				S036	S098	-2.89
				S036	S042	-2.34

[a] Total of 27 individual IDs: F-F pairs = 19 (23 IDs); M-M pairs = 2 (3 IDs); F-M pairs = 3 (5 IDs)

[b] Total of 22 individual IDs: F-F pairs = 2 (4 IDs); F-M pairs = 13 (17 IDs)

Table S4.4. Social network metrics summary (strength, clustering coefficient, and affinity) based on raw residuals of generalised affiliation indices (GAI) for 50 individual Australian humpback dolphins around the North West Cape, Western Australia. Strength = sum of all GAIs of any individual with all other individuals, and is a measure of gregariousness (Barrat et al. 2004). High strength is indicated by strong associations with other individuals (Whitehead 2009). Clustering coefficient indicates how well the associates (neighbours) of an individual are themselves associated (Holme et al. 2007). Affinity is a measure of the strength of an individuals' associates (Whitehead 2009), where high affinity is an indication of high associations with other individuals who have high strength.

ID	Strength	Clustering coefficient	Affinity
S001	0.31	-0.65	0.72
S002	0.04	-1.01	3.85
S003	-0.3	1.9	-0.22
S005	0.91	0.25	0.21
S006	-0.39	-3.52	-0.95
S008	0.51	-4.97	4.24
S009	-0.71	-0.76	-1.38
S010	-1.38	-0.14	-0.85
S012	-0.12	-0.32	-12
S013	1.05	0.67	1.34
S015	2.08	0.44	0.85
S016	1.29	0.23	0.53
S017	-0.65	0.58	-0.26
S018	0.06	-1.07	18.51
S019	-0.68	3.07	0.22
S021	0.51	0.64	-0.34
S022	-0.25	-1.06	-0.07
S024	0.23	0.86	-1.32
S025	0.86	0.03	0.81
S026	-0.26	0.99	-0.53
S027	1.5	0.19	0.43
S030	-0.92	-0.48	-0.88
S034	-0.36	1.4	-1.17
S036	-1.18	0.22	-0.25
S037	-0.68	-0.38	-0.8
S039	-0.81	-0.71	-0.74
S041	-0.21	-2.19	0.55
S042	0.85	2.37	1.74
S047	0.22	-1.73	6.68
S048	0.98	0.9	1.37
S049	0.74	0.46	0.39
S051	0.18	-2.54	-2.23
S052	-1.2	0.13	-0.63
S053	-1.05	2.54	-0.55
S056	-0.51	-2.46	-2.87
S057	-0.26	-3.29	-3.6
S058	-0.26	-3.29	-3.6
S059	-0.26	-3.29	-3.6
S060	-0.26	-3.29	-3.6
S061	-0.08	-2.46	-8.91
S062	-0.52	-0.27	-0.69
S064	1.43	0.11	0.38
S065	-0.31	-3.31	-3.23
S066	0.89	-0.2	-0.91
S067	1.86	0.26	0.58
S079	0.11	0.18	10.06
S081	-0.96	0.26	-0.69
S098	0.34	-1.79	7.12
S106	-0.84	0.56	-0.43
S111	-0.97	0.52	-0.18

Table S4.5. Summary of generalised affiliation indices (GAI) for assigned geographic location classes of East (E), West (W) and East-West (EW) amongst Australian humpback dolphins around the North West Cape, Western Australia. GAI values presented represent raw residuals. SD = standard deviation. For visual representation of assigned geographic classes see Fig. 4.3. Mantel tests for differences in associations between/within classes are indicated at the bottom of the table.

Class	Mean GAI	SD	Sum of GAIs	SD	Max. GAI	SD
E	-0.01	0.01	-0.41	0.56	0.21	0.08
EW	0.01	0.02	0.67	0.92	0.26	0.08
W	0.00	0.01	-0.04	0.67	0.21	0.09
E-E	-0.01	0.03	-0.28	0.53	0.20	0.09
E-EW	0.00	0.01	-0.02	0.11	0.07	0.06
E-W	-0.01	0.00	-0.11	0.01	-0.01	0.00
EW-E	0.00	0.01	-0.02	0.27	0.03	0.06
EW-EW	0.05	0.07	0.69	0.86	0.23	0.09
EW-W	0.00	0.03	0.00	0.45	0.09	0.10
W-E	-0.01	0.00	-0.14	0.01	-0.01	0.00
W-EW	0.00	0.02	0.00	0.32	0.11	0.13
W-W	0.01	0.04	0.09	0.55	0.19	0.06
Within	0.01	0.05	0.11	0.75	0.21	0.08
Between	0.00	0.01	-0.10	0.34	0.09	0.10
Overall	0.00	0.02	0.01	0.83	0.22	0.08

Test for differences in associations between/within classes:

Mantel test: $t = 2.15$; $p = 0.03$; matrix correlation = 0.06

Table S4.6. Summary of residency clusters (Chapter 2/Hunt et al. 2017) by sex class for adult Australian humpback dolphins around the North West Cape, Western Australia. NB. From Chapter 2/Hunt et al. 2017, long-term residents here correspond with Group A, part-time residents correspond with Group B, and occasional residents correspond with Group C.

	Total IDs	Long-term residents	Part-time residents	Occasional residents
Female	39	21	15	3
Male	10	3	7	0
Unknown	1	0	1	0
Total	50	24	23	3

Table S4.7. Models of temporal stability fitted to standardised lagged association rate (SLAR) data for Australian humpback dolphins on the North West Cape, Western Australia. A maximum time lag of 177 days was fitted to the model. For description of model equations see Whitehead (2008a). The models within ΔQAIC 0-2 of each other that best fitted the data according to Akaike's Information Criterion, corrected for small sample size and overdispersion (QAICc) are shown in bold. ΔQAIC indicates how well the data support the less favoured model (Burnham & Anderson 2002). Models ΔQAIC 0-2 are plotted in Fig. 4.4.

Category	Model equation	Model explanation	QAIC	ΔQAIC
All individuals	**a1**	**Preferred companions**	**4231.0**	**0.0**
	a2*exp(-a1*td)	**Casual acquaintances**	**4232.0**	**1.0**
	a2+a3*exp(-a1*td)	Preferred companions + casual acquaintances	4235.0	4.0
	a3*exp(-a1*td)+a4*exp(-a2*td)	Two levels of casual acquaintances	4235.8	4.8
Female to female	**a2*exp(-a1*td)**	**Casual acquaintances**	**5041.6**	**0.0**
	a3*exp(-a1*td)+a4*exp(-a2*td)	**Two levels of casual acquaintances**	**5042.2**	**0.6**
	a1	**Preferred companions**	**5042.9**	**1.3**
	a2+a3*exp(-a1*td)	Preferred companions + casual acquaintances	5046.8	5.2
Male to male	**a1**	**Preferred companions**	**337.7**	**0.0**
	a2*exp(-a1*td)	**Casual acquaintances**	**339.7**	**2.0**
	a2+a3*exp(-a1*td)	Preferred companions + casual acquaintances	341.3	3.6
	a3*exp(-a1*td)+a4*exp(-a2*td)	Two levels of casual acquaintances	343.3	4.6

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