The conservation biology of tropical inshore dolphins in north-western Australian waters

Alexander M. Brown

BSc (Hons.), Cardiff University

MRes, University of Aberdeen

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Declaration

I declare that this thesis is my own account of my research and contains as its main content work that has not previously been submitted for a degree at any tertiary education institution

Alexander M. Brown

Abstract

Concerns exist over the vulnerability of tropical inshore dolphin populations in waters off northern Australia to anthropogenic impacts, yet a lack of data precludes assessment of their conservation status and the management of threats. Three species occur in shallow, nearshore waters: the Australian snubfin (*Orcaella heinsohni*), Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*). In this thesis, I provide: i) quantitative data on the abundance and site fidelity of all three species at five sites in north-western Australia; (ii) an examination of population genetic structure in snubfin and humpback dolphins; (iii) a sex-specific investigation of the social structure of one population of snubfin dolphins; and, (iv) an analysis of sex- and geographic-differences in dorsal fin features of humpback dolphins. The abundance of each species was highly variable across the five c. 130 km^2 study sites surveyed. While the estimated abundance of most species was $\leq$ 60 individuals, and fewer than 20 humpback dolphins were identified at each site in any one sampling period, larger estimates of c. 130 snubfin and c. 160 bottlenose dolphins were obtained at two different sites. Several local populations showed evidence of site fidelity, particularly snubfin dolphins. Mitochondrial and microsatellite data revealed significant genetic differentiation of local populations separated by geographic distances of >200 km, suggesting that snubfin and humpback dolphins may exist as metapopulations of small, predominantly isolated population fragments, and should be managed accordingly. Additionally, genetic data revealed the first documented case of hybridisation between a snubfin and a humpback dolphin. I documented pronounced sex-differences in individual sociability within a small population of snubfin dolphins: males formed stronger, longer-lasting associations and were far more gregarious than females. Associations were not correlated to genetic relatedness for either sex. Based on a quantitative analysis of dorsal fin images of a sample of humpback dolphins of known sex from north-western and north-eastern Australia, I revealed that the sex of adult individuals could be distinguished with a high level of accuracy (97%) based on dorsal fin features. Additionally, significant differences in dorsal fin colouration between the two regions suggested some level of population structure. Overall, these results extend the geographic scope of quantitative population data on Australia's tropical inshore dolphins into the western third of their distribution, and provide valuable data to inform their conservation and management both within this region and throughout northern Australia.

Statement on the contribution of others

Supervision

Lars Bejder[1], Simon J. Allen[1], Kenneth H. Pollock[1,2], Celine H. Frère[3]

1. Murdoch University, WA, Australia. 2. North Carolina State University, NC, USA. 3. University of the Sunshine Coast, QLD, Australia.

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Contributions to data chapters

Chapter 2. Site-specific assessments of the abundance of three inshore dolphin species to inform conservation and management

Alex Brown: collected and analysed the data and wrote the chapter. *Kenneth Pollock*: advised on the analysis. *Simon Allen, Lars Bejder, and Kenneth Pollock*: critically reviewed the chapter.

Chapter 3. Population differentiation and hybridisation of Australian snubfin (*Orcaella heinsohni*) and humpback (*Sousa sahulensis*) dolphins in north-western Australia

Alex Brown: collected a significant proportion of the genetic samples and data on the hybrid dolphin; analysed non-genetic data; wrote the chapter. *Simon Allen, Daniele Cagnazzi, Lars Bejder, Carol Palmer, Deborah Thiele* and *Michael Krützen*: collected genetic samples. *Anna Kopps* and *Celine Frère*: conducted genetic laboratory work; analysed genetic data; contributed to writing of methods and results and critically reviewed the chapter overall. *Bethan Littleford-Colquhoun*: conducted genetic laboratory work. *SA, DC, GP, LB and DT*: critically reviewed the chapter.

Chapter 4. The social structure of Australian snubfin dolphins (*Orcaella heinsohni*): investigating sex-differences in association patterns and correlations with kinship

Alex Brown: collected the behavioural and genetic data; performed the behavioural analysis; wrote the chapter. *Lars Bejder*: advised on the behavioural analysis. *Simon Allen*: collected additional genetic data. *Celine Frère*: coordinated the genetic analysis. *LB, SA, and CF*: critically reviewed the chapter. *Felix Smith* and *Josh Smith*: collected additional behavioural data in May 2014.

Chapter 5. Sexual dimorphism and geographic variation in dorsal fin features of Australian humpback dolphins, *Sousa sahulensis*

Alex Brown: collected a significant proportion of the data; performed the analysis; wrote the chapter. *Guido Parra*, *Daniele Cagnazzi*, *Tim Hunt*, *Lars Bejder* and *Simon Allen*: contributed data. *Jennifer Smith*: advised on the statistical analysis. *GP, DC, TH, LB, SA, and JS*: critically reviewed the chapter.

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Thesis publications

The following publications are associated with the chapters of this thesis:

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Brown, A.M., Bejder, L., Parra, G.J., Cagnazzi, D., Hunt, T., Smith, J.L. and Allen, S.J. (2016). Sexual dimorphism and geographic variation in dorsal fin features of Australian humpback dolphins, *Sousa sahulensis*. *Advances in Marine Biology* **73**: 273-314. doi: 10.1016/bs.amb.2015.08.002. (Chapter 5)

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Chapter 1. General introduction

Small cetaceans, along with most marine mammals, hold important ecological roles in the upper trophic positions of marine ecosystems (Bowen 1997, Estes 2009, LeDuc 2009). They are long-lived species with slow growth, late maturation, and low reproductive rates, which rely on high levels of survival for populations to persist over time (Taylor 2002, Marsh et al. 2003, LeDuc 2009). Consequently, they are inherently vulnerable to human activities which may reduce their ability to survive and reproduce, either through direct mortality (e.g. incidental capture in fisheries) or disturbance of key processes (e.g. resting, foraging, reproducing) (e.g. Read et al. 2006, Pirotta et al. 2013, Christiansen and Lusseau 2015). Elevated levels of mortality can result in rapid declines in populations of small cetaceans, and rates of population recovery are slow (Taylor 2002, Chivers 2009, LeDuc 2009).

While human activities have caused considerable changes in almost all marine ecosystems, coastal areas are among those most impacted (Halpern et al. 2008, McCauley et al. 2015). The concentration of human populations in coastal areas gives rise to numerous anthropogenic activities, many of which negatively impact upon coastal marine environments (Millenium Ecosystem Assessment 2005, Crain et al. 2009). Many small cetacean species rely on shallow coastal and estuarine habitats, where they may be exposed to a variety of threats, including: habitat loss and degradation, acoustic disturbance, vessel strikes, environmental contaminants, and incidental capture in fisheries (e.g. Hale 1997, Jefferson et al. 2009, Ross et al. 2011, Reeves et al. 2013b). Habitat degradation and incidental capture in fisheries have contributed to the decline of several coastal populations of small cetacean, which are now threatened with extinction (e.g. Rojas-Bracho et al. 2006; Slooten et al. 2006; Reeves et al. 2008a).

Consequently, coastal cetacean populations are among those most threatened and in need of quantitative data to inform the management of potentially threatening anthropogenic activities (Wilson et al. 1999, Parra et al. 2006a). However, due to their life history characteristics and behavioural traits (i.e. long-lived, highly mobile, often problematic to observe), cetaceans are difficult, costly and time-consuming to study (Thompson et al. 2000, Taylor et al. 2007b). While coastal dolphins represent some of the most studied of

cetaceans (e.g. Wells and Scott 1999, Martinez and Slooten 2003, Cheney et al. 2014), the status of numerous species remains poorly understood, particularly in remote and/or developing regions within the Indo-Pacific (Reeves et al. 2003). A lack of baseline population data and quantification of threats have hampered efforts to assess the vulnerability of populations of coastal dolphins and implement appropriate conservation actions (Parra 2005, Cagnazzi 2011, Bejder et al. 2012).

Abundance estimation is a key element of any wildlife management strategy, and important to assessing the conservation status of a species or population (Taylor 1997, Williams et al. 2002). Abundance estimates provide a quantitative base from which to investigate: trends in abundance (Gerrodette 1987); natural vulnerability to extinction risk (Shaffer 1981); and the potential resilience to anthropogenic sources of mortality (Wade 1998). In several nations, the potential impacts of anthropogenic activities on protected species are deemed biologically significant when they are likely to have population-level consequences (e.g. NRC 2005a, JNCC 2008, Department of the Environment 2013a). Therefore, an understanding of the size of populations is fundamental to assessing the significance of potential impacts.

Determining what constitutes a 'population' for management purposes requires an understanding of structure, i.e. the level of connectivity between individuals across their distribution (Taylor 1997, Wang 2009). For example, a species distributed as a series of small, somewhat isolated population fragments will require different management to a species of the same total abundance, but which is structured as a single, well-connected population (Reed 2004). To this end, analyses of population genetic structure have been widely used to investigate the level of gene flow between adjacent populations, infer migration rates, and assist in the identification of populations which may be classified as discrete 'management units' (Taylor 1997, Palsbøll et al. 2007, Frankham et al. 2010). Additionally, a lack of gene flow between populations may be inferred through consistent geographic variation in external morphology (Perrin 2009a), and such data have also been used to inform population subdivision and the identification of management units (e.g. Perrin et al. 1991, Pitman and Ensor 2003, Wang et al. 2015).

Species of conservation concern are often characterised by small, fragmented populations with restricted gene flow and low genetic diversity (Frankham 1995a, Spielman et al.

2004). Different populations exhibit local adaptations and genetic differences, which increase the ability of a species to persist through stochastic events (Frankham et al. 2010). Additionally, the nature and severity of threatening processes vary geographically (Halpern et al. 2007), as do populations' vulnerability to such processes, making it essential to implement conservation efforts at an appropriate biogeographic scale (Wang 2009).

While data on abundance and population structure are fundamental to conservation and management, the value of behavioural data are also well-recognised (Sutherland 1998, Caro 1999, 2007, Berger-Tal et al. 2011). For example, social structure influences key population processes, including reproductive fitness (Silk et al. 2003), the flow of genetic material (Chepko-Sade and Halpin 1987), the spread of disease (Hamede et al. 2009), and the transmission of information or behaviours between conspecifics (Weilgart and Whitehead 1997, Allen et al. 2013). Social structure, therefore, represents another important element of species' population biology (Slooten et al. 1993, Whitehead 1997) and often has implications for conservation and management (Caro 1999, Berger-Tal et al. 2011). Studies of behaviour are particularly relevant to conservation biology when performed on species and populations of conservation concern, as this reduces the reliance on inferences made from similar, but not necessarily representative, species (Caro 2007).

Information on the sex of individuals is of fundamental importance in behavioural studies, and is also essential to understanding population structure and dynamics (Begon et al. 2006). For example, sex-specific ranging patterns may result in sex-biased exposure to anthropogenic impacts (Bugoni et al. 2011), while the sex-ratio of a population is an important consideration in population viability analysis (Boyce 1992). However, sex-determination may be challenging for species whose genitalia are not easily observed and/or show a lack of obvious sexual dimorphism (Gowans et al. 2000). Methods for determining the sex of free-ranging species are, therefore, of considerable value to their conservation biology.

Three species of the delphinid family occur in the shallow, inshore waters of northern Australia: the Australian snubfin (*Orcaella heinsohni*, 'snubfin dolphin' hereafter), Australian humpback (*Sousa sahulensis*, 'humpback dolphin' hereafter), and Indo-Pacific bottlenose (*Tursiops aduncus*, 'bottlenose dolphin' hereafter). For all three species, a lack of baseline population data precludes comprehensive assessment of their conservation

status under international[1] and national[2] criteria, and the management of impacts on local populations (Beasley et al. 2012, Woinarski et al. 2014).

Snubfin and humpback dolphins are of particular conservation concern (Ross 2006). Their distribution is restricted to shallow coastal and estuarine waters of northern Australia and southern New Guinea (Parra et al. 2002, 2004, Beasley et al. 2005, Jefferson and Rosenbaum 2014). Estimates of snubfin and humpback dolphin abundance from dedicated surveys are available for only a small number of sites on the east coast of Australia (Corkeron et al. 1997, Parra et al. 2006a, Cagnazzi 2011, Cagnazzi et al. 2011, 2013b) and, more recently, the Northern Territory (Palmer et al. 2014, Brooks and Pollock 2015). While the sizes of these study areas range from approximately 300-1,000 km^2, most of this research has revealed small local populations of 50-100 snubfin dolphins, and 50-150 humpback dolphins. Larger abundances of up to 200 snubfin and humpback dolphins reported at Port Essington, Northern Territory, appear to be an exception (Palmer et al. 2014). Available data suggest that these local populations exhibit site fidelity (Parra et al. 2006a, Cagnazzi et al. 2011, 2013b), occupy limited ranges (Cagnazzi 2011), and are reliant upon near-shore habitats (Parra et al. 2006b, Parra and Jedensjö 2014). A study of population genetic structure showed low levels of gene flow between several populations of snubfin and humpback dolphins on the east coast of Australia (Cagnazzi 2011). While total population sizes are unknown, both snubfin and humpback dolphins are each considered likely to number < 10,000 mature individuals (Reeves et al. 2008b, 2008c), which is the threshold number for contributing to a threatened category conservation status under criteria 'C' of the International Union for Conservation of Nature (IUCN) Red List Categories and Criteria for Species Status Assessment (IUCN 2012).

Bottlenose dolphins, by contrast, are more widely distributed; they occur in temperate to tropical inshore areas of the Indo-Pacific (Krützen and Allen 2008), and have been subject to detailed study in many locations across Australia (e.g. Krützen et al. 2005, Wiszniewski et al. 2011, Ansmann et al. 2012a, Smith et al. 2013). However, few data exist for bottlenose dolphins in northern Australia's coastal waters (Allen et al. 2012, Beasley et al. 2012).

[1] International Union for Conservation of Nature (IUCN) Categories and Criteria for Species Status Assessment (IUCN 2012).
[2] Threatened Species Scientific Committee Guidelines for assessing the conservation status of native species according to the *Environment Protection and Biodiversity Conservation Act 1999* (TSSC 2015).

Despite occupying a range of shallow water habitats and exhibiting abundances in the order of several hundred or low thousands within some sub-tropical coastal waters (e.g. Preen et al. 1997, Chilvers and Corkeron 2003, Lukoschek and Chilvers 2008, Nicholson et al. 2012), reported abundances of this species off the Northern Territory are small (< 100 individuals/study area) (Palmer et al. 2014, Brooks and Pollock 2015).

While there are insufficient data available to assess the conservation status of snubfin and humpback dolphins under the IUCN Red List Criteria, and a 'data deficient' status could be applied, both species have been assigned precautionary 'near threatened'[3] statuses by the IUCN in light of their apparent low population sizes and ongoing vulnerability to threats (Reeves et al. 2008b, 2008c, Woinarski et al. 2014). For both species, the IUCN noted that additional data would likely result in an elevation of their statuses (Reeves et al. 2008b, 2008c). The 'near threatened' status for humpback dolphins in Australia was prior to the description of *S. sahulensis* (Jefferson and Rosenbaum 2014), and therefore considered both *S. sahulensis* and *S. chinensis* as a single species (Reeves et al. 2008b). The IUCN Red List status of *S. sahulensis* is currently undergoing reassessment, as is that of the snubfin dolphin (D. Caganzzi, pers. comm.[4]). Bottlenose dolphins are considered 'data deficient' by the IUCN (Hammond et al. 2008, Woinarski et al. 2014).

In north-western Australia, all three species of inshore dolphin are listed as 'migratory'[5] under national legislation (*Environment Protection and Biodiversity Conservation* (*EPBC*) *Act 1999*) on account of their listing on Appendix II of the *Convention on Migratory Species (CMS) 1979*, of which Australia is a party. As such, they are considered Matters of National Environmental Significance, and any action likely to have a 'significant impact' on them must undergo environmental assessment (Department of the Environment 2013a). The *EPBC Act* further promotes the conservation of listed 'threatened species' following a detailed assessment of their threat status. However, nominations to list both snubfin and

[3] For humpback dolphins, the IUCN assessment considered both *S. sahulensis* and *S. chinensis* as a single species (Reeves et al. 2008b). A recent evaluation of the status of *S. sahulensis* according to the Red List criteria concluded that a precautionary 'vulnerable' status was appropriate, due to a total number of mature individuals plausibly < 10,000, an inferred continuing decline due to cumulative impacts, and all studied populations to date being < 1,000 mature individuals (Parra and Cagnazzi 2016).

[4] Daniele Cagnazzi, Southern Cross University, personal communication, August 2015

[5] Only *T. aduncus* occurring in the Arafura/Timor Sea region are listed as 'migratory' under *CMS 1979* and the *EPBC Act 1999*; *T aduncus* occurring elsewhere in Australia and beyond are not listed on either Appendix of *CMS 1979* and therefore are listed as 'cetacean' under the *EPBC Act 1999*.

humpback dolphins as 'threatened species' were found to be ineligible for assessment against the *EPBC Act* threatened species criteria (TSSC 2015) due to insufficient data on their distribution, abundance and population trends (Department of the Environment 2015a). Data deficiencies also preclude their assessment as threatened species under state legislation in Western Australia (the *Wildlife Conservation Act 1950*).

Concerns have been raised over the lack of data to support the conservation and management of tropical inshore dolphins throughout northern Australia for over two decades (Bannister et al. 1996, Hale 1997, Ross 2006, Woinarski et al. 2014). Their apparent low abundance, site fidelity and reliance on inshore habitats render them vulnerable to a variety of anthropogenic threatening processes, although these remain poorly characterised (Beasley et al. 2012). Habitat degradation through coastal development has been highlighted as a key issue (Allen et al. 2012, Beasley et al. 2012, Bejder et al. 2012). The number of large-scale port developments in this region is increasing, with notable concentrations of development on sections of the Great Barrier Reef (east) coast (Grech et al. 2013) and the Pilbara coast of north-western Australia (Bejder et al. 2012, Hanf et al. 2016). These result in considerable modification of local, inshore habitats (Jefferson et al. 2009), and the associated dredging, construction activities and vessel traffic may displace inshore dolphins from important habitats (Tougaard et al. 2009, Brandt et al. 2011, Pirotta et al. 2013, Weaver 2015). Additionally, injury and mortality in gillnet fisheries is known to occur among many *Orcaella*, *Sousa* and *Tursiops* populations in the Indian Ocean region (Reeves et al. 2013b). All three species of inshore dolphin have been recorded as incidental capture in anti-shark nets (Paterson 1990) and commercial gillnet fisheries; however, the level of bycatch mortality remains largely unknown (Harwood and Hembree 1987, Hale 1997, Parra et al. 2002, 2004, 2006a). Evidence of vessel strikes and entanglement injuries have been reported in snubfin dolphins (Thiele 2010), and elevated levels of anthropogenic contaminants have been observed in the tissue of snubfin and humpback dolphins at one site on the east coast of Australia (Cagnazzi et al. 2013a). A summary of anthropogenic activities and perceived main threats to inshore dolphins at each of the study sites included within this thesis are provided in Appendix A1.

The coastal waters of north-western Australia represent a considerable portion of the global range of snubfin and humpback dolphins. However, other than evidence of their occurrence

in the coastal waters adjacent to various urban centres (Allen et al. 2012), there is a complete absence of quantitative data on the abundance, population genetic structure and behavioural ecology of inshore dolphins in this region. Due to these data deficiencies, the threats associated with industrial-scale coastal development, and recognition of the vulnerability of tropical inshore dolphins to human impacts, there is a pressing need for baseline population data to inform the conservation and management of these species (Allen et al. 2012, Bejder et al. 2012, Brown et al. 2012).

Thesis structure

This thesis combines several fields of research, including abundance estimation (Chapter 2), population genetics (Chapter 3), behavioural ecology (Chapter 4), and morphology (Chapter 5). All address gaps in our understanding of tropical inshore dolphins, and my overarching aim is to improve the scientific basis for their conservation and management. I focus on Australian snubfin and humpback dolphins due to their greater conservation concern. However, I also present abundance data on Indo-Pacific bottlenose dolphins as they are subject to the same data deficiencies and threats across northern Australia, and they represent important components of the inshore dolphin fauna in some areas.

The specific objectives of my thesis are to:

1. Estimate the abundance of snubfin, humpback and bottlenose dolphins at selected locations in north-western Australia by conducting standardised boat-based surveys and applying capture-recapture analyses to photo-identification data (Chapter 2);
2. Examine the genetic diversity and structure of snubfin and humpback dolphins among selected locations in north-western Australia, including the occurrence of hybridisation between the two species (Chapter 3);
3. Analyse the social structure of snubfin dolphins within a specific study population; specifically, investigate sex-specific grouping, association patterns and their correlations with genetic relatedness (Chapter 4);
4. Use dorsal fin images to investigate potential sex-differences and geographic variation in dorsal fin features of humpback dolphins from north-western and north-eastern Australia; assess the utility of dorsal fin images to determine sex; and, infer potential population structure between geographic regions (Chapter 5); and,

5. Summarise key findings and make recommendations to support the conservation and management of inshore dolphins in north-western Australia (Chapter 6).

Chapters two (abundance estimation) and three (population differentiation) provide the applied core of this thesis. These chapters address two fundamental issues in conservation biology: population size and differentiation. Chapter four (social structure) improves our understanding of the behavioural ecology of snubfin dolphins markedly beyond what was previously known. Chapter five (sexual dimorphism and geographic variation) presents: a method for identifying the sex of humpback dolphins based on dorsal fin features, providing a valuable tool to inform future studies of their population biology; and, investigates geographic variation in these features to infer potential population structure.

This thesis has been written as a thesis by publication, following the Murdoch University style guideline for thesis by publication/manuscripts. A concise general introduction (Chapter 1) frames the context, research need, and objectives. Data chapters (Chapters 2-5) are presented as stand-alone documents, although they are cross-referenced as appropriate. Lastly, a general discussion (Chapter 6) summarises the findings of the data chapters and their implications, the extent to which objectives were fulfilled, study limitations, and provides recommendations for future research and management actions.

Appendix A1. Summary of anthropogenic activities and threats to inshore dolphins at thesis study sites

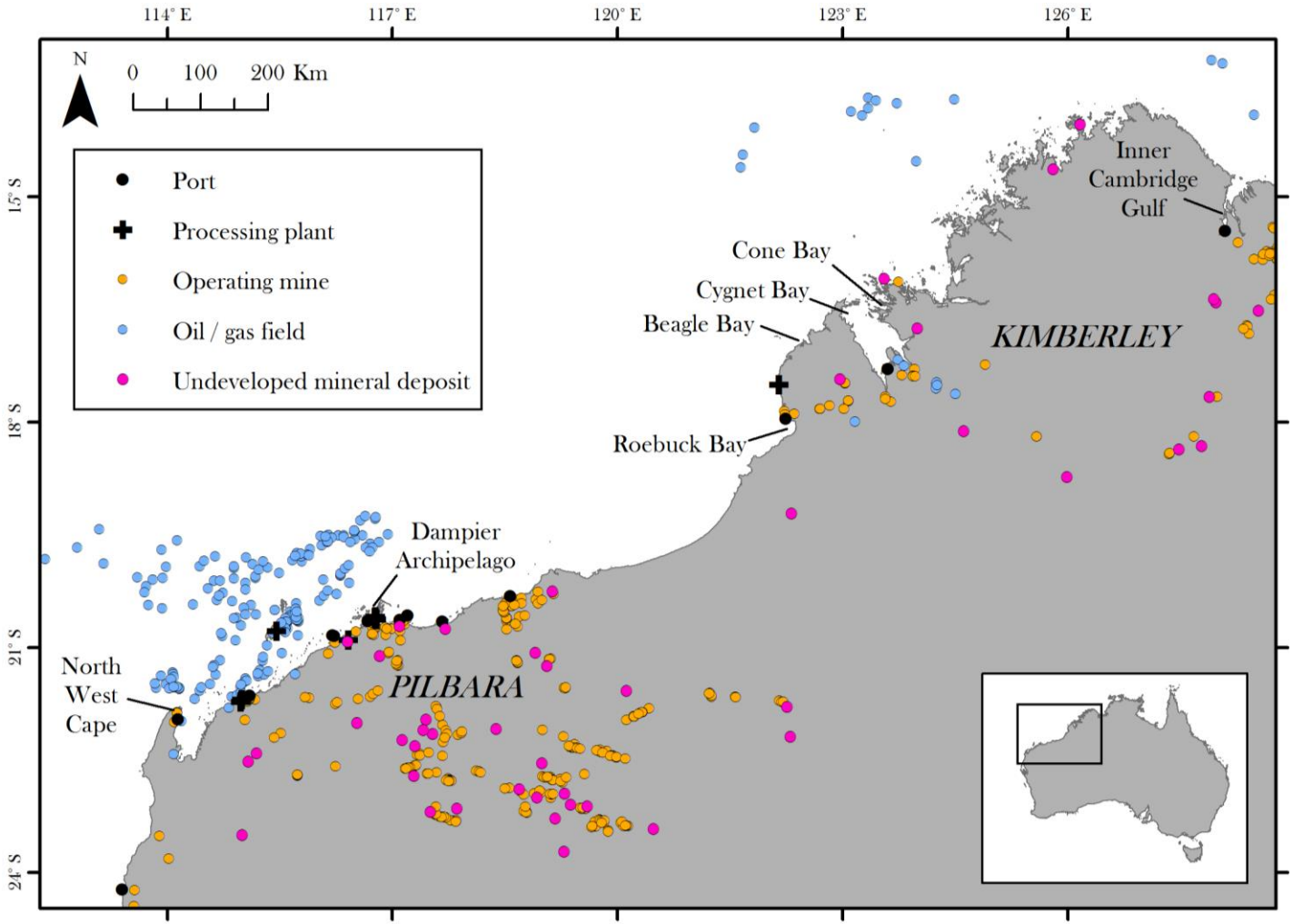


Figure A1. North-western Australia, illustrating: the Pilbara and Kimberley regions; study sites included in this thesis; and, major coastal infrastructure and resource projects (Department of Mines and Petroleum 2016). The processing plant marked north of the Roebuck Bay study site (a major liquefied natural gas processing and port export facility) indicates a proposed development.

Table A1. Level of anthropogenic activity and perceived main threats to inshore dolphins at study sites included in this thesis. *Continued overleaf.*

Study site (corresponding thesis chapters)	**Level of anthropogenic activity and threats**
North West Cape[1] (3, 5)	*Overall assessment on current level of anthropogenic activity:* low-moderate *Anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins:* • Commercial port (servicing: fishing, offshore oil and gas operations, tourism and recreational vessels). Moderate level of vessel traffic. • Commercial prawn trawl fishery operating in Exmouth Gulf. • Recreational vessel traffic (primarily small recreational fishing activities). • Commercial nature tourism vessel traffic (primarily dive/snorkel activities) *Potential future anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins:* • Port expansion or development of a new port. *Perceived main threat(s):* • Disturbance from vessel traffic. • Habitat loss, degradation and vessel disturbance associated with port operations and shipping, potentially increasing with future port expansion/development. • *Other notes:* • The study site lies within the Ningaloo Marine Park (Marine Protected Area) and World Heritage Area.
Dampier Archipelago[2] (3,5)	*Overall assessment on current level of anthropogenic activity:* high *Anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins:* • Commercial deep-water port (servicing: petrochemical, mineral and natural gas export, offshore oil and gas operations, recreational vessels). High level of vessel traffic with c. 450 vessels per month. • Small vessel traffic (primarily recreational fishing). • Several other ports in adjacent areas (i.e. within 100 km).

	Potential future anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins: • Port expansion. *Perceived main threat(s):* • Habitat degradation and vessel disturbance associated with port operations and shipping (including dredging). • Future habitat loss, degradation and increased vessel disturbance associated with port expansion and/or port development in adjacent areas. • Cumulative habitat degradation and fragmentation from multiple port developments on the adjacent coastline. • *Other notes:* • The study site lies within the proposed Dampier Archipelago Marine Park (Marine Protected Area).
Roebuck Bay[3] (2,3)	*Overall assessment on current level of anthropogenic activity:* moderate *Anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins:* • Commercial deep-water port (servicing: livestock export, offshore oil and gas operations, aquaculture, fishing, cruise liners, tourism vessels). Moderate level of vessel traffic with c. 100 vessels per month. • High level of small vessel traffic (primarily recreational fishing with low level of customary hunting (turtle/dugong)). • Commercial gillnet fishing (two licences), which ceased in late 2013 when licences bought by government and is unlikely to resume due to forthcoming protected area status. • Adjacent township of population c. 14,000 (larger during peak tourist season of May-August). *Potential future anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins:* • Broome port upgrades/expansion, including increased vessel movements. • Broome marina development. • Proposed dolphin-watching tours. • Major proposed petroleum processing plant and port development (Browse Liquefied Natural Gas Precinct) in adjacent area (c. 65 km to the north).

	Perceived main threat(s): • Disturbance from high level of small vessel traffic. • Injury to dolphins resulting from vessel strike and entanglement (with recreational fishing gear). • Habitat degradation and vessel disturbance associated with port operations and shipping. • Habitat degradation resulting from algal blooms associated with poor water quality. • Interactions (i.e. entanglement injury or mortality) with gillnet operations were a key threat up until late 2013 when these activities ceased. The impact this had on inshore dolphins in the area is unknown. • Future habitat loss, degradation and increased vessel disturbance port upgrade/expansion and/or marina development, or proposed port development in adjacent area (c. 65 km to the north). *Other notes:* • The study site lies within the proposed Roebuck Bay / Yawuru Nagulagan Marine Park (Marine Protected Area)
Beagle Bay[4] (2,5)	*Overall assessment on current level of anthropogenic activity:* low *Anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins:* • Very limited anthropogenic activities at present. • Low level of vessel traffic associated with recreational fishing and customary fishing/hunting (turtle/dugong). • Pearl oyster aquaculture has occurred in the past, but with little/no activity at present. *Potential future anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins:* • Major proposed petroleum processing plant and port development (Browse Liquefied Natural Gas Precinct) in adjacent area (c. 65 km to the south). *Perceived main threat(s):* • Potential disturbance (minor) due to small vessel traffic. • Future habitat loss, degradation and increased vessel disturbance in adjacent area associated with proposed port development (c. 65 km to the south).
Cygnet Bay[5] (2,3,4,5)	*Overall assessment on current level of anthropogenic activity:* low *Anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins:*

	• Pearl oyster aquaculture, comprising fixed ropes with small physical footprint and low level of associated small vessel movements. • Low level of small vessel traffic associated with tourism, primarily transiting northern third of study area. • Very limited small vessel traffic associated with recreational fishing within the study area. • Moderate recreational (fishing) and customary hunting (turtle/dugong) vessel traffic north of study area. • Low level of commercial gillnet fishing operating within the broader King Sound area. *Potential future anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins:* • Potential for increased small vessel movements associated with tourism. *Perceived main threat(s):* • Potential disturbance (minor) due to small vessel traffic. • Potential interactions (i.e. entanglement) with gillnet operations outside of the study area.
Cone Bay[6] (2,5)	*Overall assessment on current level of anthropogenic activity:* low (but locally moderate) *Anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins:* • Marine fin-fish aquaculture, comprising c. 20 sea cages with small physical footprint and locally moderate level of small vessel movements. Up to 2,000 tonnes fish production per annum. • Very limited small vessel traffic associated with recreational fishing and customary hunting (turtle) within the study area. • Low level of commercial gillnet fishing operating within the broader King Sound area. *Potential future anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins:* • Approved plans for expanding marine fin-fish aquaculture, resulting in increased physical footprint and moderate level of small vessel movements. Up to 20,000 tonnes of fish production per annum. *Perceived main threat(s):* • Potential disturbance (localised) due to small vessel traffic, which may increase when aquaculture operations expand.

	• Potential changes in ecosystem (i.e. prey/predator distribution and abundance) due to aquaculture operations, potentially increasing as aquaculture operations expand. • Potential interactions (i.e. entanglement) with gillnet operations outside of the study area.
Inner Cambridge Gulf[7] (2)	*Overall assessment on current level of anthropogenic activity:* low-moderate *Anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins:* • Commercial deep-water port (servicing: livestock export, mineral export, tourism vessels). Low-moderate level of vessel traffic. • Commercial gillnet fishing (one licence), primarily operating in adjacent waters of the outer Cambridge Gulf. • Low level of small vessel traffic associated with tourism, primarily fishing charters. • Very limited small vessel traffic associated with recreational fishing within the study area. *Potential future anthropogenic activities within and adjacent to the site with the potential to negatively impact upon inshore dolphins:* • Port upgrade/expansion, resulting in increased vessel traffic. *Perceived main threat(s):* • Vessel disturbance associated with port activities and shipping. • Potential disturbance due to recreational vessel traffic. • Potential interactions (i.e. entanglement) with gillnet operations

Study sites are ordered from west to east. Chapter 2 = abundance estimation; Chapter 3 = population differentiation; Chapter 4 = social structure; Chapter 5 = sexual dimorphism and geographic variation. The "overall assessments on the current levels of human activity" are based upon those suggested in Department of Environment (2015b), while the "perceived main threats" are those assessed by the author based on the nature and level of activities and those which present recognised threats to inshore dolphins documented in the literature (see Hale 1997, Beasley et al. 2012, Woinarski et al. 2014, Department of the Environment 2015b). Details of anthropogenic activities in the majority of these study sites are poorly documented, and therefore much of the information presented in this table has come from personal observations during data collection for this thesis; however, the following site-specific information sources have also been drawn upon: (CALM 2005, MPRA and CALM 2005, Thiele 2010, Department of State Development 2010, Brown et al. 2012, Dambimangari Aboriginal Corporation 2012, Department of Fisheries 2013, 2015, Department of Parks and Wildlife 2015, Pilbara Ports Authority 2016, Cambridge Gulf Limited 2016, Kimberley Ports Authority 2016).

Chapter 2. Site-specific assessments of the abundance of three inshore dolphin species to inform conservation and management[6]

2.1 Abstract

Assessing the abundance of wildlife populations is essential to their effective conservation and management. Concerns have been raised over the vulnerability of tropical inshore dolphins in waters off northern Australia to anthropogenic impacts on local populations, yet a lack of abundance data precludes assessment of their conservation status and the management of threats. Using small vessels as cost-effective research platforms, photo-identification surveys and capture-recapture models were applied to provide the first quantitative abundance data for Australian snubfin (*Orcaella heinsohni*), Australian humpback (*Sousa sahulensis*), and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) at five sites in the Kimberley region of north-western Australia. The abundance of each species was highly variable between different sites, likely reflecting species-specific habitat preferences. Within the c. 130 km^2 study sites, the estimated abundance of most species was $\leq$ 60 individuals (excluding calves), and fewer than 20 humpback dolphins were identified at each site in any one 3-5 week sampling period. However, larger estimates of c. 130 snubfin and c. 160 bottlenose dolphins were obtained at two different sites. Several local populations showed evidence of site fidelity, particularly snubfin dolphins. By implementing a standardised, multi-site approach, data on local populations were provided within a broader, regional context, and indicated that each species is patchily distributed in the region. This highlights the need for site-specific baseline data collection using appropriate survey techniques to quantitatively assess the potential impacts of threatening activities to local populations. These findings further illustrate the need to gain a greater understanding of known and potential threats to inshore dolphin populations, their relative impacts, and to mitigate where necessary. An ideal candidate site for a long-term study of snubfin dolphin population dynamics is identified, where trends in abundance and their influencing factors could be investigated. The methods employed herein provide an example of rigorous, site-specific population assessments of inshore dolphins that are broadly applicable to such studies elsewhere.

[6] Chapter publication status: published 2016.

2.2 Introduction

Estimating abundance is a key element of wildlife management strategies and important to assessing the conservation status of a species or population. They provide a base from which to investigate: trends in abundance (Gerrodette 1987), natural vulnerability to extinction risk (Shaffer 1981), the potential resilience to anthropogenic sources of mortality (Wade 1998), and the biological significance of impacts of proposed anthropogenic activities (NRC 2005b). Cetaceans are long-lived species, with late maturation, low reproductive rates and often occupy high trophic levels; consequently, they are inherently vulnerable to human impacts and often in particular need of conservation action (Taylor 2002, Lewison et al. 2004). However, due to their traits (highly mobile, problematic to observe), obtaining unbiased and precise abundance estimates of cetaceans can be difficult, expensive and time-consuming, particularly for species which are sparsely distributed across large and remote areas (Taylor and Gerrodette 1993, Williams and Thomas 2009, Peel et al. 2015). Overcoming these challenges has proven a significant impediment to cetacean research and the conservation status of numerous species and populations remains data deficient (IUCN 2015). Due to their overlap with areas of considerable human activity, cetacean populations occupying near-shore coastal habitats are among the most threatened (e.g. Rojas-Bracho et al. 2006, Slooten et al. 2006, 2013) and in most need of quantitative data to inform management (Wilson et al. 1999, Parra et al. 2006a).

Three species of coastal dolphin inhabit shallow, inshore waters of northern Australia: the Australian snubfin dolphin (*Orcaella heinsohni*, hereafter 'snubfin dolphin'), the Australian humpback dolphin (*Sousa sahulensis*, hereafter 'humpback dolphin') and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*, hereafter 'bottlenose dolphin'). For all three species, a lack of data on their distribution, abundance and their trends precludes comprehensive assessment of their conservation status and the management of impacts on local populations (Beasley et al. 2012, Woinarski et al. 2014). Snubfin and humpback dolphins are of particular conservation concern. Globally, their distribution is restricted to shallow coastal and estuarine waters of northern Australia and southern New Guinea (Parra et al. 2002, 2004, Beasley et al. 2005, 2016, Jefferson and Rosenbaum 2014). Available data suggest that both species are discontinuously distributed as small populations of 50-200 (e.g. Parra et al. 2006a, Palmer et al. 2014; Table 2.1), which exhibit site fidelity (Parra et al. 2006a, Cagnazzi et al. 2011, 2013b), limited gene flow between populations

(Cagnazzi 2011, Brown et al. 2014), and are reliant upon near-shore habitats (Parra et al. 2006b, Parra and Jedensjö 2014). While snubfin and humpback dolphins are data deficient, both species have been assigned precautionary 'near threatened'[7] statuses by the International Union for Conservation of Nature (IUCN) in light of their apparent low population sizes and ongoing vulnerability to threats (Reeves et al. 2008b, 2008c). Bottlenose dolphins are widely distributed in warm temperate to tropical shallow coastal waters of the Indo-Pacific (Krützen and Allen 2008), and exhibit locally high abundances within some sub-tropical embayments of Australia (e.g. Preen et al. 1997, Chilvers and Corkeron 2003). However, few data exist for bottlenose dolphins in waters off northern Australia (Beasley et al. 2012; Table 2.1), and, globally, they are considered 'data deficient' by the IUCN (Hammond et al. 2008).

Due to these data deficiencies, a range of potential (but largely unquantified) threats, and increasing development of coastal areas in recent decades, there have been repeated calls for improved baseline population data to support the conservation and management of inshore dolphins across northern Australia (e.g. Bannister et al. 1996, Ross 2006, Department of the Environment 2013b, Woinarski et al. 2014). All three species of inshore dolphin in north-western Australia are considered Matters of National Environmental Significance under national legislation (*Environment Protection and Biodiversity Conservation Act, EPBC Act 1999*); therefore, any action likely to have a significant impact on them must undergo environmental assessment (Department of the Environment 2013a). However, the lack of baseline data on these species has contributed to their limited consideration in the Environmental Impact Assessment (EIA) of coastal developments to date, thereby perpetuating data deficiencies (Bejder et al. 2012). Despite the presence of numerous industrial port developments, no abundance estimates are currently available for any species of inshore dolphin across north-western Australia.

[7] The IUCN Red List status assessment of 'near threatened' for humpback dolphins in Australia was prior to the description of *S. sahulensis* (Jefferson and Rosenbaum 2014) and, therefore, considered both *S. sahulensis* and *S. chinensis* as a single species (Reeves et al. 2008b). A recent evaluation of the status of *S. sahulensis* according to the Red List criteria concluded that a precautionary 'vulnerable' status was appropriate (Parra and Cagnazzi 2016).

Table 2.1. Capture-recapture abundance estimates of snubfin, humpback and bottlenose dolphins in Western Australia (WA), Northern Territory (NT) and Queensland (QLD). Only estimates for bottlenose dolphins north of the Tropic of Capricorn are shown. Differences in approximate densities between studies may reflect real differences, but may also be influenced by study area size, methodology and duration of sampling.

Species	Study site (approximate area)	Study period	Abundance estimate(s) (95% CI)	Approximate density	Source
Snubfin	Roebuck Bay, WA (100 km^2)	2013-2014	133 (127-148)	1.33	This study
	Cygnet Bay, WA (130 km^2)	2012-2013	48 (41-58) – 54 (51-60)	0.37 – 0.42	This study
	Darwin region, NT (1,086 km^2) ¶	2011-2014¶	19 (14-25) – 54 (36-72) ¶	0.02 – 0.05	Brooks & Pollock (2015)
	Port Essington, NT (325 km^2)	2008-2010	136 (58-317) – 222 (146-336)	0.42 – 0.68	Palmer et al. (2014)
	Cleveland Bay, QLD (310 km^2)	1999-2002	64 (51-80) – 76 (65-88)	0.21 – 0.25	Parra et al. (2006a)
	Keppel Bay, QLD (980 km^2)†	2006-2011†	71 (61-80) – 80 (68-93)	0.07 – 0.08†	Cagnazzi et al. (2013)
Humpback	Cygnet Bay, WA (130 km^2)	2012-2013	15 (12-20) – 20 (18-24)	0.12 – 0.15	This study
	Darwin region, NT (1,086 km^2) ¶	2011-2014¶	79 (70-111) – 95 (79-145) ¶	0.07 – 0.09	Brooks & Pollock (2015)
	Port Essington, NT (325 km^2)	2008-2010	48 (24-95) – 207 (113-379)	0.15 – 0.64	Palmer et al. (2014)
	Cleveland Bay, QLD (310 km^2)	1999-2002	34 (24-49) – 54 (38-77)	0.11 – 0.17	Parra et al. (2006a)
	Keppel Bay, QLD (980 km^2)†	2006-2008†	107 (98-117)	0.11	Cagnazzi (2011)
	Port Curtis, QLD (510 km^2)	2006-2008	85 (77-94)	0.17	Cagnazzi (2011)
	Great Sandy Strait, QLD (1,000 km^2)	2004-2007	150 (133-165)¶	0.15	Cagnazzi et al. (2011)
	Moreton Bay, QLD (1,315 km^2)	1984-1987	119 (81-166) – 163 (108-251)	0.09 – 0.12	Corkeron et al. (1997)
Bottlenose	Beagle Bay, WA (130 km^2)	2012-2013	157 (137-186)	1.21	This study
	Cygnet Bay, WA (130 km^2)	2012-2013	35 (27-48) – 60 (42-87)	0.27 – 0.46	This study
	Darwin region, NT (1,086 km^2)¶	2011-2014¶	20 (15-25) – 38 (25-51) ¶	0.02 – 0.03	Brooks & Pollock (2015)
	Port Essington, NT (325 km^2)	2008-2010	34 (14-83) – 75 (39-154)	0.10 – 0.23	Palmer et al. (2014)

Study sites are ordered from west to east. † While an area of c. 980 km^2 was surveyed in Keppel Bay, the 95% utilisation distribution of snubfin dolphins was 349 km^2, corresponding to an approximate density of 0.20-0.23.. ¶ The Darwin region includes three adjacent sites of Darwin Harbour (471 km^2), Bynoe Harbour (461 km^2) and Shoal Bay (154 km^2). At the time of publication, data collection was ongoing within the Darwin region (Brooks, L., Statplan Consulting, pers. comm.) and Keppel Bay (Cagnazzi, D., Southern Cross University, pers. comm.).

Capture-recapture methods using photo-identification (photo-ID) data are a common method of estimating the abundance of small cetaceans (Würsig and Jefferson 1990, Urian et al. 2015). These methods can be implemented from a small vessel and, with careful study design, can provide a cost-effective method of producing relatively unbiased and precise abundance estimates, albeit at a relatively small geographic scale (e.g. Wilson et al. 1999, Dawson et al. 2008, Williams and Thomas 2009). Photo-ID data also facilitate estimation of other demographic parameters such as survival rates and movement patterns, along with information such as calving rates and social structure (Hammond et al. 1990). Despite the often-cryptic behaviour of snubfin and humpback dolphins (inconspicuous surfacing pattern; vessel avoidance; occurrence in turbid waters), most individuals can be reliably photo-identified based on dorsal fin markings and capture-recapture methods have been utilised in a number of studies of inshore dolphin in northern Australia to date (see Table 2.1).

This chapter aims to provide the first measures of snubfin, humpback and bottlenose dolphin abundance in north-western Australia. Data collection focuses on the Kimberley region, a remote coastline which has been subject to increasing interest for industrial port development in recent years (Department of State Development 2010, Hanf et al. 2016 and see Appendix A1). Using small vessels as a cost-effective platform, a standardised photo-identification survey design was applied to provide rigorous, site-specific baseline data at five near-shore study sites. Encounter rates, numbers of individuals photo-identified, and capture-recapture estimates of absolute abundance are presented. Repeated sampling provides information on the fidelity of animals to some sites. By surveying multiple study sites, insight is provided into the occurrence of inshore dolphins at a broader scale within the region, and potential movements between sites. Repeated sampling provided information on the fidelity of animals to some sites. Further, I assess the utility of a series of abundance estimates for trend detection, and make corresponding recommendations for establishing an effective long-term study of population dynamics at an appropriate site. Based on these findings, a series of recommendations are made to support the conservation and management of inshore dolphins in northern Australia.

2.3 Methods

2.3.1 Study area

The Kimberley coast of north-western Australia is long and intricate, with complex habitats subject to large, semi-diurnal tides of up to 10 m range (Cresswell et al. 2011) (Fig. 2.1). Five study sites were selected: four coastal (Roebuck, Beagle, Cygnet and Cone Bays) in the western Kimberley, and one estuarine (Inner Cambridge Gulf) in the eastern Kimberley. Combined, these sites represent 6% of the c. 6,700 km length of the Kimberley mainland coastline[8]. Study sites were selected according to logistical constraints (e.g. accessibility, vessel launch facilities), reports of inshore dolphin sightings from local sources, and limited published sightings data (Thiele 2010, Allen et al. 2012). The current level of anthropogenic activity varies between these different sites and is summarised in Appendix A1 (Chapter 1).

2.3.2 Data collection

Study sites were surveyed between one and four times from 2012-2014 during the months of Apr-Jun and Sep-Oct: the dry season months which generally experience the calmest sea conditions (Table 2.3). For each site, a structured sampling procedure was adopted which conformed to the principles of the Robust Design (Pollock 1982, Pollock et al. 1990, Kendall et al. 1997, Smith et al. 2013), where multiple 'secondary' sampling events (here, 'transects') occurred in relatively short succession over a three to five week 'primary' period (here, 'sampling period'). Successive sampling periods at the same site were separated by longer time intervals of four to six months.

Using a 5.6 m research vessel, study sites were surveyed by following two pre-determined transects of c. 60 km length, configured in an offset zig-zag pattern (Fig. 2.1). At each site I aimed to cover a minimum area of c. 100 km^2 at mean high water, representing a range of water depths appropriate for the species (Parra et al. 2006b). Transects extended from the coast to approximately the 10 m (lowest astronomical tide) depth contour. The two transect routes were completed alternately to a minimum total of five repeats during each

[8] Based on the mean high water mark at 1:100,000 scale (Geoscience Australia 2004) from Eighty Mile beach (western boundary) to the Western Australia / Northern Territory border (eastern boundary); excluding islands.

sampling period. The inshore extent of survey effort varied according to the state of the tide and did not extend below 1.0 m water depth or < 200 m from shore. To reduce bias in the ability to detect dolphins, I aimed to conduct the vast majority of survey effort in Beaufort sea states ≤ two and wave height ≤ 0.3 m. Transects were completed in the shortest possible time at a survey speed of 10-12 km/h (c. 6 knots). If a transect could not be completed in a single day, effort was paused and resumed from that location at the next available opportunity (typically the following day).

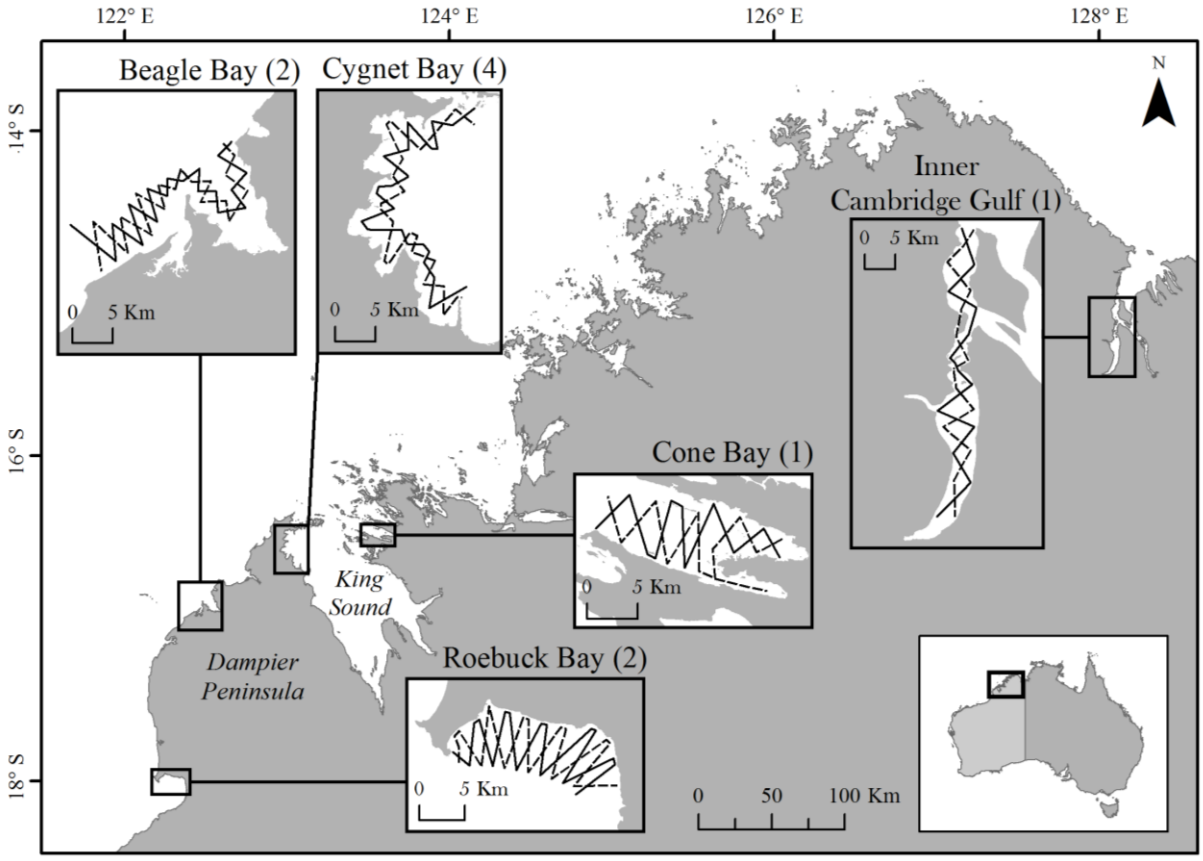


Figure 2.1. The Kimberley coastline of north-western Australia, showing study site locations. Numbers in parentheses indicate the number of sampling periods at each site. Insets show the two opposing pre-determined transect routes at each site. The coastline illustrated corresponds to the highest astronomical tide. For summary information on anthropogenic activities at each site, see Appendix A1, Chapter 1.

A crew of 3-5 (mode = four) observers searched for dolphins from the front half of the vessel. Upon sighting dolphins, I departed from the survey transect route and approached the dolphin group to record date, time, GPS location, species, and group size, composition and behaviour. Two observers with digital SLR cameras attempted to obtain multiple photographs of the dorsal fins of all dolphins present (oversampling) so that at least one

good-quality image of each individual present was obtained. A ‘group’ was defined as one or more dolphins within 100 m of any other group member and involved in the same or similar behavioural activity (Bräger 1999, Parra et al. 2006a).

2.3.3 Encounter rates

Daily vessel GPS tracks were assigned on/off effort values and interpolated to lines of effort to calculate the length of each transect, which varied according to tidal state. The total number of dolphins (including dependent calves) observed on a given transect was then divided by the transect length. Individual dolphins sighted more than once within a single transect (indicated by photo-identification) were not counted a second time. Per-transect dolphins/km values were summarised across all transects within a sampling period to provide a standardised measure of encounter rate as the mean (± SE) dolphins per km survey effort.

2.3.4 Image processing

Individual dolphins were identified from photographs based on nicks and notches on the leading and trailing edges of the dorsal fin, resulting in a catalogue of individuals for each study site (Würsig and Jefferson 1990). Three different observers independently scored each individual (excluding calves) as D1 (highly distinctive), D2 (distinctive) or D3 (indistinctive) based on the number and distinctiveness of their dorsal fin features (Urian et al. 1999, 2015). The final score was that given by ≥ two of the three observers. Both D1 and D2 individuals were included further in the analyses and are collectively referred to hereafter as ‘distinctive’ (Nicholson et al. 2012).

A selection of the best images of each individual was retained and subject to a quality assessment based on published protocols (Rosel et al. 2011). The underlying assumption was that the least distinctive individual should be readily identifiable from the lowest quality image used in the analyses (Nicholson et al. 2012, Urian et al. 2015); images not meeting this criterion were excluded from the analyses. For consistency, the lead author performed all image quality assessments.

2.3.5 Rate of new identifications, resights between sampling periods and movements of individuals between sites

Capture histories were compiled for distinctive individuals and summary statistics were generated on the number of individuals that were re-sighted across multiple sampling periods at the same site. The cumulative number of distinctive individuals identified was calculated per day of effort and plotted as a discovery curve over time. Catalogues of distinctive individuals from each study site were cross-referenced to investigate the movement of individuals between study sites over the study period.

2.3.6 Proportion of distinctive individuals in the population

The proportion of distinctive individuals in the population (θ) was estimated using a group sighting-based method (as per Nicholson et al. 2012), with results pooled across sampling periods for each site to estimate a single distinctive proportion for each site/species. In the estimation of θ, I only included group sightings where the exact group size was known, and where all individuals within the group were photographed to acceptable image quality criteria (see Section 2.3.4). The group sighting-based method was favoured over those based upon a random selection of images (e.g. Parra et al. 2006a, Palmer et al. 2014), as the random image-based method requires a conscious effort during data collection to randomly photograph individuals within a group (Eguchi 2014) – a procedure which I did not employ. Consequently, the collected photographs may be biased towards more distinctive individuals (see Read et al. 2003), more approachable individuals, or those targeted during concurrent biopsy sampling (see Chapters 3, 4, 5) within a group.

2.3.7 Abundance estimates

Where sufficient capture histories of distinctive animals were available, capture-recapture models were applied in program MARK (White and Burnham 1999) to produce estimates of abundance, capture probabilities and demographic parameters for the distinctive proportion of the population. As the number of sampling periods varied between sites, I did not restrict the choice of model to a single approach. Instead, combinations of both open and closed models were considered to investigate violations of closure assumptions and inform the selection of the most appropriate models for each site and species. I comprehensively considered the various assumptions and sources of bias in capture-recapture models using multiple validation approaches that are summarised in Table 2.2.

2.3.8 Robust Design

Four sampling periods at Cygnet Bay permitted the use of Pollock's closed Robust Design (RD) (Pollock 1982, Kendall et al. 1997), which has been increasingly applied to populations of coastal cetaceans (e.g. Silva et al. 2009, Cantor et al. 2012, Nicholson et al. 2012, Smith et al. 2013). This structured approach (which requires ≥ three sampling periods) facilitates the use of simpler and more precise closed models to estimate abundance within sampling periods, while also incorporating elements of open models to allow estimation of temporary emigration and apparent survival between sampling periods (Pollock et al. 1990, Kendall and Nichols 1995, Kendall et al. 1995, 1997).

Estimated parameters within sampling periods included the distinctive population size ($\widehat{N}_D$) and capture probability (*p*). For *p*, the probability of initial capture was set equal to the probability of subsequent capture (*p* = *c*), as 'capture' by non-invasive photo-identification was not anticipated to elicit a 'trap response' (Wilson et al. 1999; Table 2.2). Between sampling periods, temporary emigration parameters (γ", γ') were estimated, where γ" is the probability of an individual being a temporary emigrant, given it was available for capture in the previous sampling period, whereas γ' is the probability of an individual being a temporary emigrant, given it was unavailable (a temporary emigrant) in the previous sampling period. Parameter configurations include γ" = γ' = 0 (no temporary emigration); γ" = γ' (random temporary emigration); and, γ" ≠ γ' (non-random (Markovian) temporary emigration). These models also estimated apparent survival (φ), defined as the probability of surviving and staying in the study area (the product of true survival and fidelity to the study area) and scaled on an annual basis. For each temporary emigration configuration, a series of models were fitted where parameters were either constant (.) or time varying (*t*). Three configurations of capture probability were included: time-varying within and between sampling periods, *p*(*t*); time-varying between, but not within, sampling periods *p*(*s*); and, constant within and between sampling periods *p*(.).

A goodness-of-fit (GOF) test is not available in MARK for RD models (White and Burnham 1999), so I could not assess or correct for over-dispersion in the data where these models were used. The Akaike's information criterion corrected for small sample size (AICc) was used as a measure of relative GOF of each closed model. The model with the

lowest AICc was selected as the best fitting, with consideration also given to models within two AICc units, where applicable (Burnham and Anderson 2002). To account for model uncertainty, weighted model averaging was applied across all successfully run models to produce model-averaged estimates of $\widehat{N}_D$. This technique is considered to produce more stable estimates than selecting a single 'best' model from a number of closely-related models (Burnham and Anderson 2002).

2.3.9 Open models with restrictions

Open models allow for demographic changes in the population over time, providing estimates for gains (births, immigration) and losses (deaths, emigration). The sampling periods were short relative to the life history of the species, and therefore demographic closure can be assumed (Table 2.2). However, preliminary investigation of the capture histories and location of sightings within Roebuck and Beagle Bay sites suggested a lack of geographic closure; I observed highly variable captures per transect, a continuing rise in newly identified individuals throughout a sampling period (Fig. 2.2), and numerous sightings at the periphery of study sites (Appendix A2.3). Movement of animals in and out of a study site (temporary emigration) within a sampling period will not lead to biased estimates of abundance in either closed or open models if such movement is of a random nature (Kendall 1999). However, estimates will be biased if temporary emigration is non-random (i.e. Markovian).

To address suspected gains and losses within sampling periods at Roebuck and Beagle Bays, open models with various restrictions on losses and gains (see below) were implemented using the POPAN formulation of the classic Jolly-Seber open models (Schwarz and Arnason 1996). This allowed the fitting of both fully and partially closed model configurations to account for possible net gains and/or losses, along with the estimation of a 'super-population' parameter. The super-population, as introduced by Crosbie & Manly (1985) and Schwarz & Arnason (1996), is defined as the total number of animals that use the study site at any time during the course of the study. Furthermore, these models allow correction for animals that may enter and exit the study site rapidly between sampling events, therefore being unavailable for capture. Animals encountered during the sampling events (transects) represent components of the larger super-population, and a probability of entry of animals from the super-population into the sampled population

between sampling events is estimated (Carroll et al. 2013, Tyne et al. 2014). For short duration studies of long-lived species, the super-population estimate is particularly useful where the absolute size of a population is of more interest than the abundance or density of animals within a specific area at any given time (Constantine et al. 2012, Carroll et al. 2013).

Models were fitted for each sampling period and across a data set of the two periods (separated by c. five months) combined. Estimated parameters included capture probability (p), apparent survival (φ), probability of entry (P_{ent}) and the super-population size ($\widehat{N}_D$). Models constrain P_{ent} values to sum to 1 over the entire sampling period. Models were fitted with different combinations of either time-varying (t), constant (.) or varying with sampling period (s; combined periods only) apparent survival, capture probability and probability of entry. To investigate and address violation of the closure assumption, fully closed and partially closed model configurations were also fitted, where φ was fixed at 1 (closed to losses) and/or P_{ent} fixed at 0 (closed to gains). For combined period models, I fitted configurations where φ and/or P_{ent} were fixed across all sampling events and/or fixed within sampling periods, but unconstrained between periods.

The program RELEASE was used in MARK to determine GOF (Lebreton et al. 1992). Over-dispersion in the data was accounted for by estimating the over-dispersion measure ĉ using the chi-square statistic from RELEASE divided by its degrees of freedom. QAIC values were used for model selection, with the lowest QAIC value an indication of the most parsimonious model (Anderson et al. 1994). As for RD models, weighted model averaging was applied to produce model-averaged estimates of $\widehat{N}_D$.

Table 2.2. Validation of assumptions for capture-recapture models fitted to the data.

Direction of bias in abundance estimate if violated	Validation
Assumptions applicable to standard open models	
1. Marks are unique, permanent and reliably identified	
Upwards (Pollock et al. 1990, Williams et al. 2002)	1.1. Only include distinctive individuals with permanent/long-lasting marks, and only use images of sufficient quality to identify the least distinctive individual included in the analyses (Urian et al. 1999, 2015, Friday et al. 2000, Rosel et al. 2011). 1.2. Sampling occurred over a relatively short total period of time (1-2 years per site) and at intervals of 4-6 months, over which time marks are not likely to have changed much (e.g. Wilson et al. 1999). 1.3. Observer consistency, with a single experienced person overseeing all individual identification and image quality control.
2. No behavioural ('trap') response to capture	
Trap shy = upwards; trap happy = downwards (Pollock et al. 1990)	2.1. Photo-identification as a means of 'capture' offers no reward and minimal stress to 'captured' individuals as no physical capture, handling or marking occurs.
3. Homogenous probability of capture	
Downwards (Pollock et al. 1990, Williams et al. 2002)	Validation 1.1 applies. 3.1. Transects designed to give even coverage of the study site, therefore minimising heterogeneity introduced by the sampling design. 3.2 As some degree of variability in the extent of overlap between individuals' home ranges and the study sites is expected, it is inevitable that some individual heterogeneity of capture probabilities was present. Furthermore, individual differences in grouping patterns and behavioural responses to vessels may result in some level of heterogeneity of capture probabilities. Of relevance to this issue are the indications of sex-differences in capture probabilities among snubfin dolphins reported from Cygnet Bay (Chapter 4), where females were sighted less frequently than males. Conversely, analyses of photo-ID data of humpback dolphins of known sex (Chapter 5) *Continued overleaf*

Direction of bias in abundance estimate if violated	Validation
	revealed a small female-bias in the number of biopsy sampled individuals and those with the greatest image quality in photo-ID data; this provides limited evidence to suggest that female humpback dolphins may experience higher capture probabilities than males. However, I note that the image quality requirements for a successful photo-identification capture are lower (despite the controls described in validation 1.1) than those of an image-based analysis of dorsal fin morphology (Chapter 5) and, therefore, the female-bias in sample sizes observed among humpback dolphins in Chapter 5 is not directly indicative of a sex-bias in capture probabilities of humpback dolphins in photo-identification capture-recapture studies. I did not attempt to model for effects of heterogeneity in capture probabilities; incorporating covariates into capture-recapture models to address potential heterogeneity adds complexity, and may not be feasible where sample sizes are small (e.g. Palmer et al. 2014), as they were in this study. Furthermore, incomplete information on the sex of individuals included in this study limited the estimation of meaningful sex-specific capture-probabilities. Consequently, it is possible that the abundance estimates presented here (Table 2.4) are subject to some degree of downward bias. However, such downward bias is expected to be minimal, as abundance estimates within a sampling period were broadly consistent with the total number of individuals identified at a study site, which in almost all cases reached a plateau (Fig. 2.2). Such consistencies were particularly noticeable for snubfin dolphins at Cygnet Bay, illustrating that, over-time, the effects of potential heterogeneity in capture probabilities driven by sex-differences in social structure (see Chapter 4) are likely to be very small and of insufficient magnitude to affect the conclusions presented here. Future studies may seek to investigate the application of capture-recapture models within a Bayesian framework (e.g. Corkrey et al. 2008) as an alternative to the more widely-used maximum-likelihood (ML) methods implemented in Program MARK (White and Burnham 1999) and used here. Bayesian approaches to capture-recapture modelling, while more complex in their implementation, have been shown to be more suitable than ML methods in their inclusion of heterogeneous capture probabilities when sample sizes are small (Rankin et al. 2016).
4. Homogenous probability of survival	
Downwards	4.1. Influence of heterogeneous survival probability is likely to be minimal for long-lived species over a ≤ two-year study period.

Direction of bias in abundance estimate if violated	**Validation**
(Pollock et al. 1990, Williams et al. 2002)	4.2. Probability of survival may vary between age classes, although this effect is minimised by excluding dependent calves and non-distinctive individuals (which are often juveniles/sub-adults).
5. Captures are independent	
Underestimation of precision (Pollock et al. 1990, Williams et al. 2002)	5.1. Preferential associations between some individuals result in close associates having a greater probability of capture than other individuals (Connor 2000). A lack of independence will not bias estimates of $\widehat{N}_D$, but will underestimate precision. Despite some preferential associations, the fission-fusion grouping patterns exhibited by these species (Connor 2000, Parra et al. 2011) should minimise the effects of a lack of independence in captures. 5.2. In POPAN models, this was corrected for by a ĉ adjustment, resulting in an increase in SE.
6. Instantaneous sampling	
Upwards (Pollock et al. 1990, Williams et al. 2002)	6.1. Instantaneous sampling within a sampling occasion (transect) can never truly be satisfied with photo-identification of highly mobile animals from a single survey platform across a site far exceeding the visible range of observers. 6.2 Each transect was completed in the shortest time possible given the requirement for good sighting conditions; however, transects typically took 2-3 consecutive days to complete, over which time it is likely that there was some movement of individuals in/out of the study site.
7. Any temporary emigration within a specific sampling period is completely random	
Dependent upon the nature of the emigration (Otis et al. 1978, Pollock et al. 1990, Burnham 1993, Kendall et al. 1997, Kendall 1999)	7.1. For highly mobile species such as cetaceans, study sites are likely to be smaller than the home range of a local population; some movement in/out of the study site ('edge effect') by some individuals is unavoidable when sampling occurs across multiple days or weeks. 7.2. There was no *a-priori* reason to suspect that the temporary emigration described in 7.1 would be non-random (Markovian) within relatively short sampling periods of 2-5 weeks. Reported seasonal movements of coastal dolphins in relation to breeding season (e.g. Smith et al. 2013), food availability or predation risk (e.g. Heithaus and Dill 2002) occur at greater temporal scales. However, for macro-tidal environments, tidal phases (c. two weeks between spring and neap tides) may represent drivers of non-random animal movement within sampling periods and should be investigated in future studies. 7.3. Non-random temporary emigration at a seasonal time-scale may manifest as permanent gains or losses at the *Continued overleaf*

Direction of bias in abundance estimate if violated	Validation
	temporal scale of the sampling periods (2-5 weeks) implemented here; unconstrained open models allowed for such net gains and losses within a sampling period. However, these models carried little weight in comparison to closed or partially closed models, suggesting a lack of net gains or losses and either no or random temporary emigration.
Additional assumptions applicable to closed Robust Design models*	
8. Population is closed to permanent gains and losses within each sampling ('primary') period	
Dependent upon the nature of gains and losses (Pollock et al. 1990, Kendall 1999)	8.1. Sampling periods are short relative to the lifespan of the animals, therefore gains and losses through births and deaths are not anticipated. 8.2. Sampling periods were completed in the shortest time possible given the requirement for good sighting conditions, although it is highly likely that some temporary emigration occurred within sampling periods (see 7.1 above). As such, Robust design abundance estimates for individual sampling periods also represent the super-population.

*Robust Design models are subject to assumptions of closed models within sampling periods, but allow for either random or non-random (Markovian) temporary emigration between sampling periods. This is different to standard open models, which do not allow for Markovian temporary emigration.

2.3.10 Estimating total population size

Parameter estimates refer to the distinctive (marked) proportion of the population only ($\widehat{N}_D$). To estimate the total population size ($\widehat{N}_{total}$), the size of the distinctive population ($\widehat{N}_D$) was divided by the proportion of distinctive animals ($\hat{\theta}$). The standard error of the total population size was derived using a modification of the delta method (Williams et al. 2002, Nicholson et al. 2012):

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

Log-normal 95% confidence intervals for total population size were calculated using the expression:

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

with a lower limit of $\widehat{N}_{total} / C$ and upper limit of $\widehat{N}_{total} \times C$ (Burnham et al. 1987).

2.3.11 Power to detect trends in abundance

I assessed the ability of a series of abundance estimates to detect population trends using Gerrodette's (1987) inequality model:

$$r^2 n^3 \geq 12 CV^2 \left(Z_{\alpha/2} + Z_{\beta} \right)^2$$

where *r* is the rate of change in abundance, *n* is the number of abundance estimates, CV is the coefficient of variation of the abundance estimate ($\widehat{N}_{total}$), Z_{α} and Z_{β} are the normal deviates corresponding to the probability of making a Type I and Type II error, respectively. The one-tailed probability of making a Type I error (α) was set at 0.05, and the probability of making a Type II error was set at either 0.05 (i.e. high power = $1 - \beta$ = 0.95) and 0.20 (acceptable power = 0.80) (Taylor et al. 2007b). For each species and site, the mean CV of corresponding abundance estimates was calculated and these values were

used to inform the ability to detect trends. Values of CV from estimates using two sampling periods combined were excluded, so that all CV values were representative of a single sampling period of effort. Using these estimates of CV, I predicted the number of abundance estimates required to detect 5%, 10% and 20% rates of population change at annual sampling intervals.

2.3.12 Supporting information

Summary statistics were produced on the sea conditions (Beaufort sea state and wave height) during each sampling period (Appendix A2.1). Mean group sizes were compared between species using permutation tests (Appendix A2.2), and maps of sightings at each study site were plotted (Appendix A2.3).

2.4 Results

A total of ten sampling periods were completed across the five study sites (Table 2.3). Individual transects varied in length from 45-69 km according to the state of the tide and specific study site, with a mean length of 60.1 ± 0.8 SE km across all study sites. The majority of survey effort occurred in sea states ≤ two and wave height ≤ 0.2 m (Appendix A2.1).

Snubfin and humpback dolphins were encountered at all study sites; bottlenose dolphins were only encountered at Roebuck, Beagle and Cygnet Bays (Table 2.3). Encounter rates varied considerably between species and across study sites. Additionally, the results indicate fluctuations in site-specific encounter rates between sampling periods. Differences in site-specific encounter rates were most prominent for snubfin and humpback dolphins at Cygnet Bay, where very low encounter rates during the first sampling period were followed by higher values in subsequent periods. I note that the first sampling period at Cygnet Bay experienced poorer sea conditions, with greater wave heights compared to other sampling periods (Appendix A2.1).

Table 2.3. Survey effort, and number of groups observed and encounter rate of snubfin, humpback and bottlenose dolphins per site, species and sampling period.

Study site (km^2)	Sampling period (number of transect repeats)	Total effort (km)	Snubfin		Humpback		Bottlenose	
			Total groups	D/km (SE)	Total groups	D/km (SE)	Total groups	D/km (SE)
Roebuck Bay (100)	1) 04 Oct - 05 Nov 2013 (7)	419	74	0.71 (0.12)	1	0.04 (0.04)	6	0.05 (0.02)
	2) 04 Apr - 25 Apr 2014 (7)	389	74	0.57 (0.09)	0	0	5	0.04 (0.01)
	Sum / mean (SE)	**808**	**148**	**0.64 (0.07)**	**1**	**0.02 (0.02)**	**11**	**0.04 (0.01)**
Beagle Bay (130)	1) 24 Oct - 20 Nov 2012 (5)	322	0	0	4	0.05 (0.03)	39	0.41 (0.05)
	2) 01 May - 30 May 2013 (5)	337	2	0.01 (0.01)	4	0.06 (0.03)	39	0.51 (0.10)
	Sum / mean (SE)	**659**	**2**	**< 0.01**	**8**	**0.05 (0.02)**	**78**	**0.46 (0.06)**
Cygnet Bay (130)	1) 16 Apr - 07 May 2012 (5)	316	6	0.05 (0.04)	5	0.05 (0.02)	14	0.17 (0.06)
	2) 10 Sep - 27 Sep 2012 (5)	307	11	0.22 (0.09)	13	0.16 (0.05)	21	0.25 (0.11)
	3) 07 Apr - 19 Apr 2013 (5)	306	14	0.32 (0.14)	12	0.12 (0.02)	11	0.14 (0.02)
	4) 02 Sep - 20 Sep 2013 (5)	302	24	0.37 (0.05)	11	0.10 (0.03)	20	0.21 (0.02)
	Sum / mean (SE)	**1231**	**55**	**0.23 (0.02)**	**41**	**0.12 (0.01)**	**66**	**0.19 (0.02)**
Cone Bay (100)	1) 05 Sep - 21 Sep 2014 (6)	297	14	0.20 (0.08)	12	0.07 (0.03)	0	0
Inner Cambridge Gulf (180)	1) 31 May - 13 Jun 2012 (5)	313	1	< 0.01	2	< 0.01	0	0

Study sites are listed from west to east. Where the number of animals in a group was estimated as a range, the minimum estimate was used. Encounter rates (D/km) are summarised across all transect repeats within a sampling period and represent the mean (± SE) dolphins per km survey effort, including dependent calves.

2.4.1 Rate of new identifications, resights between sampling periods and movements of individuals between sites

The cumulative number of individuals identified over the course of the surveys plateaued for nearly all of the species present at each of the study sites, suggesting that the majority of animals using those sites were observed during these surveys (Fig. 2.2). Bottlenose dolphins at Beagle Bay were an exception, however, with data showing a steady increase in the number of individuals identified over the two sampling periods. This suggests that not all individuals using the site had been identified during the study.

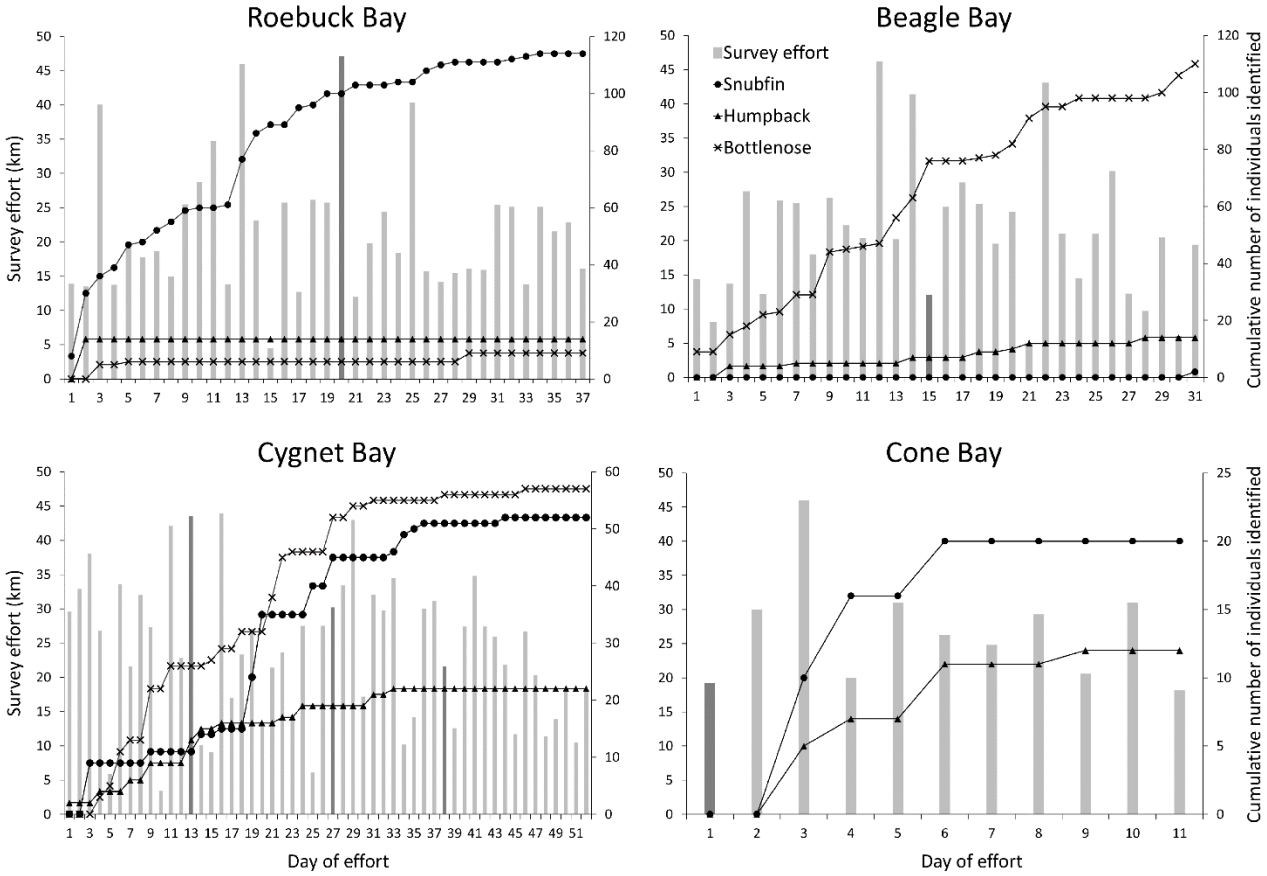


Figure 2.2. Daily survey effort and cumulative number of distinctive dolphin individuals identified at each site. Vertical bars illustrate daily survey effort (left y-axis); a darker bar indicates the first day of effort in each sampling period. Lines illustrate the cumulative number of snubfin (circles), humpback (triangles) and bottlenose (crosses) dolphin individuals photo-identified (right y-axis). No figure is provided for the Inner Cambridge Gulf, as only one distinctive humpback dolphin individual was identified on the penultimate day of effort.

It is important to note that the number of sampling periods differed between sites. Given that plateaus were often only reached within the second or third sampling periods, the apparent plateaus at Cone Bay (surveyed only once) likely represent only a subset of individuals using that site; further sampling periods are likely to yield new individuals.

The proportion of individuals resighted across multiple sampling periods (separated by c. five months) varied by species and site (Fig. 2.3). The greatest proportions of resights were of snubfin dolphins: 65% (n = 34) of individuals were sighted in ≥ three of the four sampling periods at Cygnet Bay, and 58% (n = 66) of individuals were sighted during both sampling periods at Roebuck Bay.

Individuals resighted between different study sites included two bottlenose dolphins, which were sighted at both Cygnet Bay and Beagle Bay (approximately 120 km distant). The time lags between sightings were 39 and 159 days, respectively. No other individuals of any species were sighted at more than one study site.

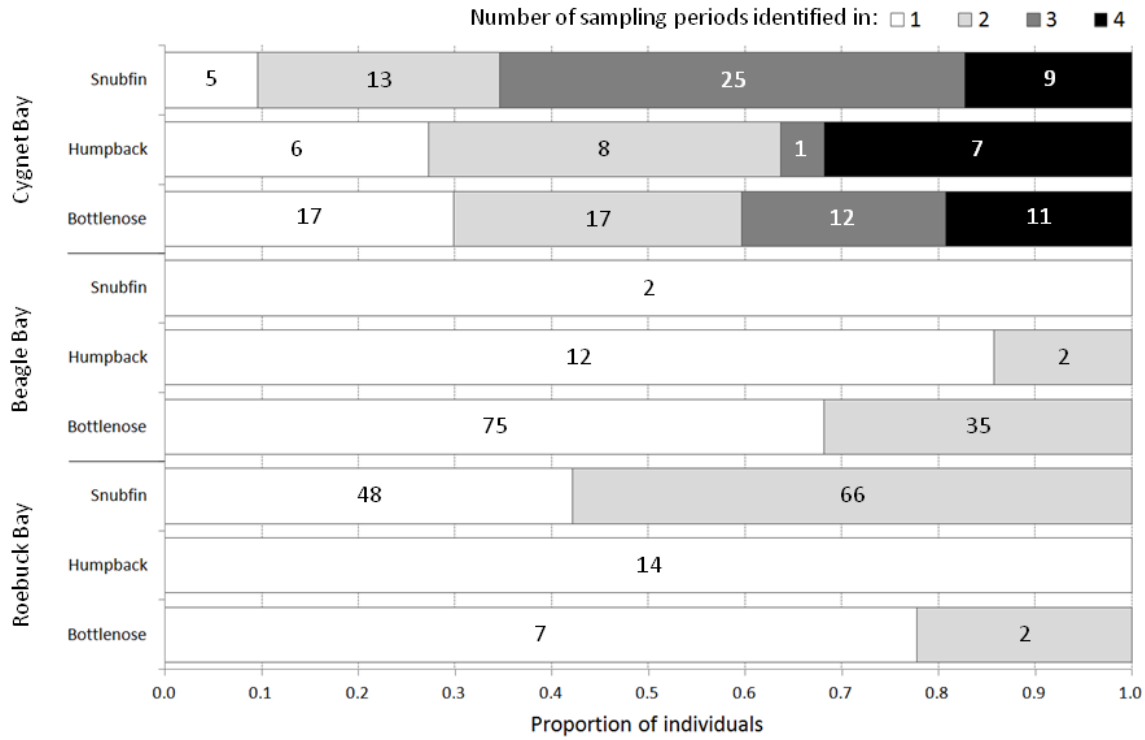


Figure 2.3. The proportion of individuals sighted in 1, 2, 3 or 4 sampling periods (where applicable) at each study site. The total number of sampling periods per site is 4 (Cygnet Bay) and 2 (Beagle Bay, Roebuck Bay). Numbers on bars represent the number of individuals per category.

2.4.2 Abundance estimates

Sufficient data were obtained to produce estimates of $\hat{\theta}$ and capture-recapture estimates of absolute abundance for snubfin dolphins at Roebuck Bay, bottlenose dolphins at Beagle Bay, and all three species at Cygnet Bay (Table 2.4 and Appendix S4). Estimates of $\hat{\theta}$ were high, at ≥ 0.89 (SE 0.02). Model selection tables and model parameter outputs are provided in Appendix A2.4. For all other sites and species, the number of distinctive individuals identified within each sampling period provides a minimum estimate of abundance during that time period. Additionally, encounter rates provide an approximate measure of relative abundance for all sites and species (Table 2.3).

Abundance estimates for snubfin dolphins at both Cygnet and Roebuck Bays were stable across sampling periods at c. 50 and c. 130, respectively (Table 2.4). Abundance estimates of humpback dolphins at Cygnet Bay were also comparable across sampling periods, ranging from 15-20. For all other sites and sampling periods, ≤ 12 distinctive humpback dolphin individuals were observed in any one sampling period, and data were insufficient to run capture-recapture models (Table 2.4). I note that the first sampling period at Cygnet Bay was anomalous, in that insufficient captures precluded estimates of absolute abundance for either snubfin or humpback dolphins. As noted above, this was coincident with poor sea conditions, which are believed to have limited the detection of these species.

Abundance estimates of bottlenose dolphins at Beagle Bay were comparable across sampling periods, though the precision corresponding to those estimates was low, particularly for sampling period one. Combining the abundance across both sampling periods generated the most precise estimate of 157 (CI 133-186) bottlenose dolphins, which fell within the confidence intervals of the single period estimates and is, therefore, considered the most reliable estimate of population size for bottlenose dolphins at Beagle Bay. Abundance estimates of bottlenose dolphins at Cygnet Bay were fairly stable across sampling periods at c. 50-60 (Table 2.4).

Table 2.4. Capture-recapture abundance estimates for snubfin, humpback and bottlenose dolphins per site, species and sampling period.

			Snubfin			**Humpback**		**Bottlenose**			
Study site (km²)	*S*	*n*	$\widehat{N}_D$ (SE, 95% CI)	$\hat{\theta}$	$\widehat{N}_{total}$ (SE, 95% CI)	*n*	$\widehat{N}_{total}$ (SE, 95% CI)	*n*	$\widehat{N}_D$ (SE, 95% CI)	$\hat{\theta}$	$\widehat{N}_{total}$ (SE, 95% CI)
Roebuck Bay	1	99	116 (9.8, 97-135)	0.89¶	130 (11.9, 109-155)	12	-	6	-	-	-
(100)	2	79	116 (17.7, 82-151)	0.89¶	130 (20.4, 96-177)	0	-	5	-	-	-
	1-2	113	119 (4.8, 113-129)	0.89¶	133 (7.0, 127-148)	12	-	9	-	-	-
Beagle Bay (130)	1	0	-	-	-	7	-	63	171 (43.0, 87-256)	0.93¶	184 (46.6, 113-300)
	2	2	-	-	-	9	-	82	145 (22.2, 101-188)	0.93¶	156 (24.4, 115-211)
	1-2	2	-	-	-	14	-	110	146 (11.8, 123-169)	0.93¶	157 (13.4, 133-186)
Cygnet Bay (130)	1	11	-	-	-	9	-	26	33 (4.9, 26-43)	0.95†	35 (5.4, 27-48)
	2	39	45 (4.2, 39-54)	0.95†	48 (4.8, 41-58)	18	20 (2.2, 18-24)	40	49 (5.0, 40-59)	0.95†	52 (5.6, 42-64)
	3	48	51 (2.2, 48-55)	0.95†	54 (3.0, 51-60)	14	17 (2.1, 14-21)	31	57 (10.4, 37-78)	0.95†	60 (11.3, 42-87)
	4	44	47 (2.5, 44-52)	0.95†	50 (3.2, 46-57)	12	15 (1.3, 12-20)	34	48 (6.8, 35-61)	0.95†	51 (7.4, 38-67)
Cone Bay (100)	1	20	-	-	-	12	-	0	-	-	-
Inner Cambridge Gulf (180)	1	0	-	-	-	1	-	0	-	-	-

Study sites are listed from west to east. *S* = sampling period; *n* = number of distinctive individuals identified; $\widehat{N}_D$ = estimated distinctive population size; $\hat{\theta}$ = estimated proportion of distinctive individuals in the population; $\widehat{N}_{total}$ = estimated total population size. See Appendix A2.4 for corresponding models. As the proportion of distinctive humpback dolphins at Cygnet Bay was 1.0, only estimates of $\widehat{N}_{total}$ are presented. ¶ SE = 0.02; † SE = 0.01. Blank cells are where insufficient data were available to estimate abundance using capture-recapture models; in these cases, the number of distinctive individuals identified (*n*) provides the minimum abundance estimate within the corresponding sampling period.

Implementation of the Robust Design permitted the estimation of apparent survival (the probability of surviving and staying in the study area) and temporary emigration rates at Cygnet Bay (Tables A2.4.11-1). For each species, the best-fitting model included constant apparent survival and no temporary emigration. Annual apparent survival (± SE) was 0.95 (± 0.05) for snubfin, 0.62 (± 0.12) for humpback and 0.86 (± 0.09) for bottlenose dolphins.

For snubfin dolphins at Roebuck Bay, fully closed models with $\varphi(.=1)$ and $P_{ent}(.=0)$ carried considerable weight in sampling period one, and also for the two sampling periods combined (Tables A2.4.1-3). Sampling period two appeared more open to losses, although estimated apparent survival was still close to one. For bottlenose dolphins at Beagle Bay, fully closed models and models closed to losses were dominant (Tables A2.4.6-8).

Capture probabilities, as estimated by capture-recapture models, varied considerably between sites, species and sampling occasions (Appendix A4), and are reflected in the precision of abundance estimates (Table 2.4). Overall, values were lowest for bottlenose dolphins at Beagle Bay, particularly during sampling period one at 0.09 (± 0.03 SE) during each transect (Table A2.4.9). This sampling period corresponded with the poorest sea conditions experienced during the entire study (Appendix A2.1). Despite considerable variability between individuals transects, estimated capture probabilities were highest for snubfin dolphins at Cygnet Bay, where they ranged from 0.04-0.79 (mean 0.38 ± 0.07 SE) (Table A2.4.14).

2.4.3 Power to detect trends in abundance

As the rate of change in abundance increases, the time required to detect a change decreases (Fig. 2.4). Accepting a lower statistical power of 80% (compared to 95% power) typically reduced the required time by approximately one year (Table 2.5). Based on estimates of abundance for snubfin dolphins at Roebuck Bay (which were intermediate in terms of precision relative to other sites/species), it would take a further eight years to detect a modest annual change in abundance of 5% with acceptable (80%) statistical power (Table 2.5). After nine years of such a decline, the original abundance would have been reduced by a total of 34%. A higher rate of decline of 20% would be detected within just four years, although with a total 45% reduction in the original abundance.

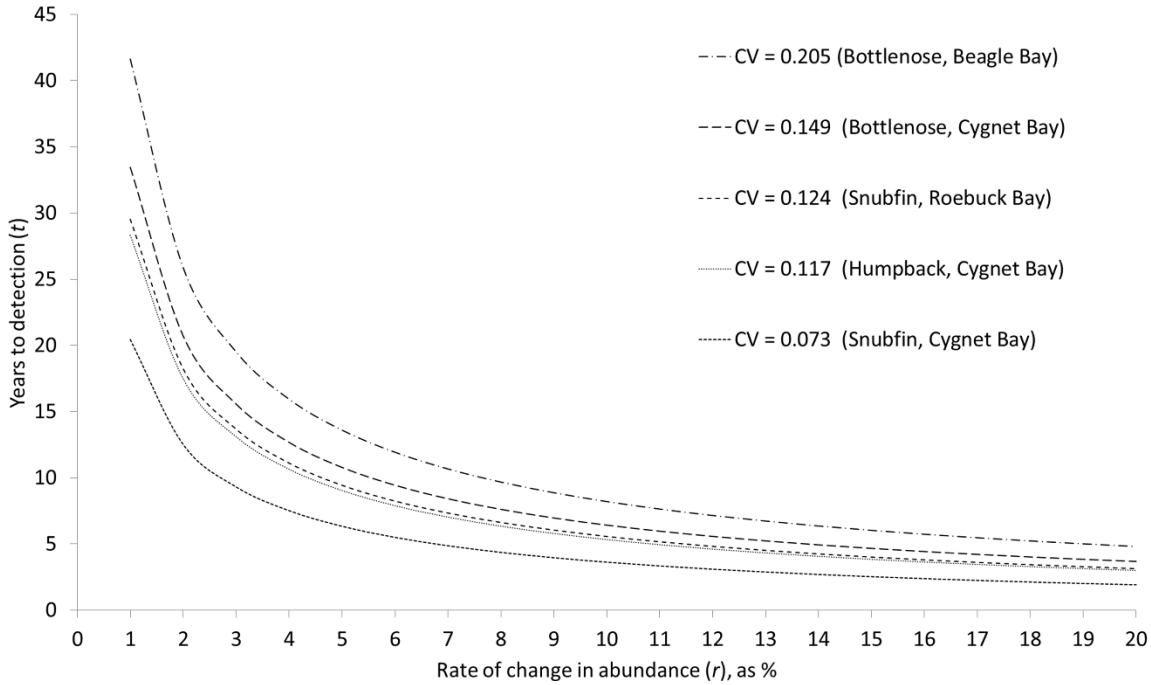


Figure 2.4. Relationship between different rates of change in abundance (*r*), and the time required to detect such a change (*t*) with a statistical power of 95%, given different levels of precision (CV) in annual abundance estimates. CVs are the mean CV of abundance estimates for single sampling periods.

2.5 Discussion

2.5.1 Abundance estimates of inshore dolphins in the Kimberley region

I applied a standardised survey design of short-duration, effort-intensive photo-identification surveys to obtain the first quantitative baseline data on the abundance and site fidelity of three inshore dolphin species in north-western Australia. Through study design and selected analytical procedures, the assumptions of the capture-recapture models used to estimate abundance are considered to be largely met, and these estimates subject to minimal bias (Table 2.2).

Table 2.5. Effects of different levels of precision (coefficient of variation, CV) of abundance estimates and statistical power on the number of years to detect different rates of change in abundance, and the corresponding total changes in abundance at the point of detecting changes. Calculations are based on Gerrodette's (1987) inequality model.

			Number of years to detection at r ($t = n - 1$)			Total % change in abundance at detection where declining at r $(1 - r)^t - 1$			Total % change in abundance at detection where increasing at r $(1 + r)^t - 1$		
Species	Site	CV	r 0.05	r 0.10	r 0.20	r 0.05	r 0.10	r 0.20	r 0.05	r 0.10	r 0.20
95% power (β = 0.05)											
Snubfin	Cygnet Bay	0.073	6	4	2	-0.28	-0.32	-0.35	0.36	0.41	0.42
Snubfin	Roebuck Bay	0.124	9	6	3	-0.38	-0.44	-0.50	0.59	0.70	0.77
Humpback	Cygnet Bay	0.117	9	5	3	-0.37	-0.43	-0.49	0.55	0.66	0.72
Bottlenose	Cygnet Bay	0.149	11	6	4	-0.42	-0.49	-0.56	0.69	0.84	0.95
Bottlenose	Beagle Bay	0.205	14	8	5	-0.50	-0.58	-0.66	0.94	1.18	1.39
80% power (β = 0.20)											
Snubfin	Cygnet Bay	0.073	5	3	2	-0.24	-0.28	-0.29	0.31	0.34	0.33
Snubfin	Roebuck Bay	0.124	8	5	3	-0.34	-0.40	-0.45	0.49	0.58	0.62
Humpback	Cygnet Bay	0.117	8	5	3	-0.33	-0.38	-0.43	0.46	0.54	0.58
Bottlenose	Cygnet Bay	0.149	9	6	3	-0.38	-0.44	-0.50	0.58	0.69	0.77
Bottlenose	Beagle Bay	0.205	12	7	4	-0.46	-0.53	-0.60	0.78	0.96	1.11

Values of CV are the mean CV of abundance estimates for single sampling periods. r = rate of change in abundance. t = number of years to detect change in abundance. n = number of annual abundance estimates. The probability of making a Type I error (α) was set at 0.05, and results are presented for both 95% (high) power and 80% (acceptable) where β = the probability of making a Type II error. See methods for more details.

The estimates of snubfin dolphin abundance presented here fall within the range of those reported elsewhere, despite other study sites being appreciably larger (Table 2.1). Consistent abundance estimates across repeated sampling periods, along with a plateau in the rate of new individual identifications, suggests that the populations of c. 50 snubfin dolphins in Cygnet Bay and c. 130 in Roebuck Bay represent largely closed, local populations. Given the c. 100 km^2 size of the area surveyed within Roebuck Bay, this site appears to contain the highest density of snubfin dolphins reported from a capture-recapture study to date (see Table 2.1). While acknowledging that differences in approximate densities of animals between studies may also reflect differences in study design, it seems appropriate to conclude that Roebuck Bay represents particularly important habitat to snubfin dolphins.

Although observed at all study sites, infrequent observations of few humpback dolphin individuals precluded capture-recapture models at all sites except Cygnet Bay, which had an approximate density comparable to those observed in studies elsewhere (Table 2.1). It is likely that the relatively small study sites surveyed only overlapped with the home ranges of a small number of individuals, and the dolphins observed in these sites represent components of larger populations ranging across a wider area (Williams et al. 2002, Nicholson et al. 2012).

The abundance estimates of bottlenose dolphins at Cygnet Bay were similar to those reported for larger sites within the Northern Territory (Palmer et al. 2014, Brooks and Pollock 2015). However, the abundance of 157 (CI 137-186) bottlenose dolphins at Beagle Bay is comparably large; this represents a density approximately comparable to those reported in high-productivity, sub-tropical embayments (e.g. Lukoschek and Chilvers 2008, Nicholson et al. 2012), and suggests particularly favourable habitat to this species.

There were considerable differences in the relative proportions of species encountered among study sites. For example, across the c. 100 km distance between the Roebuck Bay and Beagle Bay study sites, the relative proportions of snubfin and bottlenose dolphins were reversed. All study sites were dominated by water depths (< 20 m) and distances to shore (< 5 km) characteristic of those favoured by snubfin and humpback dolphins on the east coast of Australia (Parra 2006, Parra et al. 2006b, Cagnazzi 2011). However, sites were, to varying degrees, heterogeneous for several other environmental characteristics, including: bathymetric complexity, turbidity, the aspect and complexity of the coastline, and predominant shoreline

habitats (Appendix A2.3). The highly turbid and estuarine waters of the Inner Cambridge Gulf (where very few individuals of any species were observed) showed the greatest disparity to other sites. It is beyond the scope of the current study to investigate the ecological driving factors behind the observed differences in species compositions. However, it is likely that differences in habitat and prey distribution, and species-specific preferences for both, are important influences on the distribution of coastal dolphins noted in this study (Parra 2006, Parra and Jedensjö 2014). Other potential influences include predation risk (Heithaus and Dill 2002), social dynamics (Parra et al. 2011), and inter-specific competition (Parra 2005).

2.5.2 Evidence of site fidelity and lack of movement between sites

The inclusion of four sampling periods over two years at Cygnet Bay enabled investigation of site fidelity for the three dolphin species in this area. Apparent survival for snubfin dolphins was high (0.95), illustrating an almost complete lack of permanent emigration during the study and suggests residency of the local population. A well-defined plateau in the identification rate of new individuals (Figure 2.2) and stable abundance estimates across sampling periods provide support for this conclusion. There was also preliminary evidence of site fidelity within Roebuck Bay, where a majority of snubfin dolphin individuals were resighted between the two sampling periods, and very similar abundance estimates were obtained from either single or combined sampling periods. Humpback and bottlenose dolphins showed evidence of site fidelity at Cygnet Bay. However, apparent survival estimates of 0.62 for humpback and 0.85 for bottlenose dolphins are indicative of permanent emigration of individuals during the course of the study, suggesting both resident and more transient components within the sampled populations (cf. Silva et al. 2009, Palmer et al. 2014). The documented movement of two bottlenose dolphin individuals between Cygnet and Beagle Bays supports this conclusion.

Studies on snubfin and humpback dolphins on the east coast of Australia have reported either strong site fidelity within localised populations (Cagnazzi et al. 2011, 2013b), or a majority of individuals regularly occupying the same discrete area from year to year (Parra et al. 2006a). Previous studies of bottlenose dolphins have revealed variable levels of site fidelity among populations in inshore waters, although evidence of long-term residency among a proportion of the population is common (e.g. Fury and Harrison 2008, Chabanne et al. 2012). Multiple re-sights of the same individuals of all three species have been recorded across four years of sampling in the Darwin region, Northern Territory, although considerable movement of

individuals in and out of specific study sites, particularly for snubfins, also appeared to be a key feature within this region (Brooks and Pollock 2015).

A lack of observed movement of snubfin or humpback dolphin individuals between sites separated by > 100 km of coastline suggests that movements over such distances are uncommon for these species within the surveyed study area. However, the short duration of the current study is likely to have limited the ability to detect such movements. Nonetheless, genetic studies offer supporting evidence of limited connectivity between local populations for these species. Low levels of gene flow have been observed between local populations of snubfin and humpback dolphins separated by > 200 km, including snubfin dolphins at Roebuck and Cygnet Bays, to the extent that those local populations should be considered separate management units (Cagnazzi 2011, Brown et al. 2014 Chapter 3). Fine-scale population genetic structure appears to be common in coastal populations of bottlenose dolphins (e.g. Ansmann et al. 2012b, Kopps et al. 2014) and, despite evidence of individual movement between the two sites, significant genetic differentiation has been reported between bottlenose dolphins at Cygnet Bay and Beagle Bay (Allen 2015).

2.5.3 Implications for conservation and management

The considerable differences in the abundance of these species between surveyed sites highlight the need for site-specific baseline data collection and a better understanding of the distribution and habitat preferences of each species across their range. In the absence of appropriate baseline data, the assumption of similar relative abundance among these broadly sympatric species may grossly underestimate, or overestimate, the importance of a site to a single species. Multi-taxa aerial surveys to inform EIAs of port developments in north-western Australia to date have not been suitable for delineating between these similarly-sized, sympatric dolphin species and are therefore of limited value in assessing the characteristics of local populations (Bejder et al. 2012, Hanf et al. 2016). In order to quantitatively assess the potential impacts of coastal developments and other threatening activities on inshore dolphins, dedicated, well-designed survey methods which target shallow, near-shore waters using a survey platform and sea conditions favorable for detecting these often-cryptic species are required (e.g. Brooks et al. 2014, Brooks and Pollock 2015; This Chapter).

All local population sizes estimated in this study were < 160 individuals (excluding calves). While the level of connectivity between local populations of inshore dolphins in northern Australia is not well understood, evidence of site fidelity, limited movement, and genetic differentiation suggest that they are somewhat isolated (Parra et al. 2006a, Cagnazzi 2011, Cagnazzi et al. 2011, 2013b, Brown et al. 2014, Allen 2015; This Chapter and Chapter 3). Small, largely isolated populations are at greater risk of local declines than large, stable populations due to limited resilience to mortality resulting from stochastic environmental perturbations and anthropogenic activities (Shaffer 1981). For isolated populations of approximately 100 dolphins, the annual loss of a single individual above natural mortality is unsustainable (e.g. Slooten et al., 2006; Cagnazzi et al., 2013). To ensure the longevity of these populations, sources of anthropogenic mortality need to be eliminated and anthropogenic stressors that impact survival require identification and mitigation.

Northern Australia's inshore dolphins are exposed to a variety of anthropogenic activities which can negatively impact the viability of local populations, although these are generally poorly understood (reviewed in Beasley et al. 2012, Woinarski et al. 2014, Parra and Cagnazzi 2016). There are multiple avenues for both acute and chronic effects from the habitat loss and degradation caused by coastal development, which has been identified as a major threat (Jefferson et al. 2009, Allen et al. 2012, Beasley et al. 2012). The number of large-scale port developments in this region has increased considerably in recent decades, with many more planned or in development (Grech et al. 2013, Hanf et al. 2016; and see Appendix A1); the dredging, construction activities and vessel traffic associated with these developments may displace inshore dolphins from important habitats (Tougaard et al. 2009, Brandt et al. 2011, Pirotta et al. 2013, Weaver 2015). Given their small population sizes and intrinsic vulnerabilities to localised decline, even single developments have the potential to result in population-level impacts if overlap with critical habitat is high (e.g. Cagnazzi et al. 2013b). This further highlights the need for the collection of appropriate pre-development data to assess and mitigate risks, along with empirical studies to better quantify impact levels.

An additional yet largely unquantified threat to inshore dolphins in northern Australia is direct interactions with fisheries. Inshore gillnetting operations are of particular concern, and result in injury and mortality among many *Orcaella*, *Sousa* and *Tursiops* populations in the Indian Ocean region (Reeves et al. 2013b). Anti-shark nets in inshore waters off the Queensland coast have resulted in the mortality of all three species since the 1960s (Paterson 1990). The

magnitude of dolphin bycatch in the now-banned foreign gillnet fisheries across northern Australia was likely to be considerable (Harwood and Hembree 1987); however, the current level of interactions with Australia's domestic gillnet fisheries (e.g. Northern Territory Government 2014, Department of Agriculture and Fisheries 2015a, 2015b, Department of Fisheries 2015) remains unknown. Nets are often set within habitats likely to be frequented by snubfin and humpback dolphins (e.g. creek mouths, estuaries, mangroves); therefore, some mortality is considered inevitable (Parra et al. 2006a). Given the limited resilience of such small populations to anthropogenic mortality (Slooten et al. 2006, Cagnazzi et al. 2013b), quantifying the current level of direct interactions between inshore dolphins and northern Australian fisheries should be a research and management priority.

Extreme weather events (i.e. cyclones and floods) that occur in tropical northern Australia impact shallow, inshore marine habitats (e.g. seagrass loss, Preen et al. 1995). These have been linked to mortality and large-scale movements of another marine mammal, the dugong (*Dugong dugon*) (Preen and Marsh 1995, Gales et al. 2004), and research on the east coast of Australia also suggests an association between flood events and elevated mortality of inshore dolphins (Cagnazzi 2013, Meager and Limpus 2014). It is reasonable to assume that inshore dolphin populations have adapted to persist through most such natural events, for example, through the use of refugia (see Keppel et al. 2012). However, their resilience to natural perturbations may be reduced through the cumulative effects of multiple anthropogenic stressors associated with habitat degradation, such as increased contaminant burdens or a reduction in prey availability (Cagnazzi et al. 2013a, Parra and Cagnazzi 2016).

The value of long-term data to support conservation and adaptive management of wildlife populations is well-recognised (e.g. Clutton-Brock and Sheldon 2010, Cheney et al. 2014), and recent expert-led prioritisation exercises have emphasised the need for long-term studies of population dynamics of inshore dolphins in northern Australia (Department of the Environment 2013b, 2015b). They encourage multi-year, multi-disciplinary studies at appropriate reference sites (representing a range of levels of human impact), including data on abundance and habitat use, to facilitate: detecting trends in the abundance of local populations; the investigation of natural variability in characteristics of populations (e.g. abundance and habitat use) and their relationship to environmental stochastic events (e.g. cyclones); collecting life history data to inform assessments of population viability; and, developing a greater understanding of threatening processes and mitigation options (Department of the Environment 2015b). Such

long-term studies will require considerable planning and investment, and existing data are of great value to inform the selection of suitable sites. To this end, the results presented here provide an indication on the suitability of several candidate sites. Specifically, the abundance and accessibility of snubfin dolphins within Roebuck Bay present a scientifically suitable and relatively cost-effective candidate for long-term study (see recommendations). Roebuck Bay is subject to moderate levels of human activity, including: a growing adjacent township, port facilities, and considerable recreational vessel traffic in some areas (Department of Parks and Wildlife 2015), presenting opportunities for the study of impacts from threatening activities. Furthermore, the imminent establishment of a 788 km^2 multi-use Marine Protected Area (MPA) within Roebuck Bay, which aims to conserve a range of natural, cultural and recreational values, can provide the necessary management framework to facilitate such an ongoing study (Department of Parks and Wildlife 2015).

While carefully designed, multi-year studies at appropriate sites will facilitate the detection of trends in the abundance of local populations, it is important to consider the challenges involved in detecting trends within populations of the sizes reported here. Even with the most precise abundance estimates presented here, it would take a minimum of seven years to detect modest rates of change with high statistical power, by which time populations could be depleted to very low levels (Table 5). Furthermore, trends in the abundance of cetaceans can be complicated by natural variability, such as movements in or out of a study site (Forney 2000, Parra et al. 2006a, Cheney et al. 2014). This reinforces the recommendation that implementing conservation measures should not be contingent upon statistically robust proof of a decline for small populations of cetaceans (Taylor and Gerrodette 1993, Thompson et al. 2000, Taylor et al. 2007b). Monitoring trends in abundance alone will not ensure the longevity of populations (e.g. Jaramillo-Legorreta et al. 2007, McDonald-Madden et al. 2010), and must fall within an adaptive management framework which seeks to mitigate threats and specifies precautionary trigger points for intervention (e.g. Wade 1998, Thompson et al. 2000).

2.5.4 Considerations for future vessel-based studies of inshore dolphins

Photo-identification capture-recapture surveys and their associated data processing are often time-intensive (Lukoschek and Chilvers 2008). However, due to their compatibility with small vessels, they remain one of the most cost-effective methods of obtaining relatively precise abundance estimates of small cetaceans, albeit at relatively small geographic scales (Dawson

et al. 2008). Surveying larger sites with a single vessel in the same period of time would require a reduction in the intensity of effort, which may result in abundance estimates with poor precision (e.g. Palmer et al. 2014). Resources permitting, the use of multiple vessels simultaneously can allow larger sites to be surveyed within a short time period (e.g. Read et al. 2003) and, consequently, may facilitate the use of more robust and informative capture-recapture models (e.g. Brooks and Pollock 2015). The cost increases of utilising multiple vessels and additional personnel may be somewhat offset by the reduced duration of the study. Such an approach would also allow periods of favourable sea conditions to be capitalised upon (Palmer et al. 2014), and is strongly encouraged for future photo-identification surveys of inshore dolphins.

A key issue facing small vessel capture-recapture surveys for inshore dolphins in remote areas is the need for close proximity to a logistics base (i.e. accommodation, fuel, power, suitable boat launch/mooring). For the majority of the northern Australian coastline, such facilities are lacking, which presents a considerable logistical challenge to data collection. In the current study, accessibility was a key consideration in the selection of study sites; two townships and three remote aquaculture facilities were utilised. An important opportunity lies in collaborating with indigenous groups and their capacity as custodians of large areas of remote coastline throughout northern Australia[9], many of which are managed as Indigenous Protected Areas[10]. Consequently, effective engagement of indigenous communities/ranger groups and their capacity (i.e. vessel, logistics base, personnel, knowledge of local area) can be critical to surveying these remote areas (Grech et al. 2014).

2.5.5 Recommendations

I make the following specific recommendations to support the conservation and management of inshore dolphins in northern Australia:

1. *Dedicated, site-specific baseline data collection on inshore dolphins is an essential prerequisite to EIA of proposed coastal development and other potentially threatening activities.* Species-specific abundance data are critical in order to assess the relative importance of sites to each species and the population-level significance of potential impacts. Data

[9] http://www.environment.gov.au/indigenous/workingoncountry/projects/pubs/woc-projects-map.pdf
[10] http://www.environment.gov.au/indigenous/ipa/pubs/ipa-map-oct2014.pdf

collection should include vessel-based surveys of comparable design to those presented here, with a minimum of two sampling periods to add confidence to results and provide preliminary evidence of site fidelity. It is critical that such surveys are conducted in appropriate sea conditions and extend into shallow, inshore habitats. For major development proposals, the development of longer-term, Before-After-Control-Impact monitoring studies are strongly recommended (e.g. Brooks and Pollock 2015).

2. *Design and implement a long-term study of the population dynamics of snubfin dolphins within Roebuck Bay to inform conservation and adaptive management*. The study should represent a collaboration between indigenous land managers, wildlife management agencies and academic researchers, and be compatible with the management plan of the proposed Roebuck Bay MPA. The details of such a program, including the specific objectives and survey design, will require careful consideration (see Brooks et al. 2014), and are not discussed here. However, an inter-disciplinary approach is recommended, in order to answer a variety of pertinent questions, including trends in abundance and habitat use, the factors influencing these, and a greater understanding of the impacts of threatening activities.

3. *Develop a greater understanding of the distribution and habitat preferences of tropical inshore dolphins.* A compilation and spatial analysis of existing sightings data should be undertaken to investigate environmental factors influencing the distribution of each of the three species, and subsequently identify areas of likely occurrence. The results of such an exercise could inform the selection of sites for future data collection, which is of particular value to species which appear to be patchily distributed across a large, remote area.

4. *Conduct studies to investigate the potential impacts of threatening activities to inshore dolphins, including a quantitative assessment of their interactions with gillnet fisheries across northern Australia*. An independent observer program (see Allen et al. 2014) is urgently required to estimate the level of mortality resulting from incidental capture and develop appropriate management measures, particularly in areas of known inshore dolphin occurrence.

Appendix A2.1 Summary of sea conditions during each sampling period

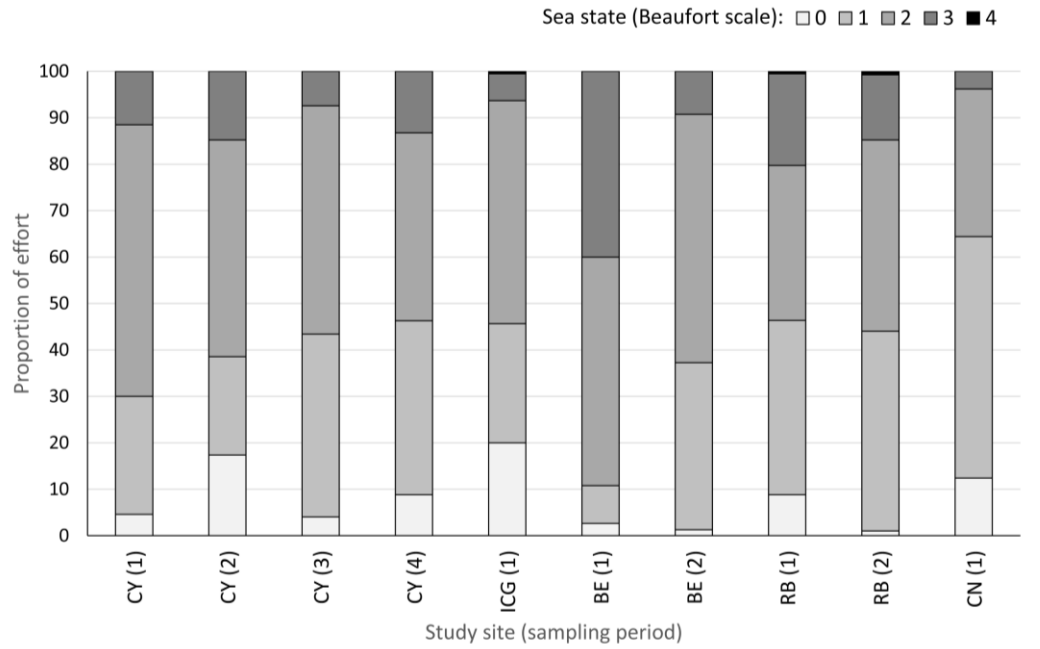


Figure A2.1.1. Proportion of effort according to sea states (Beaufort scale) per study site and sampling period. Sea state was assessed by eye by the same trained observer throughout all effort. (CY) Cygnet Bay, (ICG) Inner Cambridge Gulf, (BE) Beagle Bay, (RB) Roebuck Bay, (CN) Cone Bay.

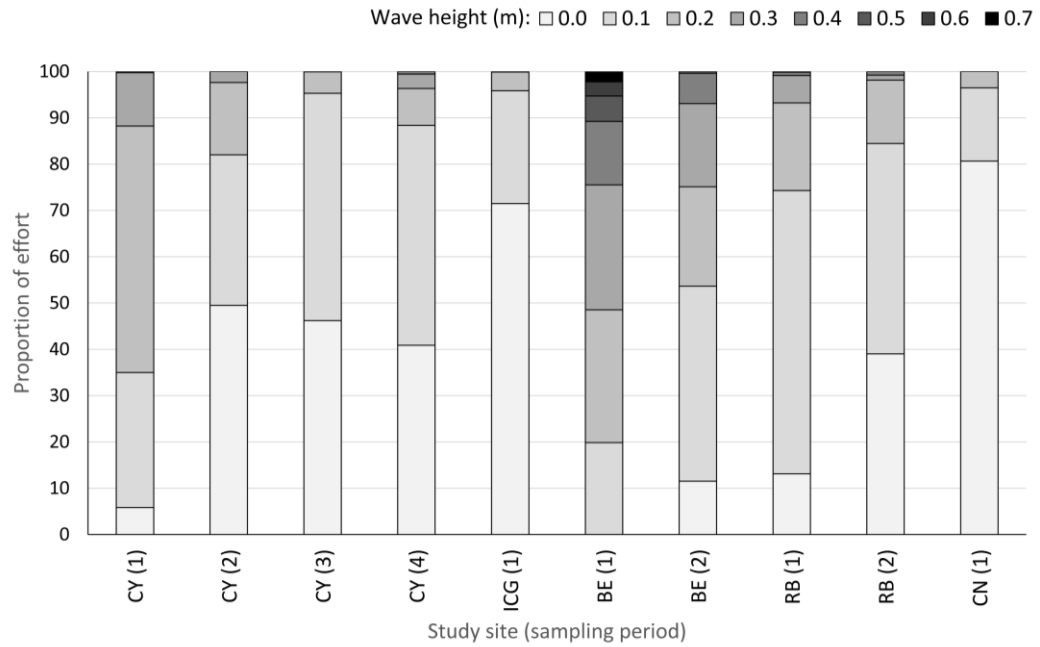


Figure A2.1.2. Proportion of effort according to wave heights (metres) per study site and sampling period. Wave heights correspond to short-period wind waves rather than long-period groundswell. Wave height was estimated by eye by the same trained observer throughout all effort. (CY) Cygnet Bay, (ICG) Inner Cambridge Gulf, (BE) Beagle Bay, (RB) Roebuck Bay, (CN) Cone Bay.

Appendix A2.2 Group size analyses

Methods

I defined a 'group' as one or more dolphins exhibiting relatively close spatial cohesion, where each member was within 100 m of any other member and involved in the same or similar behavioural activity (Bräger 1999, Parra et al. 2006a). A histogram of group size frequency distribution by species using data from all sites combined was plotted. Inter-specific differences in group sizes were investigated using randomization tests (R package "perm", Fay and Shaw 2010) employing 5,000 Monte Carlo simulations, which compared the observed difference of the mean group sizes with the difference obtained through 5,000 random allocations of the observed school sizes among the selected two species being tested (Parra et al. 2011).

Results

Snubfin dolphins formed larger groups than humpback dolphins (mean difference = 1.1, $p = < 0.01$). Bottlenose dolphin groups were also larger than those of humpback dolphins, although not significantly so (mean difference = 0.7, $p = 0.18$). The slightly larger group size of snubfin dolphins compared to bottlenose dolphins was also non-significant (mean difference 0.4, $p = 0.24$).

Table A2.2.1. Average group sizes across all study sites combined.

	Snubfin	**Humpback**	**Bottlenose**
n	223	65	156
Min-Max	1 – 22	1 – 16	1 – 18
Mean (SE)	4.4 (0.3)	3.3 (0.3)	4.0 (0.3)
Median	3	3	3
Mode	1	3	2

n = total number of groups observed

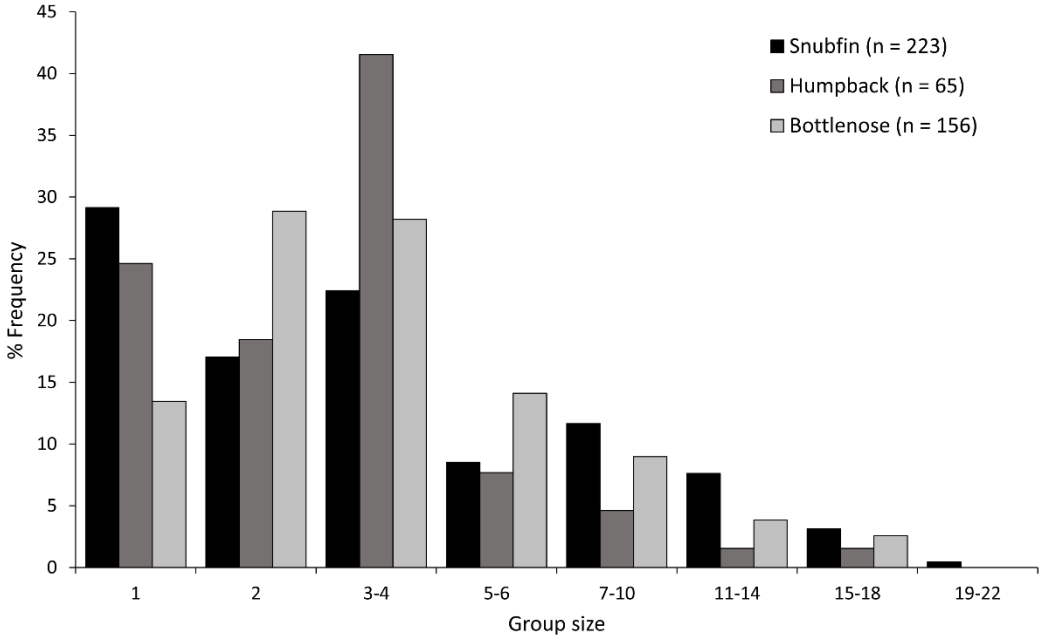


Figure A2.2.1. Group size relative frequency (%) distribution by species for all study sites combined. n = total number of groups per species.

Appendix A2.3 Maps of group sightings for each study site

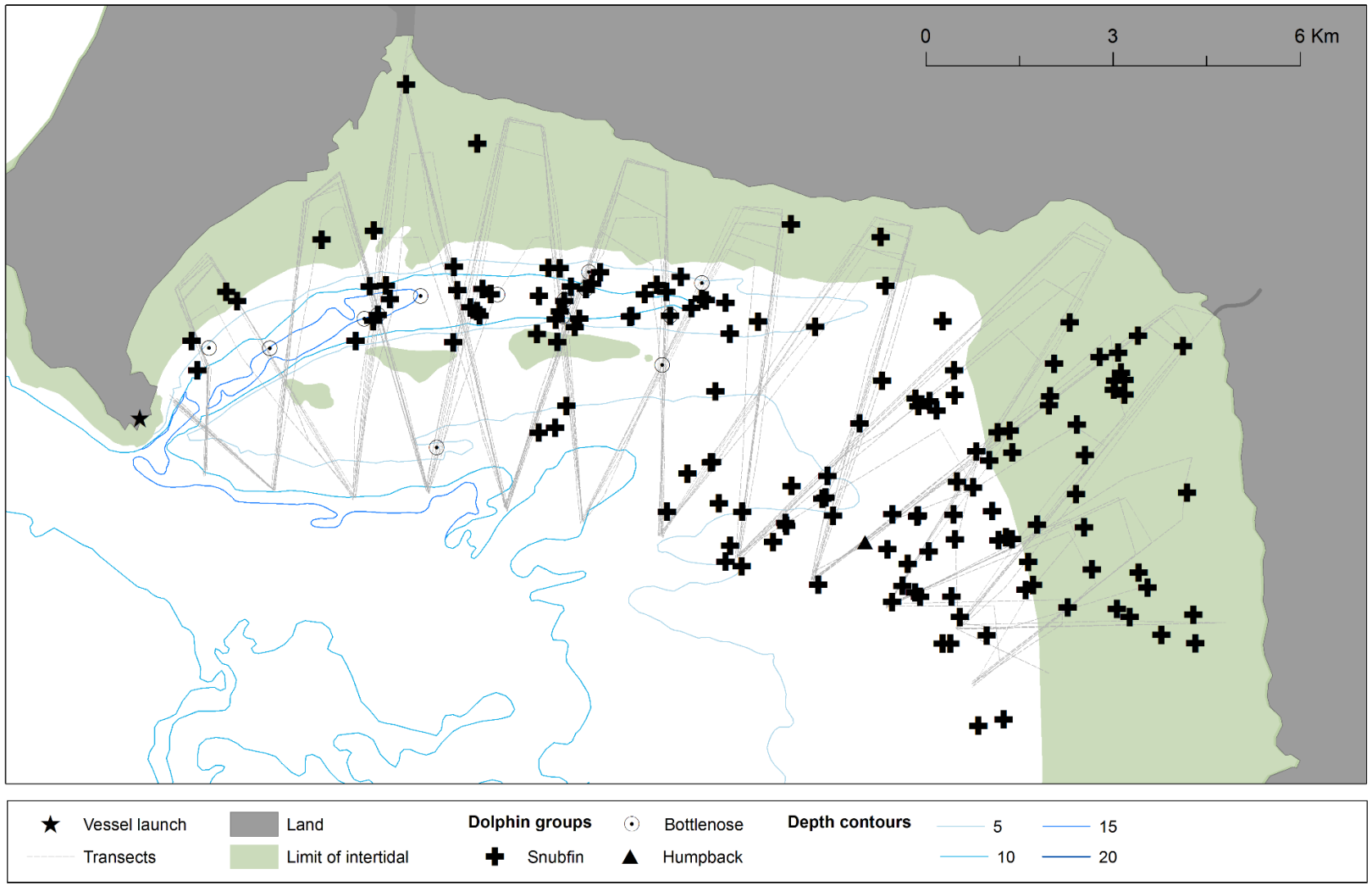


Figure A2.3.1. Survey effort (transects) and group sightings per species within Roebuck Bay across sampling periods one and two.

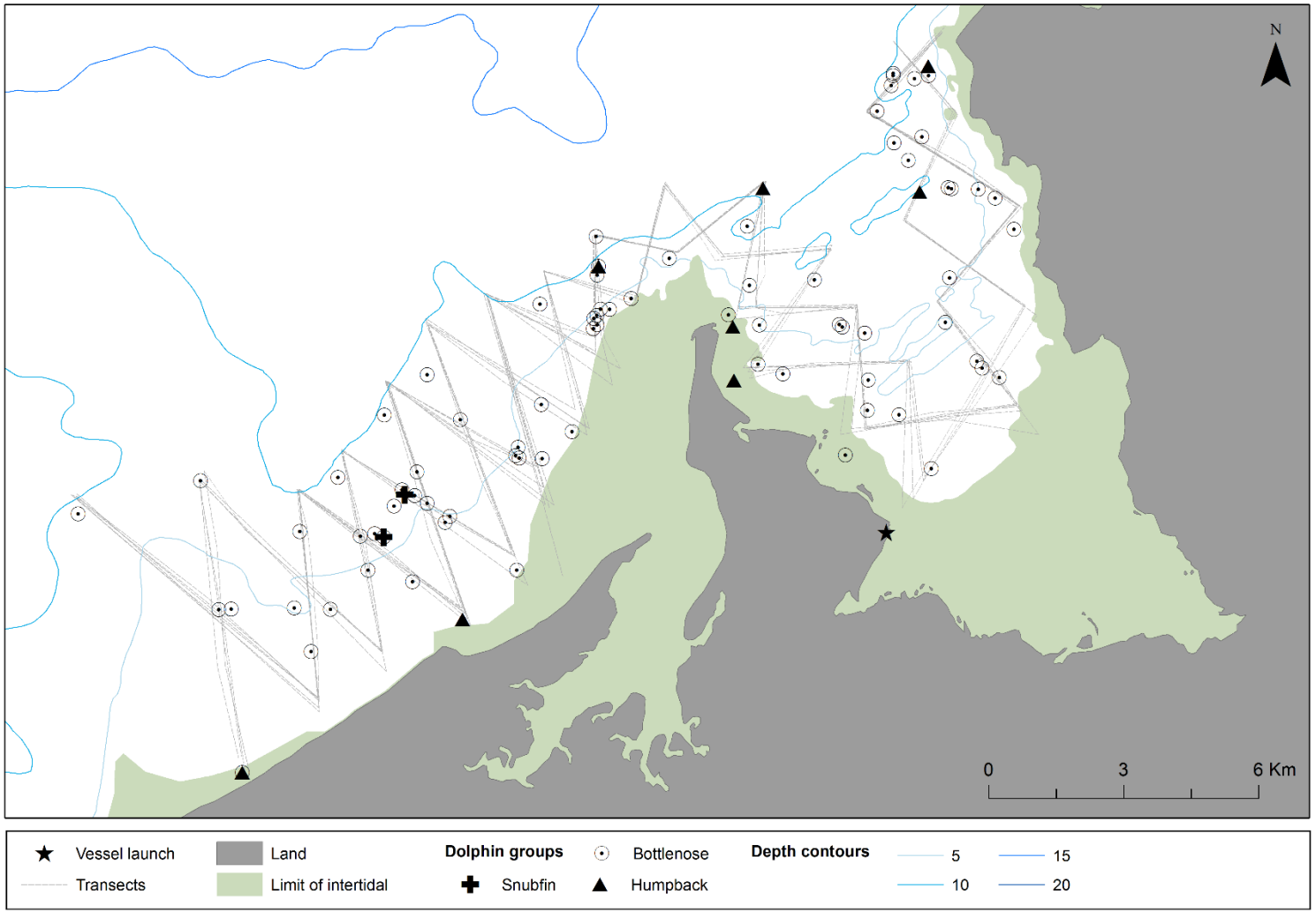


Figure A2.3.2. Survey effort (transects) and group sightings per species within Beagle Bay across sampling periods one and two. At this site, survey effort did not extend far into the intertidal areas as breaking waves (resulting from exposure to westerly swell) often made these areas inaccessible to survey.

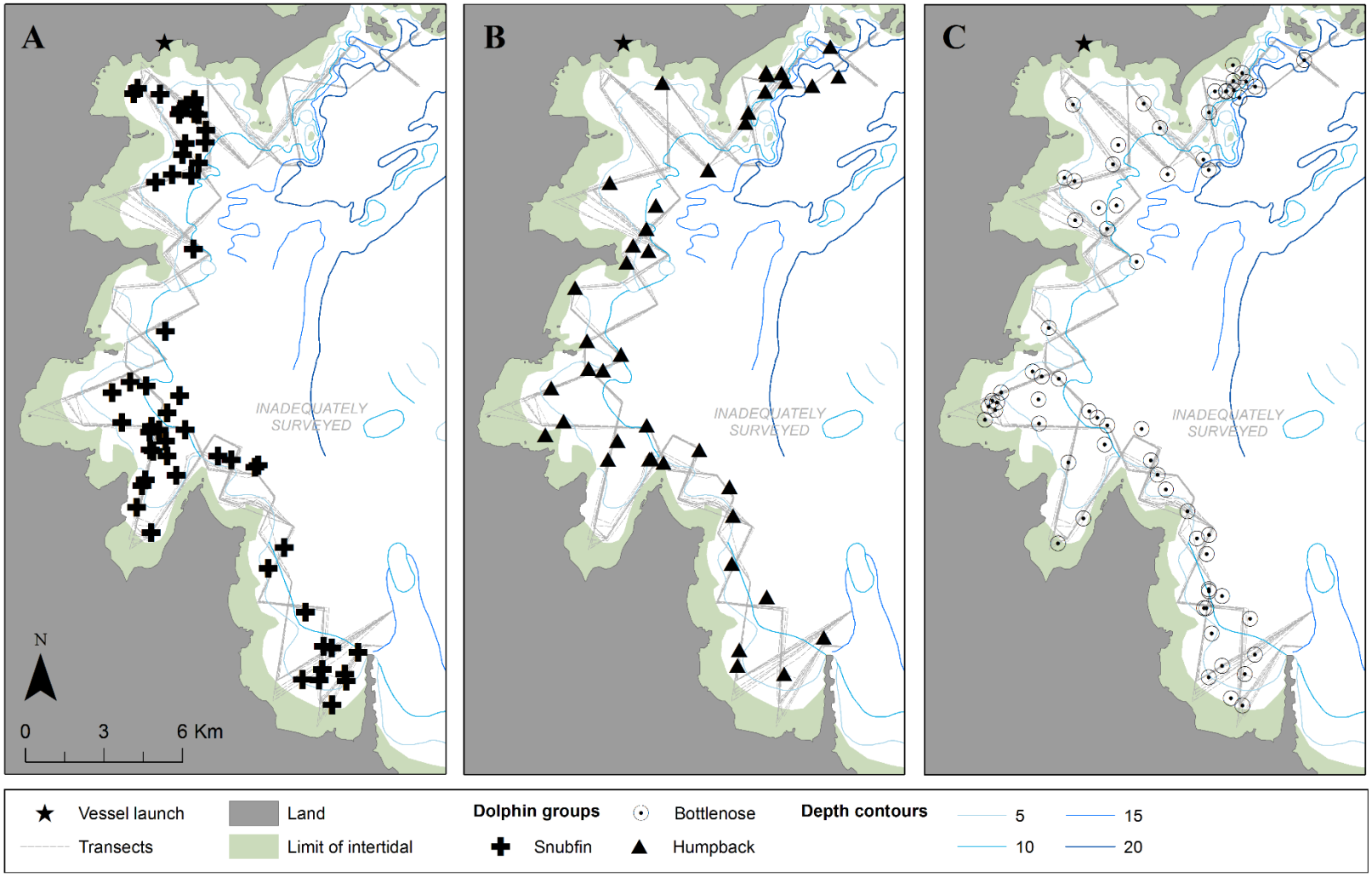


Figure A2.3.3. Survey effort (transects) and group sightings within Cygnet Bay across all sampling periods one to four. Maps illustrate snubfin (A), humpback (B) and bottlenose (C) group sightings.

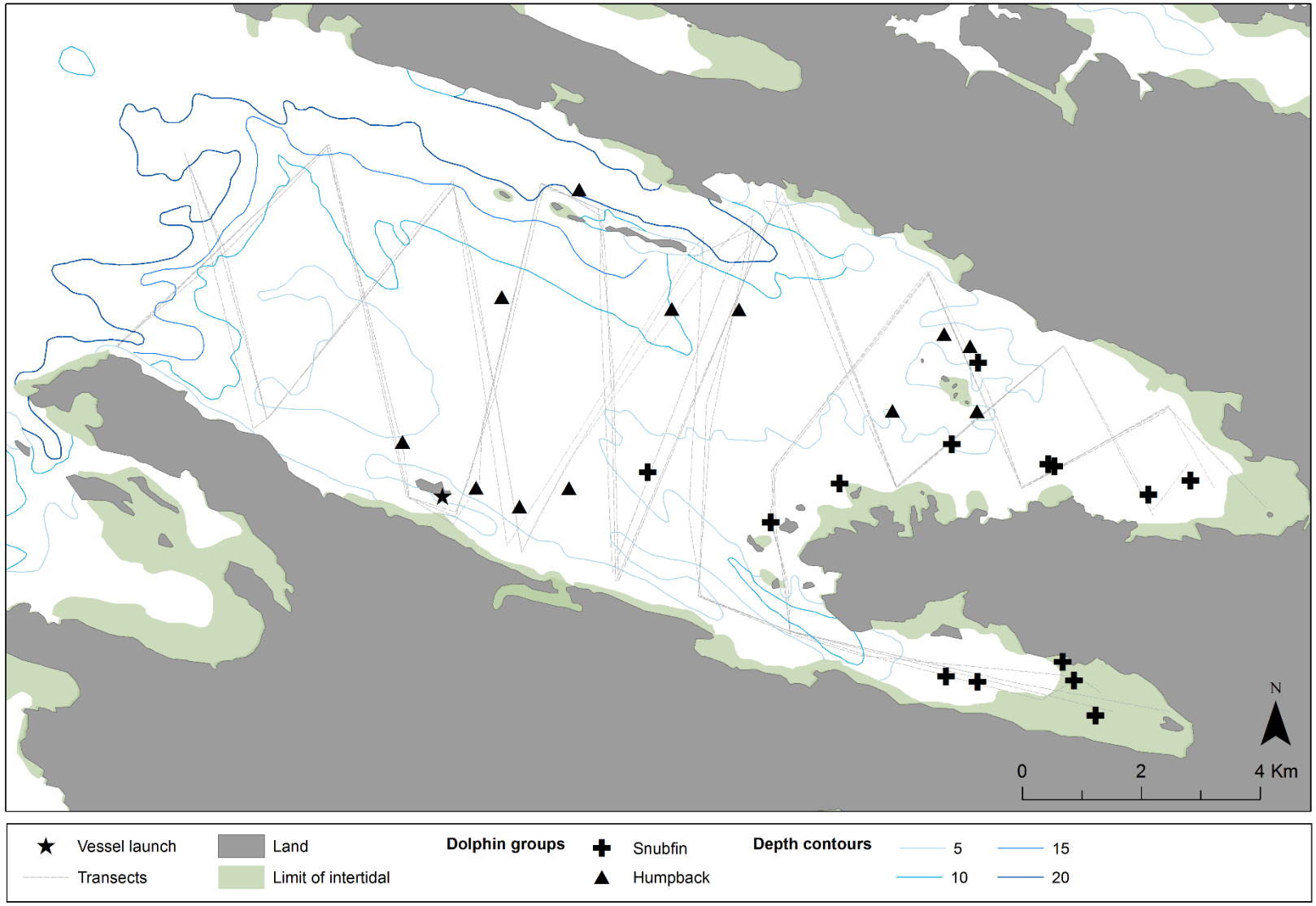


Figure A2.3.4. Survey effort (transects) and group sightings per species within Cone Bay.

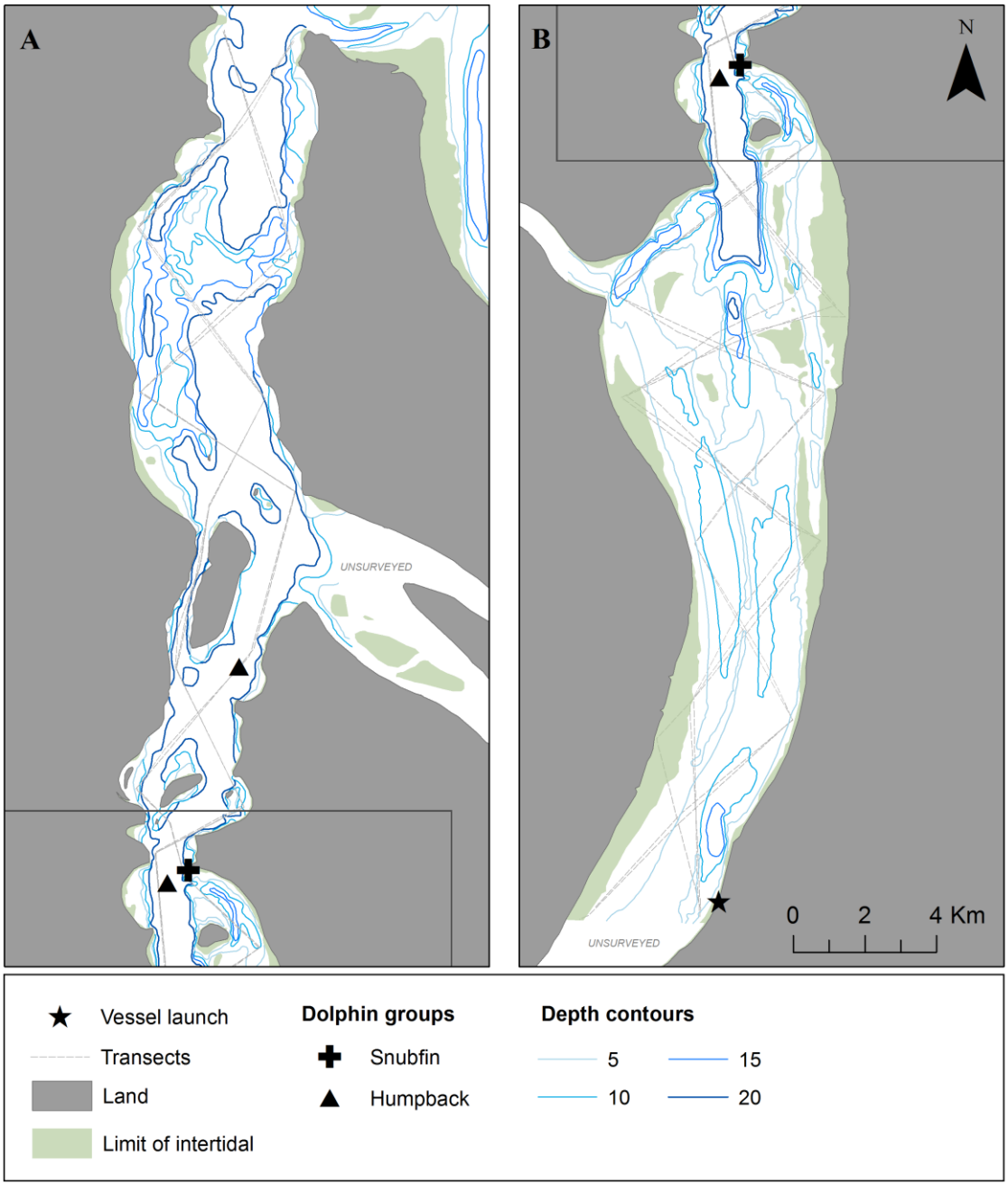


Figure A2.3.5. Survey effort (transects) and group sightings per species within the Inner Cambridge Gulf. Maps illustrate northern section (A) and southern section (B), with region of overlap indicated.

Appendix A2.4 Model selection tables and parameter estimates from capture-recapture modelling

Table A2.4.1. POPAN open models fitted to snubfin dolphins at Roebuck Bay in sampling period 1 (2013).

Model	QAICc	ΔQAICc	AICc Weight	np
$\varphi(.=1)\ p(.)\ P_{ent}(.)$	179.1	0.0	0.47	3
$\varphi(.=1)\ p(.)\ P_{ent}(.=0)$	180.2	1.1	0.27	2
$\varphi(.)\ p(.)\ P_{ent}(.=0)$	182.3	3.1	0.10	3
$\varphi(.=1)\ p(t)\ P_{ent}(.)$	183.5	4.4	0.05	7
$\varphi(.=1)\ p(t)\ P_{ent}(.=0)$	184.2	5.0	0.04	7
$\varphi(.=1)\ p(.)\ P_{ent}(t)$	185.7	6.5	0.02	7
$\varphi(.)\ p(t)\ P_{ent}(.)$	185.7	6.5	0.02	8
$\varphi(.)\ p(t)\ P_{ent}(.=0)$	186.0	6.8	0.02	6
$\varphi(.)\ p(.)\ P_{ent}(t)$	187.8	8.7	0.01	8
$\varphi(t)\ p(.)\ P_{ent}(.)$	188.5	9.4	< 0.01	8
$\varphi(.)\ p(t)\ P_{ent}(t)$	190.4	11.3	< 0.01	12
$\varphi(.=1)\ p(t)\ P_{ent}(t)$	190.4	11.3	< 0.01	12
$\varphi(t)\ p(.)\ P_{ent}(.=0)$	190.7	11.6	< 0.01	7
$\varphi(t)\ p(t)\ P_{ent}(.=0)$	194.5	15.4	< 0.01	10
$\varphi(t)\ p(.)\ P_{ent}(t)$	195.5	16.4	< 0.01	12
$\varphi(t)\ p(t)\ P_{ent}(.)$	195.8	16.6	< 0.01	12
$\varphi(t)\ p(t)\ P_{ent}(t)$	199.1	20.0	< 0.01	15

Constant (.) or time-varying (*t*) parameters of φ = apparent survival; p = capture probability; P_{ent} = probability of entry. $\varphi(.=1)$ = closed to losses; $P_{ent}(.=0)$ = closed to gains. np = number of parameters. Models with zero weight and those which did not achieve numeric convergence are not listed.

Table A2.4.2. POPAN open models fitted to snubfin dolphins at Roebuck Bay in sampling period 2 (2014).

Model	QAICc	ΔQAICc	AICc Weight	np
$\varphi(.)\ p(t)\ P_{ent}(.=0)$	220.9	0.0	0.37	6
$\varphi(.)\ p(t)\ P_{ent}(.)$	221.0	0.1	0.35	8
$\varphi(t)\ p(t)\ P_{ent}(.=0)$	224.8	3.9	0.05	10
$\varphi(.=1)\ p(.)\ P_{ent}(.=0)$	224.9	4.0	0.05	2
$\varphi(.=1)\ p(t)\ P_{ent}(.=0)$	225.0	4.1	0.05	7
$\varphi(.=1)\ p(t)\ P_{ent}(.)$	225.2	4.3	0.04	7
$\varphi(.)\ p(.)\ P_{ent}(.)$	226.2	5.3	0.03	4
$\varphi(.)\ p(t)\ P_{ent}(t)$	226.4	5.5	0.02	12
$\varphi(.=1)\ p(.)\ P_{ent}(.)$	226.9	6.0	0.02	3
$\varphi(t)\ p(.)\ P_{ent}(.)$	228.2	7.3	0.01	8
$\varphi(t)\ p(t)\ P_{ent}(.)$	229.6	8.7	< 0.01	12
$\varphi(t)\ p(.)\ P_{ent}(.=0)$	231.4	10.5	< 0.01	7
$\varphi(t)\ p(t)\ P_{ent}(t)$	232.2	11.3	< 0.01	15
$\varphi(.=1)\ p(t)\ P_{ent}(t)$	232.4	11.5	< 0.01	11
$\varphi(t)\ p(.)\ P_{ent}(t)$	232.6	11.7	< 0.01	12
$\varphi(.)\ p(.)\ P_{ent}(t)$	232.6	11.7	< 0.01	8
$\varphi(.=1)\ p(.)\ P_{ent}(t)$	235.2	14.3	< 0.01	7

Constant (.) or time-varying (*t*) parameters of φ = apparent survival; p = capture probability; P_{ent} = probability of entry. $\varphi(.=1)$ = closed to losses; $P_{ent}(.=0)$ = closed to gains. np = number of parameters. Models with zero weight and those which did not achieve numeric convergence are not listed.

Table A2.4.3. POPAN open models fitted to snubfin dolphins at Roebuck Bay for sampling periods 1 and 2 combined (2013-2014).

Model	QAICc	ΔQAICc	AICc Weight	np
$\varphi(.)\ p(s)\ P_{ent}(.)$	688.5	0.0	0.14	5
$\varphi(.=1)\ p(s)\ P_{ent}(.=0)$	688.6	0.0	0.14	3
$\varphi(.)\ p(s)\ P_{ent}(.=0)$	688.7	0.1	0.13	4
$\varphi(.=1)\ p(s)\ P_{ent}(.)$	689.2	0.7	0.10	4
$\varphi(.)\ p(.)\ P_{ent}(.=0)$	689.8	1.3	0.07	3
$\varphi(s=1)\ p(.)\ P_{ent}(.=0)$	690.0	1.4	0.07	3
$\varphi(s=1)\ p(s)\ P_{ent}(s=0)$	690.3	1.8	0.06	5
$\varphi(.=1)\ p(s)\ P_{ent}(s=0)$	690.3	1.8	0.06	4
$\varphi(.)\ p(t)\ P_{ent}(.=0)$	690.6	2.1	0.05	12
$\varphi(s=1)\ p(\mathrm{s})\ P_{ent}(.)$	690.9	2.4	0.04	5
$\varphi(.)\ p(t)\ P_{ent}(s=0)$	691.7	3.2	0.03	14
$\varphi(.)\ p(.)\ P_{ent}(s=0)$	691.8	3.3	0.03	4
$\varphi(.=1)\ p(t)\ P_{ent}(.=0)$	692.1	3.6	0.02	13
$\varphi(s=1)\ p(t)\ P_{ent}(s=0)$	692.5	4.0	0.02	13
$\varphi(.)\ p(t)\ P_{ent}(.)$	692.7	4.2	0.02	14
$\varphi(.=1)\ p(t)\ P_{ent}(\mathrm{s}=0)$	692.7	4.2	0.02	12
$\varphi(.=1)\ p(t)\ P_{ent}(.)$	692.9	4.4	0.02	13
$\varphi(s=1)\ p(t)\ P_{ent}(.)$	698.2	9.7	< 0.01	14
$\varphi(.=1)\ p(.)\ P_{ent}(.=0)$	698.2	9.7	< 0.01	2
$\varphi(.=1)\ p(.)\ P_{ent}(t)$	699.3	10.8	< 0.01	3
$\varphi(.=1)\ p(.)\ P_{ent}(.)$	700.2	11.7	< 0.01	3
$\varphi(.=1)\ p(.)\ P_{ent}(s=0)$	700.2	11.7	< 0.01	3
$\varphi(s=1)\ p(s)\ P_{ent}(t)$	702.7	14.2	< 0.01	15
$\varphi(.=1)\ p(s)\ P_{ent}(t)$	702.9	14.4	< 0.01	14
$\varphi(t)\ p(.)\ P_{ent}(.)$	703.5	15.0	< 0.01	14
$\varphi(t)\ p(t)\ P_{ent}(s=0)$	703.5	15.0	< 0.01	23
$\varphi(t)\ p(.)\ P_{ent}(.=0)$	703.8	15.3	< 0.01	13
$\varphi(t)\ p(s)\ P_{ent}(.=0)$	704.6	16.1	< 0.01	14
$\varphi(.=1)\ p(t)\ P_{ent}(\mathrm{t})$	705.2	16.6	< 0.01	23
$\varphi(t)\ p(.)\ P_{ent}(s=0)$	705.7	17.2	< 0.01	14
$\varphi(t)\ p(t)\ P_{ent}(.)$	706.4	17.9	< 0.01	24
$\varphi(t)\ p(s)\ P_{ent}(\mathrm{s}=0)$	706.7	18.1	< 0.01	15
$\varphi(.)\ p(t)\ P_{ent}(t)$	707.1	18.6	< 0.01	24
$\varphi(.)\ p(s)\ P_{ent}(t)$	707.6	19.1	< 0.01	15

Constant (.), time-varying (t) or varying with sampling period (s) parameters of φ = apparent survival; p = capture probability; P_{ent} = probability of entry. $\varphi(.=1)$ = closed to losses; $P_{ent}(.=0)$ = closed to gains; (s=1/0) = closed within periods but open between periods. np = number of parameters. Models with zero weight and those which did not achieve numeric convergence are not listed.

Table A2.4.4. Model averaged parameter estimates for snubfin dolphins at Roebuck Bay in sampling periods 1 (2013) and 2 (2014).

	Sampling period 1 (2013)				Sampling period 2 (2014)			
Parameter	**Estimate**	**SE**	**LCI**	**UCI**	**Estimate**	**SE**	**LCI**	**UCI**
$\varphi\ t_{1\text{-}2}$	1.00	0.01	0.98	1.00	0.95	0.04	0.79	0.99
$\varphi\ t_{2\text{-}3}$	1.00	0.01	0.98	1.00	0.94	0.04	0.78	0.98
$\varphi\ t_{3\text{-}4}$	1.00	0.00	1.00	1.00	0.95	0.04	0.79	0.99
$\varphi\ t_{4\text{-}5}$	1.00	0.00	1.00	1.00	0.95	0.04	0.79	0.99
$\varphi\ t_{5\text{-}6}$	1.00	0.00	1.00	1.00	0.95	0.04	0.79	0.99
$p\ t_1$	0.32	0.06	0.22	0.44	0.21	0.06	0.12	0.34
$p\ t_2$	0.32	0.06	0.21	0.44	0.21	0.06	0.12	0.33
$p\ t_3$	0.31	0.05	0.22	0.42	0.22	0.06	0.13	0.36
$p\ t_4$	0.31	0.05	0.22	0.42	0.19	0.06	0.10	0.33
$p\ t_5$	0.31	0.05	0.22	0.42	0.35	0.10	0.19	0.55
$p\ t_6$	0.33	0.06	0.22	0.46	0.44	0.13	0.22	0.69
$P_{ent}\ t_{1\text{-}2}$	0.03	0.04	0.00	0.27	0.00	0.01	0.00	0.03
$P_{ent}\ t_{2\text{-}3}$	0.03	0.04	0.00	0.29	0.01	0.07	0.00	1.00
$P_{ent}\ t_{3\text{-}4}$	0.04	0.06	0.00	0.44	0.00	0.01	0.00	0.03
$P_{ent}\ t_{4\text{-}5}$	0.03	0.05	0.00	0.37	0.00	0.02	0.00	0.03
$P_{ent}\ t_{5\text{-}6}$	0.04	0.05	0.00	0.34	0.00	0.01	0.00	0.03
$\widehat{N}_D$	115.86	9.84	96.56	135.15	116.21	17.65	81.61	150.81

Estimates are derived from the models listed in Table A2.4.1 and A2.4.2. φ = apparent survival; p = capture probability; P_{ent} = probability of entry; t_i = parameter estimate at transect i; $\widehat{N}_D$ = estimated super-population abundance of distinctive animals; SE = standard error (unconditional); LCI and UCI = lower and upper 95% confidence intervals respectively.

Table A2.4.5. Model averaged parameter estimates for snubfin dolphins at Roebuck Bay in sampling periods 1 and 2 combined (2013-2014).

Parameter	Estimate	SE	LCI	UCI
$\varphi\ t_{1\text{-}2}$	1.00	0.00	1.00	1.00
$\varphi\ t_{2\text{-}3}$	1.00	0.00	1.00	1.00
$\varphi\ t_{3\text{-}4}$	1.00	0.00	1.00	1.00
$\varphi\ t_{4\text{-}5}$	1.00	0.00	1.00	1.00
$\varphi\ t_{5\text{-}6}$	1.00	0.00	1.00	1.00
$\varphi\ t_{6\text{-}7}$	1.00	0.00	1.00	1.00
$\varphi\ t_{7\text{-}8}$	1.00	0.00	1.00	1.00
$\varphi\ t_{8\text{-}9}$	1.00	0.00	1.00	1.00
$\varphi\ t_{9\text{-}10}$	1.00	0.00	1.00	1.00
$\varphi\ t_{10\text{-}11}$	1.00	0.00	1.00	1.00
$\varphi\ t_{11\text{-}12}$	1.00	0.00	1.00	1.00
$p\ t_{1}$	0.30	0.04	0.22	0.39
$p\ t_{2}$	0.29	0.04	0.23	0.37
$p\ t_{3}$	0.29	0.04	0.22	0.37
$p\ t_{4}$	0.29	0.04	0.22	0.37
$p\ t_{5}$	0.29	0.04	0.22	0.37
$p\ t_{6}$	0.32	0.07	0.21	0.46
$p\ t_{7}$	0.22	0.04	0.15	0.31
$p\ t_{8}$	0.22	0.04	0.15	0.31
$p\ t_{9}$	0.21	0.04	0.14	0.31
$p\ t_{10}$	0.21	0.05	0.12	0.32
$p\ t_{11}$	0.23	0.04	0.15	0.32
$p\ t_{12}$	0.24	0.05	0.15	0.36
$P_{ent}\ t_{1\text{-}2}$	0.01	0.05	0.00	0.98
$P_{ent}\ t_{2\text{-}3}$	0.00	0.01	0.00	0.02
$P_{ent}\ t_{3\text{-}4}$	0.00	0.01	0.00	0.02
$P_{ent}\ t_{4\text{-}5}$	0.00	0.01	0.00	0.02
$P_{ent}\ t_{5\text{-}6}$	0.00	0.01	0.00	0.02
$P_{ent}\ t_{6\text{-}7}$	0.01	0.03	0.00	0.72
$P_{ent}\ t_{7\text{-}8}$	0.00	0.01	0.00	0.02
$P_{ent}\ t_{8\text{-}9}$	0.00	0.01	0.00	0.02
$P_{ent}\ t_{9\text{-}10}$	0.00	0.01	0.00	0.02
$P_{ent}\ t_{10\text{-}11}$	0.00	0.01	0.00	0.02
$P_{ent}\ t_{11\text{-}12}$	0.00	0.01	0.00	0.02
$\widehat{N}_D$	119.04	4.84	109.56	128.52

Estimates are derived from the models listed in Table A2.4.3. φ = apparent survival; p = capture probability; P_{ent} = probability of entry; t_i = parameter estimate at transect i; $\widehat{N}_D$ = estimated super-population of distinctive animals; SE = standard error; LCI and UCI = lower and upper 95% confidence intervals respectively.

Table A2.4.6. POPAN open models fitted to bottlenose dolphins at Beagle Bay in sampling period 1 (2012).

Model	AICc	ΔAICc	AICc Weight	np
$\varphi(.=1)\ p(.)\ P_{ent}(.=0)$	112.1	0.0	0.46	2
$\varphi(.)\ p(.)\ P_{ent}(.=0)$	113.9	1.8	0.18	3
$\varphi(.=1)\ p(.)\ P_{ent}\ (.)$	114.2	2.2	0.15	3
$\varphi(.)\ p(.)\ P_{ent}\ (.)$	116.1	4.0	0.06	4
$\varphi(.=1)\ p(t)\ P_{ent}(.=0)$	117.1	5.1	0.04	6
$\varphi(.)\ p(t)\ P_{ent}\ (.=0)$	117.2	5.1	0.03	5
$\varphi(.=1)\ p(t)\ P_{ent}(.)$	117.4	5.3	0.03	6
$\varphi(t)\ p(.)\ P_{ent}(.)$	119.2	7.2	0.01	7
$\varphi(.)\ p(t)\ P_{ent}(.)$	119.8	7.7	0.01	7
$\varphi(.=1)\ p(t)\ P_{ent}(t)$	121.1	9.0	0.01	9
$\varphi(.=1)\ p(.)\ P_{ent}(t)$	121.1	9.0	< 0.01	6
$\varphi(.)\ p(.)\ P_{ent}(t)$	121.1	9.1	< 0.01	7
$\varphi(t)\ p(t)\ P_{ent}(.=0)$	123.3	11.2	< 0.01	8
$\varphi(.)\ p(\mathrm{t})\ P_{ent}(\mathrm{t})$	123.4	11.4	< 0.01	10
$\varphi(t)\ p(t)\ P_{ent}(.)$	124.0	12.0	< 0.01	9
$\varphi(t)\ p(.)\ P_{ent}(t)$	125.0	13.0	< 0.01	10
$\varphi(t)\ p(t)\ P_{ent}(t)$	127.9	15.9	< 0.01	12

Constant (.) or time-varying (*t*) parameters of φ = apparent survival; p = capture probability; P_{ent} = probability of entry. $\varphi(. = 1)$ = closed to losses; $P_{ent}(. = 0)$ = closed to gains. np = number of parameters. Models with zero weight and those which did not achieve numeric convergence are not listed.

Table A2.4.7. POPAN open models fitted to bottlenose dolphins at Beagle Bay in sampling period 2 (2013).

Model	AICc	ΔAICc	AICc Weight	np
$\varphi(.=1)\ p(t)\ P_{ent}(.)$	178.8	0.0	0.54	6
$\varphi(.=1)\ p(t)\ P_{ent}(.=0)$	180.7	1.9	0.21	6
$\varphi(.)\ p(t)\ P_{ent}(.)$	181.1	2.3	0.17	7
$\varphi(.=1)\ p(t)\ P_{ent}(t)$	183.6	4.8	0.05	9
$\varphi(.)\ p(t)\ P_{ent}(t)$	186.0	7.2	0.01	10
$\varphi(.=1)\ p(.)\ P_{ent}(t)$	188.3	9.5	< 0.01	6
$\varphi(.)\ p(.)\ P_{ent}(t)$	190.5	11.6	< 0.01	7
$\varphi(t)\ p(.)\ P_{ent}(t)$	195.6	16.7	< 0.01	10
$\varphi(t)\ p(t)\ P_{ent}(t)$	199.7	20.8	< 0.01	12
$\varphi(.=1)\ p(.)\ P_{ent}(.)$	200.4	21.6	< 0.01	3

Constant (.) or time-varying (*t*) parameters of φ = apparent survival; p = capture probability; P_{ent} = probability of entry. $\varphi(. = 1)$ = closed to losses; $P_{ent}(. = 0)$ = closed to gains. np = number of parameters. Models with zero weight and those which did not achieve numeric convergence are not listed.

Table A2.4.8. POPAN open models fitted to bottlenose dolphins at Beagle Bay for sampling periods 1 and 2 combined (2012-2013).

Model	QAICc	ΔQAICc	AICc Weight	np
$\varphi(.=1)\ p(t)\ P_{ent}(.=0)$	366.6	0.0	0.40	11
$\varphi(.=1)\ p(t)\ P_{ent}\ (.)$	366.8	0.2	0.36	11
$\varphi(s=1)\ p(t)\ P_{ent}\ (.)$	368.9	2.3	0.13	12
$\varphi(.)\ p(t)\ P_{ent}\ (.)$	369.1	2.5	0.11	12
$\varphi(.=1)\ p(s)\ P_{ent}\ (.=0)$	379.1	12.5	< 0.01	3
$\varphi(.=1)\ p(s)\ P_{ent}\ (.)$	381.1	14.6	< 0.01	4
$\varphi(s=1)\ p(s)\ P_{ent}\ (.=0)$	381.1	14.6	< 0.01	4
$\varphi(.)\ p(s)\ P_{ent}(.)$	381.2	14.6	< 0.01	4
$\varphi(.=1)\ p(s)\ P_{ent}(s=0)$	381.2	14.6	< 0.01	4
$\varphi(.=1)\ p(.)\ P_{ent}(.)$	381.9	15.3	< 0.01	3
$\varphi(.=1)\ p(.)\ P_{ent}(s=0)$	382.1	15.5	< 0.01	3
$\varphi(.=1)\ p(.)\ P_{ent}(.=0)$	383.0	16.5	< 0.01	2
$\varphi(s=1)\ p(s)\ P_{ent}(.)$	383.2	16.6	< 0.01	5
$\varphi(.)\ p(s)\ P_{ent}(.)$	383.2	16.7	< 0.01	5
$\varphi(s=1)\ p(s)\ P_{ent}(s=0)$	383.3	16.7	< 0.01	5
$\varphi(.=1)\ p(t)\ P_{ent}(t)$	383.9	17.4	< 0.01	19
$\varphi(s=1)\ p(.)\ P_{ent}(.)$	384.0	17.4	< 0.01	4
$\varphi(s=1)\ p(.)\ P_{ent}(s=0)$	384.1	17.6	< 0.01	4
$\varphi(.)\ p(.)\ P_{ent}(s=0)$	384.1	17.6	< 0.01	4
$\varphi(.)\ p(.)\ P_{ent}(.=0)$	385.1	18.5	< 0.01	3
$\varphi(s=1)\ p(.)\ P_{ent}(.=0)$	385.1	18.5	< 0.01	3
$\varphi(.)\ p(t)\ P_{ent}(t)$	386.1	19.5	< 0.01	20

Constant (.), time-varying (t) or varying with sampling period (s) parameters of φ = apparent survival; p = capture probability; P_{ent} = probability of entry. $\varphi(. = 1)$ = closed to losses; $P_{ent}(. = 0)$ = closed to gains; (s = 1/0) = closed within periods but open between periods. np = number of parameters. Models with zero weight and those which did not achieve numeric convergence are not listed.

Table A2.4.9. Model averaged parameter estimates for bottlenose dolphins at Beagle Bay in sampling periods 1 (2012) and 2 (2013).

	Sampling period 1 (2012)				Sampling period 2 (2013)			
Parameter	**Estimate**	**SE**	**LCI**	**UCI**	**Estimate**	**SE**	**LCI**	**UCI**
$\varphi\ t_{1\text{-}2}$	0.99	0.04	0.91	1.00	1.00	0.00	1.00	1.00
$\varphi\ t_{2\text{-}3}$	1.00	0.01	0.97	1.00	1.00	0.00	1.00	1.00
$\varphi\ t_{3\text{-}4}$	0.99	0.08	0.00	1.00	1.00	0.00	1.00	1.00
$\varphi\ t_{4\text{-}5}$	1.00	0.01	0.98	1.00	1.00	0.00	1.00	1.00
$p\ t_1$	0.09	0.03	0.05	0.18	0.20	0.07	0.09	0.39
$p\ t_2$	0.09	0.03	0.05	0.18	0.20	0.08	0.09	0.39
$p\ t_3$	0.09	0.03	0.05	0.17	0.18	0.05	0.10	0.29
$p\ t_4$	0.09	0.03	0.04	0.17	0.06	0.03	0.03	0.14
$p\ t_5$	0.09	0.03	0.05	0.17	0.30	0.06	0.20	0.43
$P_{ent}\ t_{1\text{-}2}$	0.00	0.04	0.00	0.07	0.08	0.07	0.01	0.36
$P_{ent}\ t_{2\text{-}3}$	0.01	0.07	0.00	0.15	0.09	0.09	0.01	0.47
$P_{ent}\ t_{3\text{-}4}$	0.00	0.04	0.00	0.07	0.08	0.07	0.01	0.36
$P_{ent}\ t_{4\text{-}5}$	0.00	0.04	0.00	0.09	0.11	0.11	0.01	0.54
$\widehat{N}_D$	171.45	42.95	87.26	255.64	144.73	22.21	101.20	188.26

Estimates are derived from the models listed in Table A2.4.6 and A2.4.7. φ = apparent survival; p = capture probability; P_{ent} = probability of entry; t_i = parameter estimate at transect i; $\widehat{N}_D$ = estimated super-population abundance of distinctive animals; SE = standard error; LCI and UCI = lower and upper 95% confidence intervals respectively.

Table A2.4.10. Model averaged parameter estimates for bottlenose dolphins at Beagle Bay in sampling periods 1 and 2 combined (2012-2013).

Parameter	Estimate	SE	LCI	UCI
$\varphi\ t_{1\text{-}2}$	1.00	0.00	1.00	1.00
$\varphi\ t_{2\text{-}3}$	1.00	0.00	1.00	1.00
$\varphi\ t_{3\text{-}4}$	1.00	0.00	1.00	1.00
$\varphi\ t_{4\text{-}5}$	1.00	0.00	1.00	1.00
$\varphi\ t_{5\text{-}6}$	1.00	0.00	1.00	1.00
$\varphi\ t_{6\text{-}7}$	1.00	0.00	1.00	1.00
$\varphi\ t_{7\text{-}8}$	1.00	0.00	1.00	1.00
$\varphi\ t_{8\text{-}9}$	1.00	0.00	1.00	1.00
$\varphi\ t_{9\text{-}10}$	1.00	0.00	1.00	1.00
$p\ t_1$	0.12	0.03	0.07	0.18
$p\ t_2$	0.11	0.03	0.07	0.17
$p\ t_3$	0.12	0.03	0.07	0.19
$p\ t_4$	0.06	0.02	0.03	0.13
$p\ t_5$	0.11	0.03	0.06	0.19
$p\ t_6$	0.14	0.04	0.08	0.22
$p\ t_7$	0.12	0.03	0.07	0.21
$p\ t_8$	0.15	0.04	0.09	0.23
$p\ t_9$	0.06	0.02	0.02	0.12
$p\ t_{10}$	0.30	0.05	0.21	0.42
$P_{ent}\ t_{1\text{-}2}$	0.00	0.00	0.00	0.00
$P_{ent}\ t_{2\text{-}3}$	0.00	0.01	0.00	0.01
$P_{ent}\ t_{3\text{-}4}$	0.00	0.00	0.00	0.00
$P_{ent}\ t_{4\text{-}5}$	0.00	0.00	0.00	0.00
$P_{ent}\ t_{5\text{-}6}$	0.00	0.00	0.00	0.01
$P_{ent}\ t_{6\text{-}7}$	0.00	0.00	0.00	0.00
$P_{ent}\ t_{7\text{-}8}$	0.00	0.00	0.00	0.00
$P_{ent}\ t_{8\text{-}9}$	0.00	0.00	0.00	0.00
$P_{ent}\ t_{9\text{-}10}$	0.00	0.00	0.00	0.00
$\widehat{N}_D$	146.14	11.84	122.94	169.34

Estimates are derived from the models listed in Table A2.4.8. φ = apparent survival; p = capture probability; P_{ent} = probability of entry; t_i = parameter estimate at transect i; $\widehat{N}_D$ = estimated abundance of distinctive animals; SE = standard error; LCI and UCI = lower and upper 95% confidence intervals respectively.

Table A2.4.11. Robust design models fitted for snubfin dolphins at Cygnet Bay.

Model	AICc	ΔAICc	AICc weight	np
$\varphi(.)$ $\gamma''(.) = \gamma'(.) = 0$ $p(t)$	-12.5	0.0	0.43	17
$\varphi(t)$ $\gamma''(.) = \gamma'(.) = 0$ $p(t)$	-11.3	1.2	0.24	18
$\varphi(.)$ $\gamma''(.) = \gamma'(.)$ $p(t)$	-10.5	2.0	0.16	18
$\varphi(t)$ $\gamma''(.) = \gamma'(.)$ $p(t)$	-8.9	3.6	0.07	19
$\varphi(.)$ $\gamma''(t) = \gamma'(t)$ $p(t)$	-8.9	3.6	0.07	19
$\varphi(t)$ $\gamma''(t) = \gamma'(t)$ $p(t)$	-6.5	5.9	0.02	20

Constant (.), time-varying (t) or varying with sampling period (s) parameters of apparent survival (φ); capture probability (p); and temporary emigration (γ'', γ'), including random temporary emigration ($\gamma'' = \gamma'$) or no temporary emigration ($\gamma'' = \gamma' = 0$). np = number of parameters. Akaike information criterion corrected for small sample sizes (AICc) was used to determine the best-fitting model. Models with zero weight and those which did not achieve numeric convergence are not listed.

Table A2.4.12. Robust design models fitted for humpback dolphins at Cygnet Bay.

Model	AICc	ΔAICc	AICc weight	np
$\varphi(.)$ $\gamma''(.) = \gamma'(.) = 0$ $p(t)$	-12.5	0.0	0.35	17
$\varphi(t)$ $\gamma''(.) = \gamma'(.) = 0$ $p(t)$	-11.3	1.2	0.22	18
$\varphi(.)$ $\gamma''(.) = \gamma'(.)$ $p(t)$	-10.5	2.0	0.11	18
$\varphi(t)$ $\gamma''(.) = \gamma'(.)$ $p(t)$	-8.9	3.6	0.11	19
$\varphi(.)$ $\gamma''(t) = \gamma'(t)$ $p(t)$	-8.9	3.6	0.07	19
$\varphi(t)$ $\gamma''(t) = \gamma'(t)$ $p(t)$	-6.5	5.9	0.04	20
$\varphi(.)$ $\gamma''(.) = \gamma'(.) = 0$ $p(s)$	82.5	95.0	0.03	7
$\varphi(t)$ $\gamma''(.) = \gamma'(.) = 0$ $p(s)$	83.6	96.1	0.03	8
$\varphi(.)$ $\gamma''(.) = \gamma'(.)$ $p(s)$	84.6	97.1	0.02	8
$\varphi(t)$ $\gamma''(.) = \gamma'(.)$ $p(s)$	85.8	98.2	0.01	9
$\varphi(.)$ $\gamma''(t) = \gamma'(t)$ $p(s)$	85.8	98.2	0.01	9
$\varphi(.)$ $\gamma''(.) = \gamma'(.) = 0$ $p(.)$	85.8	98.3	< 0.01	5
$\varphi(t)$ $\gamma''(.) = \gamma'(.) = 0$ $p(.)$	86.7	99.2	< 0.01	6
$\varphi(.)$ $\gamma''(.) = \gamma'(.)$ $p(.)$	87.9	100.4	< 0.01	6
$\varphi(t)$ $\gamma''(t) = \gamma'(t)$ $p(s)$	87.9	100.4	< 0.01	10
$\varphi(t)$ $\gamma''(t) = \gamma'(t)$ $p(.)$	91.0	103.5	< 0.01	8
$\varphi(t)$ $\gamma''(.) = \gamma'(.)$ $p(.)$	93.2	105.7	< 0.01	9
$\varphi(.)$ $\gamma''(t) = \gamma'(t)$ $p(.)$	93.2	105.7	< 0.01	9

Constant (.), time-varying (t) or varying with sampling period (s) parameters of apparent survival (φ); capture probability (p); and temporary emigration (γ'', γ'), including random temporary emigration ($\gamma'' = \gamma'$) or no temporary emigration ($\gamma'' = \gamma' = 0$). np = number of parameters. Akaike information criterion corrected for small sample sizes (AICc) was used to determine the best-fitting model. Models with zero weight and those which did not achieve numeric convergence are not listed.

Table A2.4.13. Robust design models fitted for bottlenose dolphins at Cygnet Bay.

Model	AICc	ΔAICc	AICc weight	np
$\varphi(.)\ \gamma''(.) = \gamma'(.) = 0\ \ p(t)$	118.6	0.0	0.66	24
$\varphi(.)\ \gamma''(.) = \gamma'(.)\ \ p(t)$	121.2	2.6	0.18	25
$\varphi(.)\ \gamma''(.) \neq \gamma'(.)\ \ p(t)$	123.4	4.8	0.06	26
$\varphi(t)\ \gamma''(.) = \gamma'(.) = 0\ \ p(t)$	123.6	5.0	0.05	26
$\varphi(.)\ \gamma''(t) \neq \gamma'(.)\ \ p(t)$	126.0	7.4	0.02	27
$\varphi(t)\ \gamma''(.) = \gamma'(.)\ \ p(t)$	126.4	7.8	0.01	27
$\varphi(.)\ \gamma''(t) = \gamma'(t)\ \ p(t)$	126.5	7.9	0.01	27
$\varphi(t)\ \gamma''(.) \neq \gamma'(.)\ \ p(t)$	128.7	10.1	< 0.01	28
$\varphi(t)\ \gamma''(t) = \gamma'(t)\ \ p(t)$	129.1	10.5	< 0.01	28
$\varphi(t)\ \gamma''(t) \neq \gamma'(.)\ \ p(t)$	131.5	12.9	< 0.01	29

Constant (.), time-varying (*t*) or varying with sampling period (*s*) parameters of apparent survival (φ); capture probability (*p*); and temporary emigration (γ'', γ'), including no temporary emigration ($\gamma'' = \gamma' = 0$), random temporary emigration ($\gamma'' = \gamma'$) or Markovian temporary emigration ($\gamma'' \neq \gamma'$). np = number of parameters. Akaike information criterion corrected for small sample sizes (AICc) was used to determine the best-fitting model. Models with zero weight and those which did not achieve numeric convergence are not listed.

Table A2.4.14. Parameter estimates for snubfin dolphins at Cygnet Bay, based on the best-fitting model of constant apparent survival, no temporary emigration and time-varying capture probability.

Parameter	Estimate	SE	LCI	UCI
φ	0.95	0.05	0.68	0.99
$\gamma'' = \gamma' = 0$ (fixed)	0.00	0.00	0.00	0.00
$p\ S_2\ t_1$	0.07	0.04	0.02	0.19
$p\ S_2\ t_2$	0.04	0.03	0.01	0.16
$p\ S_2\ t_3$	0.66	0.09	0.46	0.82
$p\ S_2\ t_4$	0.51	0.09	0.34	0.67
$p\ S_3\ t_1$	0.34	0.07	0.22	0.48
$p\ S_3\ t_2$	0.22	0.06	0.12	0.35
$p\ S_3\ t_3$	0.79	0.06	0.65	0.89
$p\ S_3\ t_4$	0.42	0.07	0.29	0.56
$p\ S_4\ t_1$	0.36	0.07	0.24	0.51
$p\ S_4\ t_2$	0.18	0.06	0.10	0.32
$p\ S_4\ t_3$	0.45	0.07	0.31	0.59
$p\ S_4\ t_4$	0.49	0.07	0.35	0.63
$p\ S_4\ t_5$	0.40	0.07	0.28	0.55
$\widehat{N}_D\ S_2$	45.28	4.20	37.04	53.51
$\widehat{N}_D\ S_3$	50.69	2.21	46.36	55.03
$\widehat{N}_D\ S_4$	47.42	2.47	42.58	52.25

Estimates are derived from model $\varphi(.)\ \ \gamma''(.) = \gamma'(.) = 0\ \ p(t)$ listed in Table A2.4.11, with the exception of $\widehat{N}_D$ estimates which were derived from weighted model-averaging across all models in table A2.4.11. φ = apparent survival; $\gamma''\gamma'$ = temporary emigration parameters; $p\ S\ t_i$ = capture probability for transect i within sampling period S; $\widehat{N}_D\ S_i$ = estimated abundance of distinctive animals within sampling period i; SE = standard error; LCI and UCI = lower and upper 95% confidence intervals respectively.

Table A2.4.15. Parameter estimates for humpback dolphins at Cygnet Bay, based on the best-fitting model of constant apparent survival, no temporary emigration and constant capture probability.

Parameter	Estimate	SE	LCI	UCI
φ	0.62	0.12	0.37	0.82
$\gamma'' = \gamma' = 0$ (fixed)	0.00	0.00	0.00	0.00
p	0.35	0.04	0.28	0.42
$\widehat{N}_D S_2$	20.08	2.01	16.13	24.03
$\widehat{N}_D S_3$	16.70	1.84	13.09	20.31
$\widehat{N}_D S_4$	15.12	2.08	11.04	19.20

Estimates are derived from model $\varphi(.)$ $\gamma''(.) = \gamma'(.) = 0$ $p(.)$ listed in Table A2.4.12, with the exception of $\widehat{N}_D$ estimates which were derived from weighted model-averaging across all models in table A2.4.12. φ = apparent survival; $\gamma''\gamma'$ = temporary emigration parameters; p = capture probability; $\widehat{N}_D S_i$ = estimated abundance of distinctive animals within sampling period i; SE = standard error; LCI and UCI = lower and upper 95% confidence intervals respectively.

Table A2.4.16. Parameter estimates for bottlenose dolphins at Cygnet Bay, based on the best-fitting model of constant apparent survival, no temporary emigration and time-varying capture probability.

Parameter	Estimate	SE	LCI	UCI
φ	0.86	0.09	0.59	0.97
$\gamma'' = \gamma' = 0$ (fixed)	0.00	0.00	0.00	0.00
$p\ S_1\ t_1$	0.09	0.05	0.03	0.25
$p\ S_1\ t_2$	0.39	0.10	0.22	0.60
$p\ S_1\ t_3$	0.45	0.11	0.26	0.66
$p\ S_1\ t_4$	0.24	0.08	0.12	0.43
$p\ S_2\ t_1$	0.10	0.04	0.04	0.22
$p\ S_2\ t_2$	0.22	0.06	0.13	0.36
$p\ S_2\ t_3$	0.12	0.05	0.06	0.25
$p\ S_2\ t_4$	0.65	0.08	0.48	0.79
$p\ S_2\ t_5$	0.08	0.04	0.03	0.20
$p\ S_3\ t_1$	0.19	0.06	0.11	0.32
$p\ S_3\ t_2$	0.21	0.06	0.12	0.34
$p\ S_3\ t_3$	0.09	0.04	0.04	0.20
$p\ S_3\ t_4$	0.16	0.05	0.08	0.28
$p\ S_3\ t_5$	0.05	0.03	0.02	0.15
$p\ S_4\ t_1$	0.04	0.03	0.01	0.15
$p\ S_4\ t_2$	0.16	0.05	0.08	0.30
$p\ S_4\ t_3$	0.30	0.07	0.18	0.46
$p\ S_4\ t_4$	0.45	0.08	0.29	0.61
$p\ S_4\ t_5$	0.02	0.02	0.00	0.13
$\widehat{N}_D\ S_1$	33.37	4.92	23.73	43.01
$\widehat{N}_D\ S_2$	49.19	4.96	39.46	58.91
$\widehat{N}_D\ S_3$	57.23	10.38	36.87	77.58
$\widehat{N}_D\ S_4$	47.98	6.77	34.71	61.25

Estimates are derived from model $\varphi(.)\ \ \gamma''(.) = \gamma'(.) = 0\ \ p(t)$ listed in Table A2.4.13, with the exception of $\widehat{N}_D$ estimates which were derived from weighted model-averaging across all models in table A2.4.13. φ = apparent survival; $\gamma''\gamma'$ = temporary emigration parameters; $p\ S_i\ t_i$ = capture probability for transect t_i within sampling period S_i; $\widehat{N}_D\ S_i$ = estimated abundance of distinctive animals within sampling period i; SE = standard error; LCI and UCI = lower and upper 95% confidence intervals respectively.

Chapter 3. Population differentiation and hybridisation of Australian snubfin and Australian humpback dolphins in north-western Australia[1]

3.1 Abstract

Little is known about the Australian snubfin (*Orcaella heinsohni*) and humpback (*Sousa sahulensis*) dolphins ('snubfin' and 'humpback' dolphins, hereafter) of north-western Australia. While both species are listed as 'near threatened' by the IUCN, data deficiencies are impeding rigorous assessment of their conservation status across Australia. Understanding the genetic structure of populations, including levels of gene flow among populations, is important for the assessment of conservation status and the effective management of species. Using nuclear and mitochondrial DNA markers, population genetic diversity and differentiation was assessed between snubfin dolphins from Cygnet (n = 32) and Roebuck Bays (n = 25), and humpback dolphins from the Dampier Archipelago (n = 19) and the North West Cape (n = 18). All sampling locations were separated by geographic distances > 200 km. For each species, significant genetic differentiation between sampling locations was observed based on 12 (for snubfin dolphins) and 13 (for humpback dolphins) microsatellite loci (F_{ST} = 0.05-0.09; P < 0.001) and a 422 bp sequence of the mitochondrial control region (F_{ST} = 0.50-0.70; P < 0.001). The estimated proportion of migrants in a population ranged from 0.01 (95% CI 0.00-0.06) to 0.13 (0.03-0.24). These are the first estimates of genetic diversity and differentiation for snubfin and humpback dolphins in Western Australia, providing valuable information towards the assessment of their conservation status in this rapidly developing region. The results suggest that north-western Australian snubfin and humpback dolphins may exist as metapopulations of small, largely isolated population fragments, and should be managed accordingly. Management plans should seek to maintain effective population size and gene flow. Additionally, while interactions of a socio-sexual nature between these two species have been observed previously, this study provides strong evidence for the first documented case of hybridisation between a female snubfin dolphin and a male humpback dolphin.

[1] Chapter publication status: published 2014.

3.2 Introduction

Maintaining genetic diversity is a key objective of biodiversity conservation (McNeely et al. 1990). Species of conservation concern are often characterised by small, fragmented populations with restricted gene flow and low genetic diversity (Frankham 1995a, Spielman et al. 2004). Small and fragmented populations with severely restricted gene flow are more vulnerable to the accumulation of deleterious mutations, the loss of genetic diversity through random genetic drift, and inbreeding depression than single populations of the same effective population size (Frankham 1995b, Lynch et al. 1995, Keller and Waller 2002, Reed 2004). Additionally, further isolation and decline of fragmented populations within species may, through mate limitation, increase the probability of hybridisation with related, sympatric species (e.g. Lehman 1991, Willis et al. 2004). These processes may reduce the fitness of populations and impede their ability to adapt to environmental change, resulting in a reduced evolutionary potential and greater risk of extinction (Reed and Frankham 2003, O'Grady et al. 2006, Frankham et al. 2010). Understanding the genetic structure of populations, including levels of gene flow among populations and genetic diversity, is therefore important for the assessment of a species' conservation status, as well as the effective management of a species, particularly where anthropogenic activities may contribute to population fragmentation (Mace and Lande 1991).

Inshore dolphins occupying coastal and estuarine areas frequently overlap with areas of high human activity, exposing them to a variety of threats, including habitat loss and degradation, acoustic disturbance, vessel strikes, pollution and incidental capture in fisheries (Jefferson et al. 2009). These threats, combined with the late maturation, slow reproduction, often low abundance and restricted ranges of inshore dolphins, have resulted in priority conservation status being afforded to a number of geographically isolated populations (Rojas-Bracho et al. 2006, Reeves et al. 2008d, 2013a).

The Australian snubfin dolphin (*Orcaella heinsohni*, 'snubfin dolphin' hereafter) and Australian humpback dolphin (*Sousa sahulensis*, 'humpback dolphin' hereafter) occur in tropical coastal waters of northern Australia and southern New Guinea (Beasley et al. 2005, Jefferson and Rosenbaum 2014). At an international level, the conservation status of snubfin

and humpback dolphins was assessed as 'near threatened'[1] by the International Union for Conservation of Nature (IUCN), with caveats noting that additional data would likely result in an elevated status (Reeves et al. 2008b, 2008c). While both species receive protection under Australian national (the *Environment Protection and Biodiversity Conservation Act, 1999*) and Western Australian State (the *Wildlife Conservation Act 1950*) legislation, insufficient data exists for their conservation status to be rigorously assessed against threatened species listing criteria (Beasley et al. 2012, Bejder et al. 2012, Woinarski et al. 2014).

The distribution, abundance and population structure of snubfin and humpback dolphins are poorly understood throughout the majority of their ranges in Australian waters. Studies at a small number of sites on the east coast of Australia, primarily in waters adjacent to urban centres in Queensland, suggest that snubfin and humpback dolphins exhibit a discontinuous distribution of small populations of 50-100 animals (Corkeron et al. 1997, Parra et al. 2004, 2006a, Cagnazzi 2011, Cagnazzi et al. 2011, 2013b). These populations have relatively small ranges of approximately 200-350 km^2 and a preference for inshore habitats of waters < 15 m deep and within 5 km of the coast (Parra 2006, Parra et al. 2006b, Cagnazzi 2011). More recent studies in north-western Australia and the Northern Territory have revealed a similarly patchy distribution of small populations, although some larger populations of 100-200 animals have been recorded (Palmer et al. 2014, Brooks and Pollock 2015; Chapter 2).

Snubfin and humpback dolphins are sympatric throughout most of their distribution, which also overlaps that of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, 'bottlenose dolphin' hereafter). Where species are sympatric, inter-species associations and inter-species mating may facilitate hybridisation. This phenomenon has been reported between several cetacean species (review in Bérubé 2009, Schaurich et al. 2012), particularly among small cetaceans (Herzing and Johnson 1997, Willis et al. 2004, Acevedo-Gutiérrez et al. 2005, Miralles et al. 2013). To date, no hybrids have been confirmed between snubfin, humpback, or bottlenose dolphins. However, associations between snubfin and humpback dolphins have been reported at several locations along the Queensland coast (Parra 2005, Cagnazzi 2011). Associations have also been reported between humpback and bottlenose dolphins, and snubfin and bottlenose dolphins in north-western Australia (Bejder et al. 2012, Brown et al. 2012). In Cleveland Bay,

[1] The IUCN status assessment of 'near threatened' for humpback dolphins in Australia was prior to the description of *S. sahulensis* (Jefferson and Rosenbaum 2014), and therefore considered both *S. sahulensis* and *S. chinensis* as a single species (Reeves et al. 2008b). The status of *S. sahulensis* is currently being assessed.

Queensland, the majority (58%, n = 11) of snubfin-humpback dolphin associations were of an aggressive-sexual nature where, in all cases, humpback dolphins were identified as the aggressors (Parra 2005). Although the benefits and costs of these interactions are not fully understood, they suggest that inter-specific mating is possible.

Wild hybridisation is typically a conservation concern; when mediated by anthropogenic translocation of species and habitat modification, it has led to the extinction of many animal species and is particularly problematic for species of low abundance (Rhymer and Simberloff 1996, Allendorf et al. 2001). Several studies have reported hybridisation events among mammalian species within modified habitats and/or where populations have undergone a decline (Carr et al. 1986, Lehman 1991, Bérubé and Aguilar 1998). However, there is evidence that natural hybridisation may play an important role in the evolution of animals (e.g. Dowling and Secor 1997, Amaral et al. 2014), as has long been recognised for plants (Stebbins 1950).

Examining the structure of populations in the marine environment presents a particular challenge due to the absence of obvious barriers to gene flow, and the highly mobile nature of many marine species. Robust demographic and movement data are often costly and logistically difficult to acquire, while similar challenges exist for the identification of hybridisation through morphological data and observations of species interactions. To this end, molecular tools have been employed to address a variety of questions in mobile marine taxa of conservation and management importance, such as teleost fish (e.g. Knutsen et al. 2003, Mariani et al. 2005), elasmobranchs (e.g. Dudgeon et al. 2012), marine reptiles (e.g. Carreras et al. 2013, Dutton et al. 2013) and marine mammals (e.g. Garcia-Rodriguez et al. 1998, Rosenbaum et al. 2000, Hamner et al. 2012). In marine mammals, analyses of molecular markers have often contributed towards the identification of appropriate management units to inform decision-makers (LeDuc et al. 2002, Segura et al. 2006, Wiemann et al. 2010), including the identification of cryptic taxa and genetically-isolated populations of conservation concern (Pichler et al. 1998, Beasley et al. 2005, Natoli et al. 2005, Mirimin et al. 2011). Furthermore, molecular tools have permitted the investigation of hybridisation in the absence of other conclusive evidence (Willis et al. 2004, Miralles et al. 2013).

Molecular studies of snubfin and humpback dolphins are largely restricted to investigations of taxonomy (Beasley et al. 2005, Frère et al. 2011, Palmer et al. 2011, Mendez et al. 2013). The exception is Cagnazzi (2011), who examined genetic population structure based on

microsatellites of both species sampled at several locations along the Queensland coast. For snubfin dolphins, no structure was found between three populations within a 200 km stretch of coast, but significant differentiation was found between this region and a population approximately 600 km distant. The latter population, which numbers fewer than 100 individuals and is threatened by loss of habitat from port development, has been suggested as qualifying for 'endangered' status under IUCN Red List criteria for regional populations (Cagnazzi et al. 2013b). For humpback dolphins, significant genetic differentiation was detected between almost all putative populations, even when separated by only a few kilometres, such as in the Great Sandy Strait (Cagnazzi 2011).

The lack of information on the genetic population structure of snubfin and humpback dolphins is of particular concern in the north-west of Australia, where data deficiencies are coupled with a resources extraction boom, resulting in widespread and large-scale habitat modification of the inshore environment associated with port development (Allen et al. 2012, Bejder et al. 2012). The development of the coastal zone may introduce anthropogenic barriers to dispersal and cause fragmentation of inshore dolphin populations. However, in the absence of any understanding of the genetic diversity or connectivity between populations, the likelihood or significance of these potential effects on inshore dolphins remains unknown. Information on the genetic population structure of these species in this region is essential to determining an appropriate management scale at which to assess potential anthropogenic effects and inform conservation strategies.

In this study, mitochondrial DNA (mtDNA) sequence data and nuclear microsatellite markers were used to examine the genetic diversity and structure of snubfin and humpback dolphins among a limited number of study sites in north-western Australia. In addition to population structure, the possible existence of hybrid dolphins across the study area was also investigated.

3.3 Materials and Methods

3.3.1 Study sites and sample collection

A total of 110 skin tissue samples were obtained from free-ranging dolphins across north-western Australia between 2008 and 2013 using a biopsy darting system from small research vessels (Krützen et al. 2002). Snubfin dolphin samples were obtained from Cygnet Bay and Roebuck Bay, and humpback dolphin samples were obtained from Cygnet Bay, the Dampier

Archipelago and the North West Cape (Fig. 3.1). To assist in identifying the parental species of a suspected hybrid, I also collected biopsy samples from Indo-Pacific bottlenose dolphins from Cygnet Bay, so as to include all three dolphin species regularly encountered in Cygnet Bay into these analyses. Tissue samples were stored in either 100% ethanol or saturated NaCl/20% dimethyl sulfoxide (Amos and Hoelzel 1991). Sampled sites represent those accessible by small research vessel and where snubfin or humpback dolphins were sufficiently approachable to distances suitable for successfully obtaining biopsy samples. Samples were primarily collected on an opportunistic basis during another research project on bottlenose dolphin (*Tursiops* spp.) population structure across north-western Australia (see Allen et al. 2012), and also in parallel to demographic and behavioural studies of snubfin and humpback dolphins at these locations (Chapters 2 and 4).

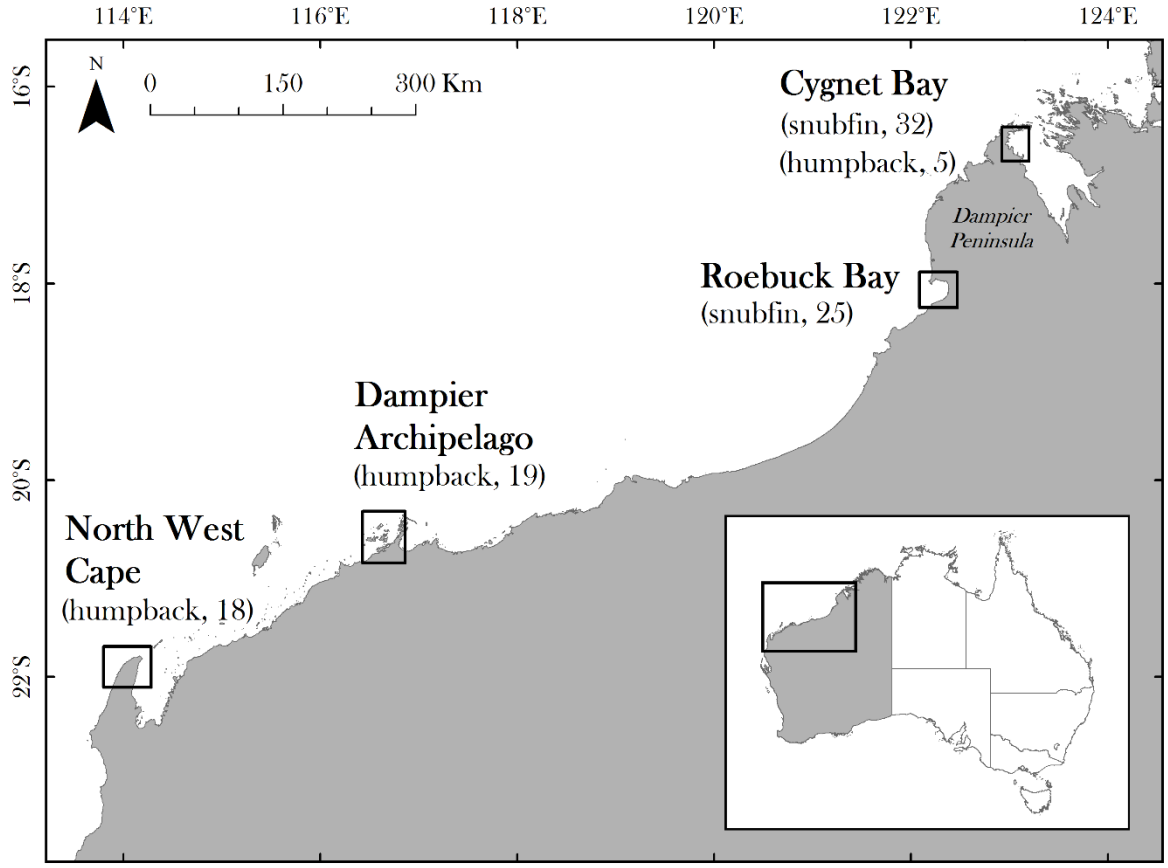


Figure 3.1. Biopsy sampling locations and sample sizes of Australian snubfin and humpback dolphins in north-western Australia.

3.3.2 Genetic analyses

Genomic DNA was extracted using the DNeasy Blood & Tissue Kit (Qiagen) following the manufacturer's instructions. Sex was determined genetically using sex chromosome-specific

primers. Loci ZFX and SRY (Gilson et al. 1998) were coamplified in a single PCR reaction. PCR products were run on a 1.5 % agarose gel and sex determined based on the number of different fragments amplified.

Mitochondrial DNA (mtDNA) haplotypes were assigned based on a 422 base pair (bp) sequence. The fragment was amplified by the primers dlp1.5 and dlp5 (Baker et al. 1993). The PCR conditions described in Bacher et al. (2010) were followed. Haplotypes were assigned with the software Geneious R6.1 (Biomatters).

Fourteen microsatellite loci were amplified in four 10 µl volume multiplex PCRs using Qiagen Multiplex Kit^{TM} (Qiagen). The microsatellite markers used were: DIrFCB1, DIrFCB4 (Buchanan et al. 1996), LobsDi_7.1, LobsDi_9, LobsDi_19, LobsDi_21, LobsDi_24, LobsDi_39 (Cassens et al. 2005), SCA9, SCA22, SCA27 SCA39 (Chen and Yang 2009), TexVet5, TexVet7 (Rooney et al. 1999). The PCR conditions as described in Frère et al. (2010c) were followed. The single stranded PCR products were run on an ABI 3730 DNA Sequencer (Applied Biosystems). Alleles were scored with Genemapper Software 3.7 (Applied Biosystems). Duplicate samples, i.e. samples that were genotyped for at least 10 microsatellite loci and matched 95%, were identified using the Microsatellite Toolkit (Park 2001) and, from these, the sample with the most complete genotype was retained. Microsatellites were checked for Hardy-Weinberg equilibrium and linkage disequilibrium in GenePop (Rousset 2008).

Several measures of population differentiation were calculated for the sampled study sites. The suspected hybrid and the bottlenose dolphins were excluded from all analyses comparing population structure and diversity within snubfin and humpback dolphins. F_{ST} values (for microsatellites and mtDNA) and Φ_{ST} values (for mtDNA) were calculated in Arlequin (Excoffier et al. 2005).

Contemporary migration rates were calculated in BayesAss 1.3 (Wilson and Rannala 2003) using 10^7 iterations, a burn-in length of 10^6 and a sampling interval of 1,000 steps. Three runs per species with different seeds were performed to confirm that similar mean posterior migration rates and 95% confidence intervals were obtained. An admixture model without information on sampling location was run in STRUCTURE [version 2.2.3 (Pritchard et al. 2000, Falush et al. 2003)] to examine differentiation patterns between populations, with a burn-in length of 10^5 and 10^6 Markov chain Monte Carlo (MCMC) steps. The most likely number of

genetically homogeneous clusters (if greater than two) was determined based on 10 iterations for each population (k) = 1-4 by calculating Δk, an ad hoc statistic proposed by Evanno et al. (2005). Δk was calculated in STRUCTURE HARVESTER [Web v0.6.93 (Earl and von Holdt 2012)]. Results from STRUCTURE were also compared to those of the recently published software FLOCK [FLOCK_MSAT 3.0 (Duchesne and Turgeon 2012)] using default parameters. Compared to the MCMC-based STRUCTURE, FLOCK uses an iterative method, which makes it faster and computationally more efficient.

Effective population (N_e) sizes were calculated for snubfin dolphins based on the linkage-disequilibrium (LD) method using LNDe v1.31 (Waples and Do 2008). For small effective population sizes of <500, the LD method has been shown to be reliable with the use of 10-20 microsatellite loci and samples of 25-50 individuals (Waples and Do 2010). Due to small sample sizes (< 25 samples per population), I did not calculate N_e for humpback dolphins.

An underlying assumption of the LD method of estimating N_e is non-overlapping generations. This assumption is violated within the long-lived, polygamous populations examined here, and may lead to a downward bias in estimates of N_e (Palstra and Ruzzante 2008, Waples and Do 2010, Robinson and Moyer 2013). Despite this, Robinson & Moyer (2013) showed that, for populations with small N_e, the LD method performed relatively well for species with overlapping generations under a variety of life history scenarios and sampling strategies. Random sampling of mature individuals, as was the case in the current study, has been shown to produce the best estimates of N_e by LD (Robinson and Moyer 2013). The lowest allele frequency considered in the analyses was set to 0.03 to ensure that single copy alleles were filtered out; N_e estimates were correspondingly corrected for downward bias by multiplying the estimate by 1.25 (Waples and Do 2010, Ansmann et al. 2013). Due to the paucity of information on snubfin dolphin life history traits, I used a correction factor suggested for bottlenose dolphins (Ansmann et al. 2013).

To test whether any population had recently undergone a bottleneck, a graphical method was used to detect allele frequency distortion, where a mode-shift away from the lowest allele frequency class is indicative of a recently bottlenecked population (Luikart et al. 1998). Tests for recent bottlenecks were also performed using the software BOTTLENECK [v1.2.02 (Piry et al. 1996)]. A total of 1,000 iterations were specified and Wilcoxon sign rank tests were used to assess significance. BOTTLENECK v1.2.02 provides results for three models of the

generation of new alleles; the stepwise mutation model (SMM), the infinite allele model (IAM) and the two-phased model of mutation (TPM). In the software manual, the authors recommend the use of TPM for microsatellite datasets; in their paper (Cornuet and Luikart 1996), by contrast, IAM is recommended for microsatellites with fewer than 3 bp repeats.

3.3.3 Hybrid investigation

In Cygnet Bay, a dolphin was encountered that, phenotypically, could not be identified as a humpback, snubfin or bottlenose dolphin. All three of these species are regularly encountered within Cygnet Bay. To confirm hybrid status and to identify the suspected hybrid's parental species, the suspected hybrid's mtDNA haplotype was compared to those of humpback, snubfin and bottlenose dolphins. Additionally, the microsatellite genotype of the suspected hybrid was compared to alleles found in the three dolphin species at Cygnet Bay. This permitted the parental species of the suspected hybrid to be assigned based on species-specific alleles. Furthermore, STRUCTURE was used to obtain a measure of likelihood to which species the suspected hybrid belongs. All samples collected at Cygnet Bay were included in the STRUCTURE analysis using the same parameters as above.

Microsatellite genotypes used in this study are available in the supplementary material and mtDNA haplotype sequences have been archived on GenBank (Accession numbers KJ530719-KJ530740).

3.4 Results

3.4.1 Population differentiation

After having removed duplicate samples, analyses were conducted on the following populations and sample sizes: snubfin dolphins from Cygnet Bay (n = 32) and Roebuck Bay (n = 25), and humpback dolphins from Cygnet Bay (n = 5), the Dampier Archipelago (n = 19) and the North West Cape (n = 18) (Fig. 3.1). No $F_{ST,}$ Φ_{ST} or contemporary migration rate values for humpback dolphins from Cygnet Bay are presented due to the small sample size. Additionally, one sample of a suspected hybrid and six samples from bottlenose dolphins were collected from Cygnet Bay.

Twelve of the 14 genotyped microsatellite loci were polymorphic in snubfin dolphins and 13 microsatellite loci were polymorphic in humpback dolphins (Table 3.1, Table A3.4). On

average, 95% of loci were genotyped per individual. For both species, none of the microsatellite loci appeared out of Hardy-Weinberg Equilibrium after sequential Bonferroni correction (Rice 1989b), nor linked after sequential Bonferroni correction. Six mtDNA haplotypes were found each in snubfin and humpback dolphins (Fig. 3.2). Within species, all population pairs were significantly differentiated based on microsatellites (F_{ST} = 0.05-0.09) and mtDNA loci (F_{ST} = 0.50-0.70, Φ_{ST} = 0.17-0.45) (Table 3.2). STRUCTURE assigned most individuals sampled at the same location to the same cluster (Fig, 3.3A-3.3C). For snubfin dolphins, Δk analysis and FLOCK showed that the most likely k was ≤ 2 (Fig. A3.1). For humpback dolphins, the most likely number of k was four based on STRUCTURE (Fig. A3.1), and three based on FLOCK. Three equals the number of sampled populations.

Contemporary migration rates (i.e. within the last few generations) revealed an estimated proportion of 0.04 (95% CI 0.01-0.10) of snubfin dolphins in Cygnet Bay derived from Roebuck Bay and 0.03 (0.00-0.08) of Roebuck Bay individuals derived from Cygnet Bay. For humpback dolphins, I estimated a proportion of 0.01 (0.00-0.06) individuals from the Dampier Archipelago derived from the North West Cape and 0.13 (0.03-0.24) of North West Cape individuals derived from the Dampier Archipelago.

Table 3.1. Microsatellite characteristics for snubfin and humpback dolphins.

	N_A	N_E	F_{IS}	H_E	H_O
Snubfin dolphins					
Cygnet Bay	4.25	2.65	0.00	0.57	0.58
Roebuck Bay	4.25	2.88	-0.01	0.58	0.60
Humpback dolphins					
Dampier Archipelago	3.73	2.09	-0.07	0.44	0.46
North West Cape	3.58	2.16	0.06	0.40	0.35

N_A = Number of Alleles, N_E = Number of effective Alleles, F_{IS} = Inbreeding Coefficient, H_E = expected heterozygosity, H_O = observed heterozygosity. Numbers are averages over polymorphic loci. See Tables A1 and A2 for locus specific microsatellite characteristics.

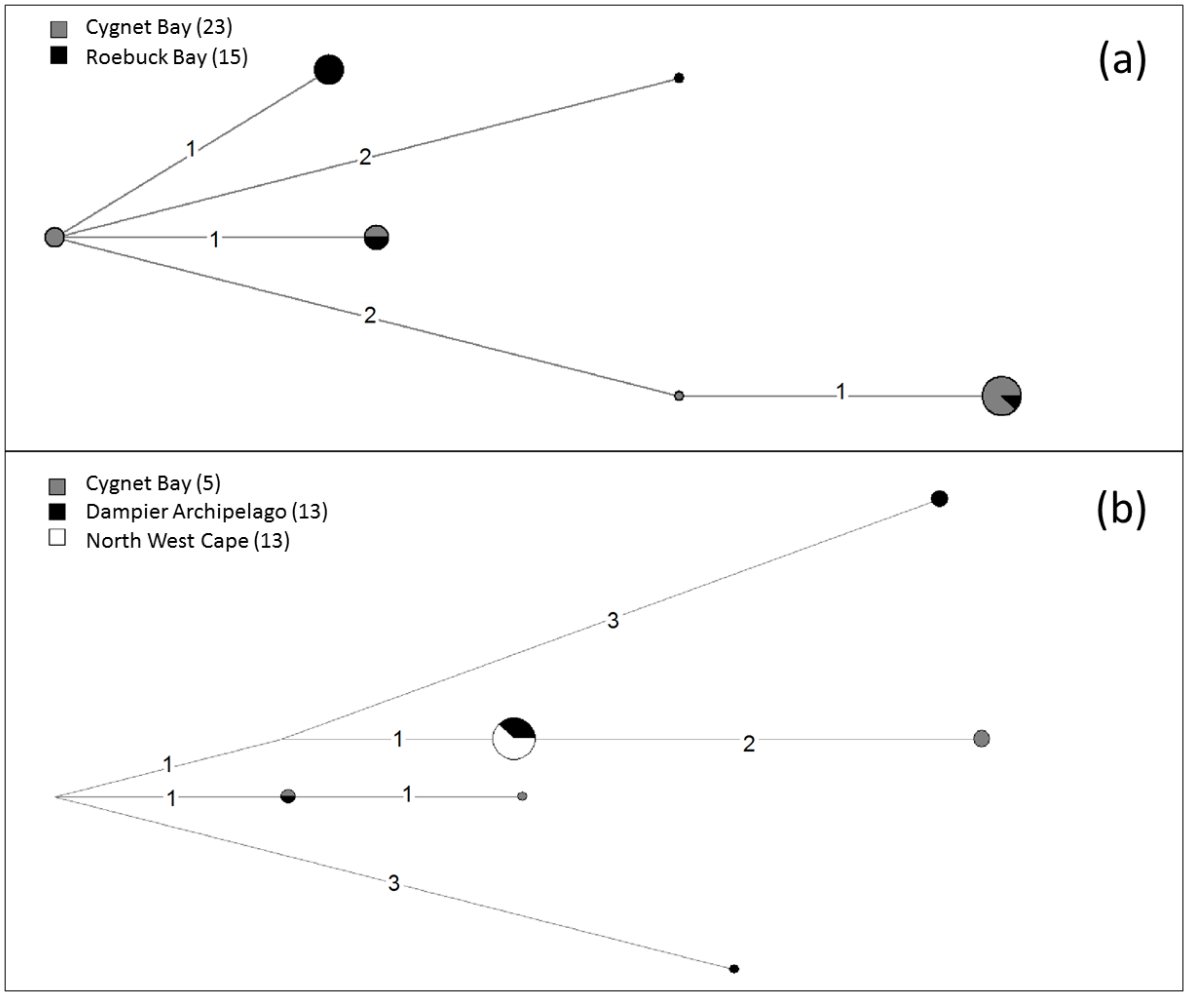


Figure 3.2. mtDNA networks for (a) snubfin and (b) humpback dolphins. Sample sizes are shown in parentheses. Branch numbers indicate the number of nucleotide differences between mtDNA haplotypes.

Table 3.2. Genetic differentiation of mtDNA and microsatellite loci for snubfin and humpback dolphins.

	Measure of differentiation	**mtDNA**	**microsatellites**
Snubfin dolphins (CY-RB)	F_{ST}	0.500**	0.091**
	Φ_{ST}	0.446**	na
Humpback dolphins (DA-NWC)	F_{ST}	0.699**	0.046**
	Φ_{ST}	0.167*	na

Asterisks indicate *P* values (* $P < 0.05$, ** $P < 0.001$). CY = Cygnet Bay, RB = Roebuck Bay, DA = Dampier Archipelago, NWC = North West Cape. For the mtDNA based estimates, a lower sample size was used for both species; 15 samples from RB, 23 samples from CY, and 13 samples each from DA and NWC.

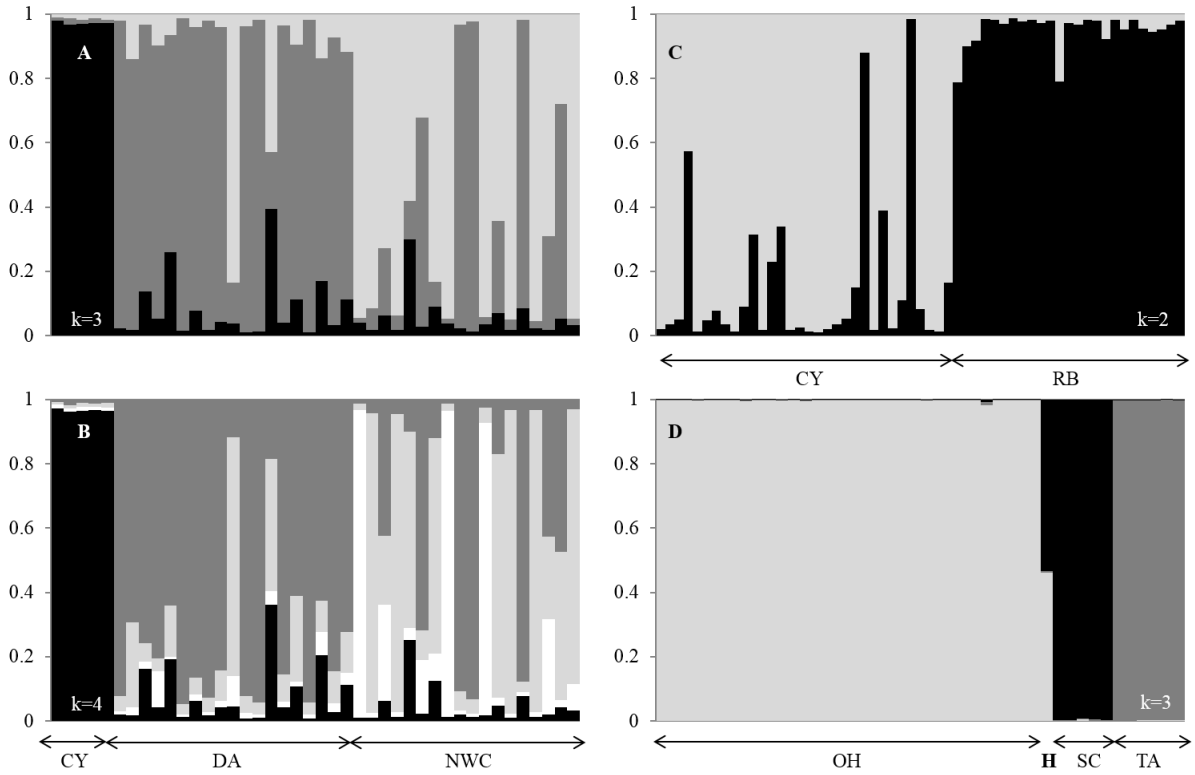


Figure 3.3. Structure plots for humpback dolphins where (A) k = 3 and (B) k = 4, for (C) snubfin dolphins, and (D) the three regularly encountered dolphin species at Cygnet Bay. k = number of clusters. Each bar on the x-axis corresponds to an individual. The y-axis indicates the proportion of population/species membership. CY = Cygnet Bay, DA = Dampier Archipelago, NWC = North West Cape, RB = Roebuck Bay, OH = snubfin dolphins, SC = humpback dolphins, TA = bottlenose dolphins, H = suspected hybrid.

3.4.2 Effective population size and evidence of bottlenecks

For snubfin dolphins, N_e (95% CI) was estimated to be 49.1 (28.6-112.1) for Cygnet Bay and 56.0 (24.3-77,180.6) for Roebuck Bay. The wide confidence intervals are revisited in the discussion. Conflicting results were obtained on recent bottlenecks depending on the method used (see Table A3.3 for *P* values and Fig. A3.3 for visualisations of potential mode shifts).

3.4.3 Suspected hybrid

The Cygnet Bay individual that could not be visually assigned to species level exhibited a length, girth and light grey colouration typical of adult humpback dolphins in the region. The low, triangular dorsal fin was also indicative of a humpback dolphin, although the position of the dorsal fin was posterior to the mid-point of the body, as in a snubfin dolphin. The surfacing movement was comparable to that of a snubfin dolphin, tilting back the head to breathe, with faint neck creases visible (although without the prominent sunken post-cranial region of a

snubfin dolphin). A short rostrum was visible, being noticeably shorter than that of a bottlenose dolphin and far shorter than that of a humpback dolphin (Fig. 3.4).

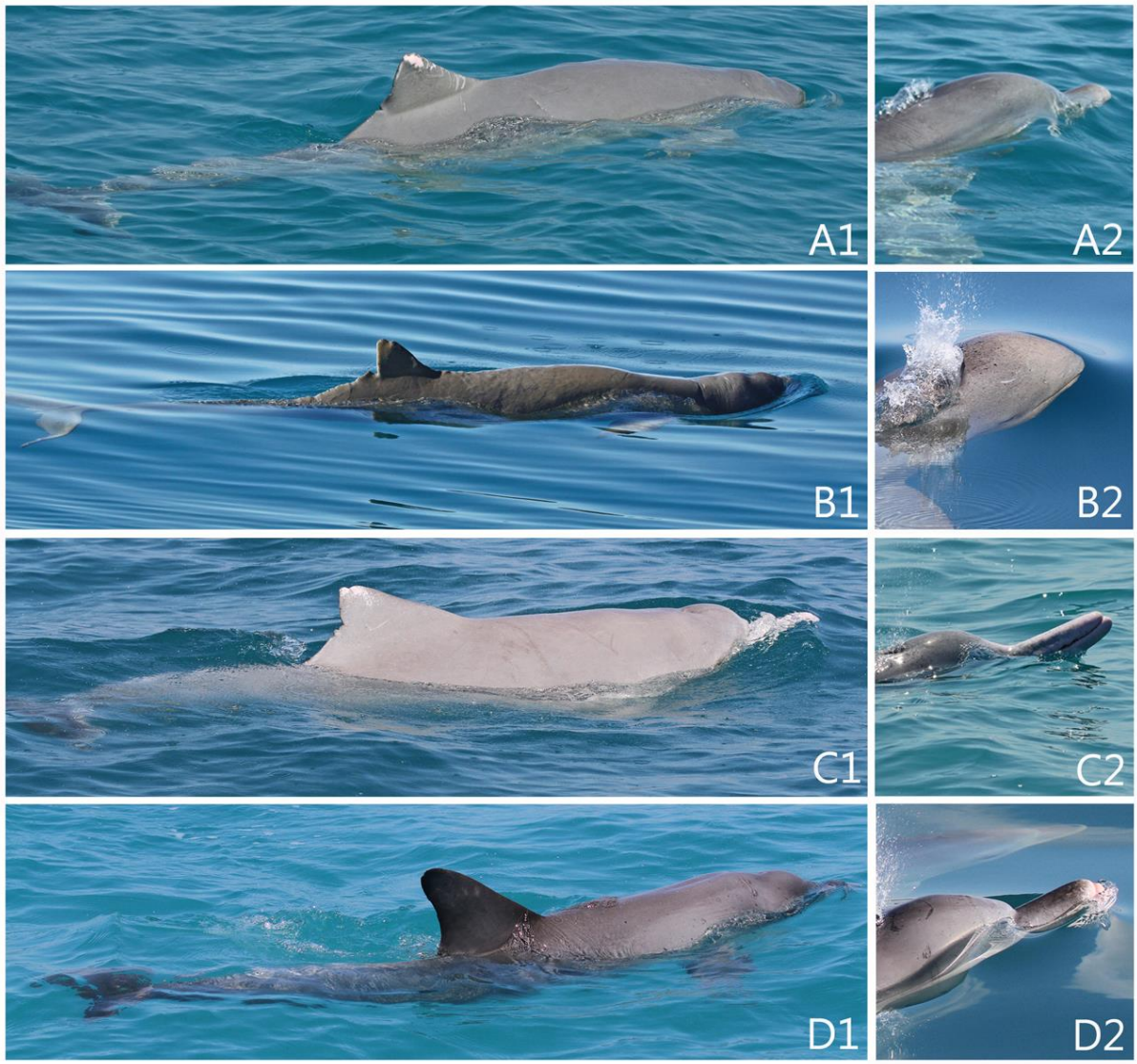


Figure 3.4. Images of hybrid (A1-2), adult snubfin (B1-2), humpback (C1-2) and bottlenose (D1-2) dolphins encountered at Cygnet Bay. Left images show relative dorsal proportions; right images compare head/rostrum characteristics.

Over four × one month seasons of photo-identification and biopsy sampling surveys at Cygnet Bay from 2012-2013, the suspected hybrid was observed 22 times on 17 different days (Brown et al., unpublished data). Over these observations, a total of eight hours were spent in the presence of the suspected hybrid; 23% of the time the animal was alone (defined as > 100 m from any other individual) and 77% in close (< 10 m) association with one or more snubfin dolphins. Only two brief close associations with humpback and bottlenose dolphins were recorded; in both encounters the suspected hybrid was also in close association with one or

more snubfin dolphins. The majority of associations with snubfin dolphins were small groups (< 5 individuals) with female individuals (confirmed through genetics or presence of dependent calf) (Chapter 5).

Genetic analyses revealed that the individual was a female and supported its status as a hybrid. The comparison of the hybrid's genotype to alleles found in the three resident dolphin species within Cygnet Bay indicated the majority of alleles (84.4%) found were species-specific. The hybrid shares at least one allele of each microsatellite locus with snubfin dolphins and at least one allele of each microsatellite locus for 11 out of the 14 loci with humpback dolphins (Table 3.3). At one locus, the hybrid is homozygote and this allele is only shared with snubfin dolphins. At five loci, the hybrid shares an allele with bottlenose dolphins, however, only one of them has not been found in either snubfin or humpback dolphins (Table 3.3).

STRUCTURE analyses including snubfin, humpback and bottlenose dolphins from Cygnet Bay estimated that the sample originated to 53.4 ± 0.05% (mean of 10 iterations ± SD, k = 3) from a snubfin dolphin, to 46.2 ± 0.05% from a humpback dolphin and to 0.4 ± 0.00% from a bottlenose dolphin (as indicated by the proportion of shading in individual bars in Fig. 3.3D). The mtDNA haplotype of the suspected hybrid matched a haplotype found in snubfin dolphins (Fig. A3.4), suggesting that she most likely had a snubfin dolphin mother. The STRUCTURE results and allele comparisons suggest a humpback dolphin father.

From all samples included in this study, other than the hybrid, only one other, a male snubfin dolphin from Roebuck Bay, showed some signs of mixed species ancestry. Images of this individual suggest a normal snubfin dolphin phenotype. STRUCTURE assigned this individual by 16.7% (10 iterations, SD = 0.00) to humpback dolphin (Fig. A3.2) and 83.1% (0.00) to snubfin dolphin. This is suggestive of post-F1 hybrid status, although the small number of microsatellite markers used in this study restricts the interpretation of such results.

Table 3.3. Alleles shared by the suspected hybrid and the three regularly present dolphin species (snubfin, humpback and bottlenose) at Cygnet Bay.

	Allele 1			Allele 2				
Locus	**OH**	**SC**	**TA**	**OH**	**SC**	**TA**	**Hybrid homozygote**	**Support of hybrid hypothesis? If not, what are potential explanations?**
DIrFCB4	y				y			y
DIrFCB5	y				y			y
Lobs7.1	y				y			y
LobsDi9	y			y			y	n; null allele or allele might not have been sampled in SC due to small sample size or rare allele
LobsDi19	y				y			y
LobsDi21	y		y		y			y
LobsDi24	y			y				n; allele 1 or allele 2 might not have been sampled in SC due to small sample size or rare allele
LobsDi39	y				y	y		y
SCA9	y				y			y
SCA22	y	y	y			y		n; allele 2 might not have been sampled in SC and/or OH due to small sample size, or rare allele
SCA27	y		y		y			y
SCA39	y		y		y	y		y
Tex5	y	y		y	y		y	y
Tex7	y				y			y

OH = snubfin dolphin, SC = humpback dolphin, TA = bottlenose dolphin, y = yes, n = no

3.5 Discussion

3.5.1 Population differentiation

Snubfin and humpback dolphins showed significant levels of population structure at both the mitochondrial and microsatellite DNA level between the sampling locations. Significant F_{ST} and Φ_{ST} values for snubfin dolphins between Roebuck Bay and Cygnet Bay provide genetic evidence for the presence of discrete populations with limited gene flow. The two populations shared two out of six mtDNA haplotypes and 15 private microsatellite alleles were detected (Table A3.1). Within each of these sampling locations, STRUCTURE assigned most snubfin individuals to the same cluster. However, three individuals (9%) at Cygnet Bay were

predominately assigned to the Roebuck Bay cluster, suggesting that they were Roebuck Bay migrants or of migrant ancestry (Fig. 3.3C).

Humpback dolphins from the Dampier Archipelago and the North West Cape also exhibit significant population structure with limited gene flow. Significant F_{ST} and Φ_{ST} values were obtained between two sampling locations, and the results of STRUCTURE and FLOCK assigned the majority of animals at these two locations to separate clusters. However, there was some evidence of movement of individuals between sites, particularly from the Dampier Archipelago to the North West Cape, the latter of which included five individuals (26%) predominately assigned to the dominant cluster at the Dampier Archipelago (Fig. 3.3A). Humpback dolphins occur along a further 400 + km of coastline south of the North West Cape (Allen et al. 2012). The results of STRUCTURE at k = 4 further illustrate admixture within North West Cape humpback dolphins and suggest the existence of a potential fourth, not yet sampled, humpback population, possibly to the south of the North West Cape. The sample size for humpback dolphins from Cygnet Bay (n = 5) was too small to calculate meaningful F_{ST} and Φ_{ST} values with samples from the other two locations. However, Cygnet Bay humpback dolphins appear to be genetically differentiated from the other two sampling locations, based on the strong partitioning in the STRUCTURE results. Based on all three sampling sites, two out of six mtDNA haplotypes were shared among dolphins from two out of three different sampling locations, and there were 16 private microsatellite alleles detected (Table A3.2).

For both species, most contemporary migration rates were low, with estimated proportions of migrants ≤ 0.04 between sites. Confidence intervals around these estimates were wide, owing to the relatively small sample sizes. However, for most sites, the upper confidence interval of the proportion of migrants was ≤ 0.1. The exception was migration rates of humpback dolphins from the Dampier Archipelago to the North West Cape, which were slightly higher at 0.13 (95% CI 0.03-0.24) – a result supported by the greater admixture of humpback dolphins at the North West Cape revealed by STRUCTURE. Confidence in this apparent directionality of gene flow for humpback dolphins between the Dampier Archipelago and the North West Cape is limited by largely overlapping confidence intervals between the two estimates of migration rates. A greater number of samples is required to further investigate the potential source-sink pattern of population structure (e.g. Andreasen et al. 2012).

Demographic data, while of limited temporal extent, support the findings of population differentiation for snubfin dolphins in this study. Photo-identification studies conducted over two years at Cygnet Bay suggests the population of approximately 50 snubfin dolphins to be resident to this site (Chapter 2, Chapter 5). There is also some evidence of site-fidelity of snubfin dolphins to Roebuck Bay; photo-identification data showed a majority of individuals to be present in both 2013 and 2014 study periods (Chapter 2). Additionally, photo-identification data have not revealed any movement of snubfin dolphin individuals between Cygnet Bay and Roebuck Bay to date (Chapter 2). Studies on snubfin and humpback dolphins from the east coast of Australia have revealed either a majority of individuals regularly using the same discrete area from year to year (Parra et al. 2006a), or strong site fidelity within resident populations (Cagnazzi et al. 2011, 2013b). These patterns of site fidelity support my finding of genetic structuring of snubfin and humpback dolphins of north-western Australia.

In the current study, it is acknowledged that distances between sampling locations were large (> 200 km) and, therefore, it cannot be ruled out that a pattern of isolation-by-distance could explain the significant genetic structuring. However, it is not possible to test for isolation-by distance based on only two sampling locations for each species. Despite the limitations of these data, there are several lines of evidence to support that snubfin dolphins at Cygnet Bay and Roebuck Bay represent neighbouring populations, and that the observed genetic differentiation is not an artefact of sampling two locations at the extreme ends of a continuous distribution of more connected population fragments. Firstly, no snubfin dolphins were observed during exploratory survey effort around the northern section of the Dampier Peninsula (to the north and west of Cygnet Bay; see Fig. 3.1) (Brown, unpublished data; S. Allen, Murdoch University, pers. com.). Secondly, two separate months of survey effort between the two sampling locations across c. 30 km of coastline around Beagle Bay, representing a range of habitats, recorded only two sightings of two snubfin dolphin individuals (Brown et al. 2016; Chapter 2). Lastly, limited survey effort and discussions with recreational fishers, aquaculture operators and land owners suggest that sightings of snubfin dolphins on the west side of the Dampier Peninsula, between the two sampling locations, are restricted to occasional sightings of single individuals and small groups (Brown, unpublished data; S. Allen, Murdoch University, pers. comm.).

While acknowledging differences in distances between studies, my results support the conclusions of Cagnazzi (2011) for humpback dolphins along the east coast of Queensland. In his study, Cagnazzi (2011) found significant genetic differentiation between populations

separated by *ca*. 200 km, but also between populations separated by only a few kilometres, where a bathymetric feature (area of shallow water with narrow channel) was suggested to provide a barrier to dispersal. In contrast to the current results and those of Cagnazzi (2011), a study in Chinese waters of the related species, Indo-Pacific humpback dolphins (*Sousa chinensis*), found no evidence of population structure among three resident populations, each separated by approximately 500 km of coastline (Lin et al. 2012). Potentially suitable habitat (river mouths) is distributed along much of the coastline (Chen et al. 2008), and a maximum dispersal distance of 300 km has been recorded for an individual in this region (Jefferson and Hung 2004). This suggests that a stepping-stone pattern of gene flow may be occurring, to a level sufficient to prevent differentiation. It was also suggested that gene flow might be of a recently interrupted form, where insufficient time has passed for detectable differentiation to develop (Lin et al. 2012).

Humpback dolphins have been observed in areas between the sampling locations of this study (Allen et al. 2012), although their distribution along the north-western Australian coast remains poorly understood. Individual movements of up to 130 km have been recorded off the east coast of Australia (Cagnazzi 2011). No obvious natural geographic barriers to dispersal exist along the 350 km of coastline between the Dampier Archipelago and North West Cape, so the significant genetic differentiation found between animals at these two locations may be a result of their geographic separation exceeding individual dispersal distances. Further evidence for limited dispersal among humpback dolphins, which may contribute to population differentiation, is provided by observations of site fidelity from photo-identification studies. Site fidelity across multiple years has been reported among several populations of humpback dolphins on the east coast of Australia (Parra et al. 2006a, Cagnazzi 2011, Cagnazzi et al. 2011), and, more recently, at the North West Cape (T. Hunt, Flinders University, pers. comm.).

The identification of genetic population structure in snubfin dolphins on the Queensland coast by Cagnazzi (2011) was somewhat restricted by the distribution of sampling locations. No structure was found between three relatively close populations (within a 200 km stretch of coast), although significant differentiation was found at a much greater separation of approximately 600 km. Cygnet Bay and Roebuck Bay are separated by approximately 250 km of coastline. Based on our current understanding of the habitat requirements of snubfin dolphins (Parra et al. 2006b), no obvious barriers to dispersal exist between the two sites: the coastline is currently undeveloped and shallow inshore waters are present throughout. Recorded sightings

between the two sites are largely restricted to reports of small groups immediately north of Roebuck Bay (Allen et al. 2012), in addition to the sighting of just two snubfin individuals over two months of dedicated boat survey effort along a 30 km stretch of coast approximately equidistant between Cygnet and Roebuck Bays (Chapter 2). The maximum reported distance travelled by an individual snubfin dolphin is 70 km (Cagnazzi 2011), suggesting that the geographic distance between Cygnet Bay and Roebuck Bay is likely a key driver of the restricted gene flow documented here.

Interestingly, a recent study on bottlenose dolphins also found significant genetic differentiation between animals sampled at Cygnet Bay and populations only 130 km further west (Allen 2015). In his study, Allen (2015) noted that habitat immediately north of Cygnet Bay, characterised by narrow channels with very strong tidal currents, may represent a barrier to dispersal. While barriers to dispersal are rarely obvious in marine habitats, significant genetic structure over relatively small spatial scales has been observed in numerous species of coastal dolphins - e.g. *Tursiops* spp. (Krützen et al. 2004, Sellas et al. 2005, Rosel et al. 2009, Ansmann et al. 2012b); *Cephalorhynchus hectori* spp. (Hamner et al. 2012); *Sotalia guianesis* (Hollatz et al. 2011). For bottlenose dolphins (*Tursiops* spp.), a range of environmental, habitat and resource specialisation, and social factors have been suggested as drivers of fine-scale population structure (e.g. Bilgmann et al. 2007, Möller et al. 2007, Rosel et al. 2009, Wiszniewski et al. 2009b, Ansmann et al. 2012b, Kopps et al. 2014). Future studies of the population genetic structure of snubfin and humpback dolphins, which incorporate a larger number and geographic spread of samples, could seek to investigate patterns of isolation-by-distance and the possible isolating influence of eco-geographical features (e.g. Fontaine et al. 2007, Mendez et al. 2010).

3.5.2 Effective population size and evidence of bottlenecks

For successful conservation strategies, it can be important to have an understanding of the effective population size (N_e), which provides an indicator of the number of individuals contributing genes to the next generation (Wright 1969). The effective population size is usually lower than the census size and, by definition, describes the rate of inbreeding accumulation and loss of genetic diversity (Robinson and Moyer 2013). A rule of thumb suggests that N_e should not fall below 50 in the short-term and should be above 500 in the long-term (Franklin 1980). Mace & Lande (1991) suggest that, subject to additional criteria (e.g. population decline), a population of $N_e < 50$ should be considered in a critical state (i.e. 50% probability of extinction

within five years or two generations). I found that N_e estimates are close to this theoretical lower limit for snubfin dolphins at Cygnet Bay (N_e = 49.1, 95% CI 28.6-112.1) and Roebuck Bay (56.0, 95% CI 24.3-77,180.6), potentially raising conservation concerns. While confidence intervals are wide, the N_e estimate for Cygnet Bay is very similar to the current abundance estimate of c. 50 derived from photo-identification data (Chapter 2). The very wide confidence intervals for Roebuck Bay indicate considerable uncertainty in the estimate of N_e, most likely due to the small sample size (n = 25 individuals) providing insufficient data upon which to produce an informative estimate of N_e. For both populations, a greater number of samples are required to accurately estimate N_e.

The results on recent bottlenecks are ambiguous for the four sampling sites investigated. Depending on the mutation model, significant and non-significant results were obtained for each site. The graphical allele frequency distortion method indicated a mode shift of humpback dolphins at the North West Cape. The presence of a recent bottleneck is supported by a low mtDNA diversity (one haplotype) identified at this sampling location. However, under the two-phased model of mutation there was no indication for a recent bottleneck at the North West Cape. The results of these assessments of recent bottlenecks should be interpreted with caution due to ambiguity and large confidence intervals.

3.5.3 Hybridisation

There was strong genetic evidence that the suspected hybrid found at Cygnet Bay is the offspring of a snubfin dolphin mother and a humpback dolphin father. While alleles at three microsatellite loci (Table 3.3) were not shared between the hybrid and humpback dolphins, it is most likely that these alleles also exist in humpback dolphins, but have not been sampled as yet due to the small sample size from this species at Cygnet Bay (n = 5). The absence of these alleles within these samples could also be due to the presence of null alleles, in particular, for the locus LobsDi9 (Table 3.3).

This is the first documented case of hybridisation between snubfin and humpback dolphins. The hybrid is a female, seemingly fully grown and in good body condition, which associates primarily with snubfin dolphins – her maternal species. Despite a predominance of male sterility among mammalian hybrids (see Wu et al. 1996), there are several examples of fertility among female cetacean hybrids, e.g. within the Genus *Phocoena* (Willis et al. 2004); *Balaenoptera* (Spilliaert et al. 1991, Glover et al. 2013); and *Pseudorca* × *Tursiops* (Schaurich et al. 2012),

and one record of fertility of a male hybrid of the *Globicephala* genus (Miralles et al. 2013). In the absence of any evidence of the reproductive history of the snubfin-humpback hybrid identified here, no assessment of her fertility can be made at this stage.

Snubfin and humpback dolphins are sympatric across much of their range, occasionally form mixed groups, and aggressive-sexual inter-specific interactions have been documented (Parra 2005). Snubfin-humpback dolphin associations within Cygnet Bay appear to be uncommon and typically affiliative, although one observation of repeated mating attempts by a male humpback dolphin with a female snubfin has been observed. Frequent hybridisation has been documented between Dall's (*Phocoena dalli*) and harbour (*P. phocoena*) porpoises in a localised area of the northeast Pacific (Willis et al. 2004). In all hybrids examined, Willis *et al*. (2004) revealed Dall's porpoise to be the maternal species, and suggested that the highly promiscuous male harbour porpoise's indiscriminate pursuit of females of either species could be a driving factor of this hybridisation. In this region, the harbour porpoise is the rarer species, having apparently declined in recent decades (Baird 2003). Humpback dolphins, identified as the paternal species of the hybrid in the current study, are the least numerous of the three dolphin species within Cygnet Bay (Chapter 2). I hypothesise that the observed propensity of humpback dolphins to initiate aggressive-sexual interactions with snubfin dolphins (Parra 2005), along with a low availability of conspecific potential mates at the Cygnet Bay study site, are potential drivers of the hybrid dolphin reported here.

This discovery of a snubfin-humpback dolphin hybrid shows that these two sympatric species are capable of inter-generic hybridisation. There are no indications that snubfin and humpback dolphins interbreed regularly from my data, and molecular studies of these animals on the east coast of Australia have not revealed any evidence of hybridisation to date (Cagnazzi 2011). However, total sample sizes are small for both species, with limited survey effort throughout the majority of their range in Australia. This phenomenon likely represents a low-frequency, natural hybridisation, facilitated by a fragmented distribution and potentially low abundance (Lehman 1991, Bérubé and Aguilar 1998, Willis et al. 2004). Further isolation of already fragmented populations may facilitate further hybridisation and, hence, raise conservation concerns (Allendorf et al. 2001).

3.5.4 Conservation and management implications

The definition of populations, stocks or management units (MUs) is typically based on ecological or evolutionary criteria, or a combination of the two (Waples and Gaggiotti 2006). Many different definitions of a population are in use and the criteria used vary according to the purpose for which a population is being defined (Waples and Gaggiotti 2006). Genetic data have been widely used to examine the structure of cetacean populations and to make recommendations on the identification of MUs (e.g. Sellas et al. 2005, Bilgmann et al. 2008, Mendez et al. 2010). Indeed, the level of differentiation identified in this study, in terms of significant F_{ST} values, supports the criteria for separate MUs as proposed by Moritz (Moritz 1994). However, many authors argue that identifying MUs from genetic data alone is unwise (Paetkau 1999, Crandall et al. 2000, Waples and Gaggiotti 2006), particularly via the use of F_{ST} alone to infer gene flow, as it relies on several simplifying assumptions, which typically are not met for natural populations (Pearse and Crandall 2004, Palsbøll et al. 2007). Furthermore, an absence of historical gene flow may not correspond to current demographic isolation, yet it is the contemporary movement of animals which may be more pertinent in conservation and management actions (Palsbøll et al. 2007). While a combination of demographic, ecological and genetic data will provide the most robust assessments of MUs (e.g. Paetkau 1999, Taylor and Dizon 1999, Olsen et al. 2014), such inter-disciplinary approaches require considerable resources and lengthy time-frames (Olsen et al. 2014).

Palsbøll et al. (2007) advocate an approach to defining MUs based on a predefined threshold level of genetic divergence, rather than the rejection of panmixia. They encourage a demographic interpretation, with the dispersal rate (i.e. migration rates) of individuals of greater relevance to conservation and management than historical gene flow. A commonly cited threshold for demographic dependence is at least 10% exchange (Hastings 1993). Among the results reported here, the estimated upper confidence intervals for migrant proportions were $\leq$ 0.1 for snubfin dolphins, which supports, with reasonable confidence, the notion of separate MUs based on dispersal rates. The large confidence intervals around the estimated migration rates for humpback dolphins include the value of 0.1, making it difficult to determine if the two sampled locations represent independent MUs based upon proposed dispersal thresholds (Palsbøll et al. 2007). A larger number of samples is required to more accurately estimate contemporary migration rates of humpback dolphins.

While based on limited sample sizes, these results suggest that north-western Australian snubfin and humpback dolphins may exist as metapopulations of small, genetically largely isolated population fragments. As such, they are vulnerable to genetic characteristics associated with small, fragmented populations; these include the accumulation of deleterious mutations, the loss of genetic diversity through random genetic drift, inbreeding depression, and a reduced ability to adapt to environmental change (Frankham et al. 2010). These data, when combined with our (albeit limited) understanding of their movements, ecology and population structure from elsewhere in their range, suggest that the sampled populations are somewhat isolated and should be managed accordingly. For both species, further data are required to gain a better understanding of their genetic population structure, movements and demographics. However, it would seem appropriate to manage the two sampled populations of snubfin dolphins at Cygnet and Roebuck Bays as independent MUs. Despite the uncertainty around contemporary migration rates between humpback dolphins at the Dampier Archipelago and North West Cape, there is significant population structure and limited gene flow between these sampled populations; in light of the threat of coastal development in this region (described below), a precautionary approach of managing the sampled populations as independent MUs is recommended until further data become available.

Concerns have been raised with regard to the rate of industrial development along the coast of north-western Australia given the lack of appropriate baseline data on inshore dolphins in this region (Allen et al. 2012, Bejder et al. 2012, Brown et al. 2012). A resources boom, focussing on offshore hydrocarbon reserves and terrestrial mineral deposits, has been driving the rapid development of port and coastal processing facilities. The scale of these developments and, in particular, the volume of dredging, is large by global standards. Individual projects are responsible for tens of millions of cubic metres of seafloor dredging; combined dredging volumes for the region are in the hundreds of millions of cubic metres (Bejder et al. 2012, EPA 2013). Several such developments (either constructed, under-construction or in-planning) lie within 100 km of the Dampier Archipelago sampling site, while a plan for the world's largest liquefied natural gas processing facility was approved (but subsequently abandoned by the proponents) at a site 50 km north of Roebuck Bay (DMP 2014).

For tropical inshore dolphins, which are reliant upon the near-shore environment, the habitat modification associated with such coastal development presents multiple pathways for potential effects (Jefferson et al. 2009). For snubfin and humpback dolphins in particular, data

deficiencies are precluding assessment of their conservation status and, therefore, their effective management in this rapidly developing region (Allen et al. 2012, Bejder et al. 2012). Given the results presented here, it is recommended that conservation actions should include efforts to reduce extinction risk by maintaining effective population size and gene flow. Further restrictions on gene flow or a reduction in effective population size may compromise their evolutionary potential and, therefore, the longevity of these populations.

3.5.5 Recommendations

The following conservation actions are recommended:

1. *Broad-scale baseline data collection*. These results are based on a limited sample size, representing a small proportion of the several thousand kilometres of coastline of north-western Australia. The collection of baseline data on the distribution and abundance of inshore dolphins is required to identify and characterise local populations. Similarly, a greater number of biopsy samples across a broader geographic range is required to gain a more detailed understanding of their population genetic structure and connectivity.

2. *Improved understanding and protection of identified local populations.* Each local population identified in this study is likely to serve a critical role as a stepping-stone for gene flow among a fragmented metapopulation. For each local population, baseline data should be collected on abundance, effective population size, habitat use and potential or realised threatening processes. Data should inform management plans, which identify and assess the risk of potential threats to local populations, and make recommendations on actions required to minimise anthropogenic threats.

3. *Greater consideration of movement corridors between local populations.* The occasional dispersal of breeding individuals between local populations results in the gene flow required to maintain the evolutionary potential of these small populations of dolphins. As such, proponents of development along the coast should consider their environmental footprint in relation to local populations of snubfin and humpback dolphins and the influence their activities (e.g. prolonged acoustic disturbance) may have on the movement of animals between populations, regardless of the density of animals observed in the vicinity. Management agencies and decision-makers are urged to consider the potential cumulative impacts of multiple developments and other threatening processes on dolphins.

Appendix A3 Supporting information to Chapter 3

Table A3.1. Locus-specific microsatellite characteristics for snubfin dolphins.

	Cygnet Bay (n = 32)					**Roebuck Bay** (n = 25)				
Locus	N_A	N_E	N_P	H_E	H_O	N_A	N_E	N_P	H_E	H_O
DIrFCB4	11	5.306	5	0.812	0.813	9	5.919	3	0.831	1
DIrFCB5	5	2.332	1	0.571	0.567	4	2.935	-	0.659	0.737
LobsDi7.1	4	3.012	1	0.668	0.625	4	2.290	1	0.563	0.522
LobsDi9	1	1	-	0	0	1	1	-	0	0
LobsDi19	2	1.789	-	0.441	0.406	2	1.814	-	0.449	0.440
LobsDi21	5	3.391	-	0.705	0.688	5	3.086	-	0.676	0.760
LobsDi24	3	2.073	-	0.518	0.500	3	1.580	-	0.367	0.280
LobsDi39	1	1	-	0	0	1	1	-	0	0
SCA9	4	3.489	-	0.713	0.875	4	2.890	-	0.654	0.727
SCA22	3	2.476	-	0.596	0.656	3	2.237	-	0.553	0.522
SCA27	7	2.790	1	0.642	0.719	10	6.187	3	0.838	0.739
SCA39	3	1.679	-	0.404	0.375	3	1.788	-	0.441	0.360
Tex5	2	1.519	-	0.342	0.250	2	1.891	-	0.471	0.520
Tex7	2	1.897	-	0.473	0.500	2	1.956	-	0.489	0.550
Mean*	4.25	2.65		0.57	0.58	4.25	2.88		0.58	0.60

N_A = Number of Alleles, N_E = Number of effective Alleles, N_P = Private Alleles, H_E = expected heterozygosity, H_O = observed heterozygosity, * = excluding monomorphic loci.

Table A3.2. Locus-specific microsatellite characteristics for humpback dolphins.

	Cygnet Bay (n = 5)					**Dampier Archipelago** (n = 19)					**North West Cape** (n = 18)				
Locus	**N_A**	**N_E**	**N_P**	**H_E**	**H_O**	**N_A**	**N_E**	**N_P**	**H_E**	**H_O**	**N_A**	**N_E**	**N_P**	**H_E**	**H_O**
DIrFCB4	5	4.000	1	0.750	1	5	2.234	1	0.552	0.611	2	1.220	-	0.180	0.200
DIrFCB5	2	2.000	-	0.500	1	1	1	-	-	-	2	1.061	-	0.057	0.059
LobsDi7.1	4	2.941	1	0.660	0.600	5	3.238	1	0.691	0.526	3	1.684	-	0.406	0.375
LobsDi9	2	1.220	1	0.180	0.200	1	1	-	-	-	1	1.000	-	0.000	0.000
LobsDi19	4	3.846	-	0.740	1	6	2.843	-	0.648	0.737	6	3.461	-	0.711	0.706
LobsDi21	2	1.220	1	0.180	0.200	2	1.111	-	0.100	0.105	2	1.117	-	0.105	0.111
LobsDi24	5	4.167	1	0.760	1	3	1.875	-	0.467	0.632	5	3.880	-	0.742	0.667
LobsDi39	3	2.778	1	0.640	1	2	1.385	-	0.278	0.333	2	1.301	-	0.231	0.267
SCA9	6	3.333	1	0.700	0.800	5	3.153	1	0.683	0.579	8	4.208	2	0.762	0.556
SCA22	5	3.571	1	0.720	0.800	5	2.725	1	0.633	0.526	5	3.400	-	0.706	0.647
SCA27	2	1.471	-	0.320	0.400	3	1.174	-	0.148	0.158	3	1.325	-	0.245	0.167
SCA39	4	2.381	1	0.580	0.600	3	2.105	-	0.525	0.684	3	2.219	-	0.549	0.444
Tex5	1	1	-	-	-	1	1	-		-	1	1.000	-	0.000	0.000
Tex7	2	1.471	1	0.320	0.400	2	1.166	-	0.142	0.154	2	1.057	-	0.054	0.056
Mean*	3.54	2.65		0.54	0.69	3.73	2.09		0.44	0.46	3.58	2.16		0.40	0.35

N_A = Number of Alleles, N_E = Number of effective Alleles, N_P = Private Alleles, H_E = expected heterozygosity, H_O = observed heterozygosity, *excluding monomorphic loci.

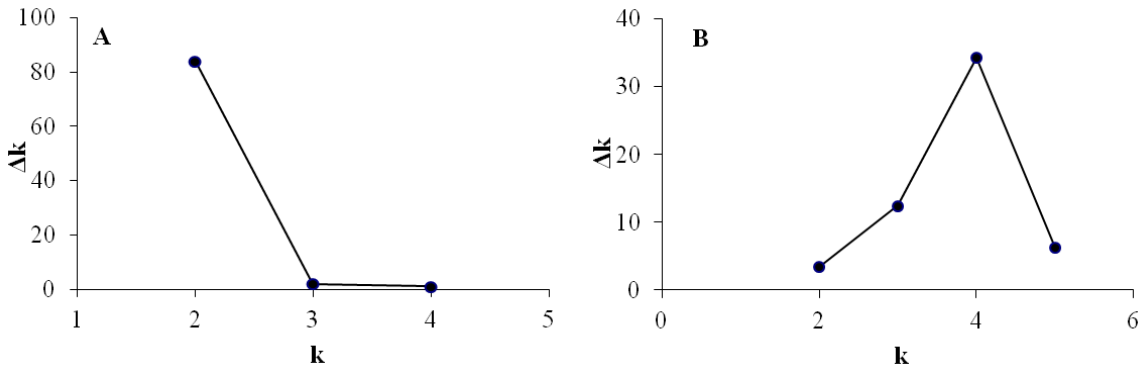


Figure A3.1. Δk plot for (A) snubfin dolphins and (B) humpback dolphins. In B, Δk peaks at k = 4, indicating that the most likely number of clusters equals 4.

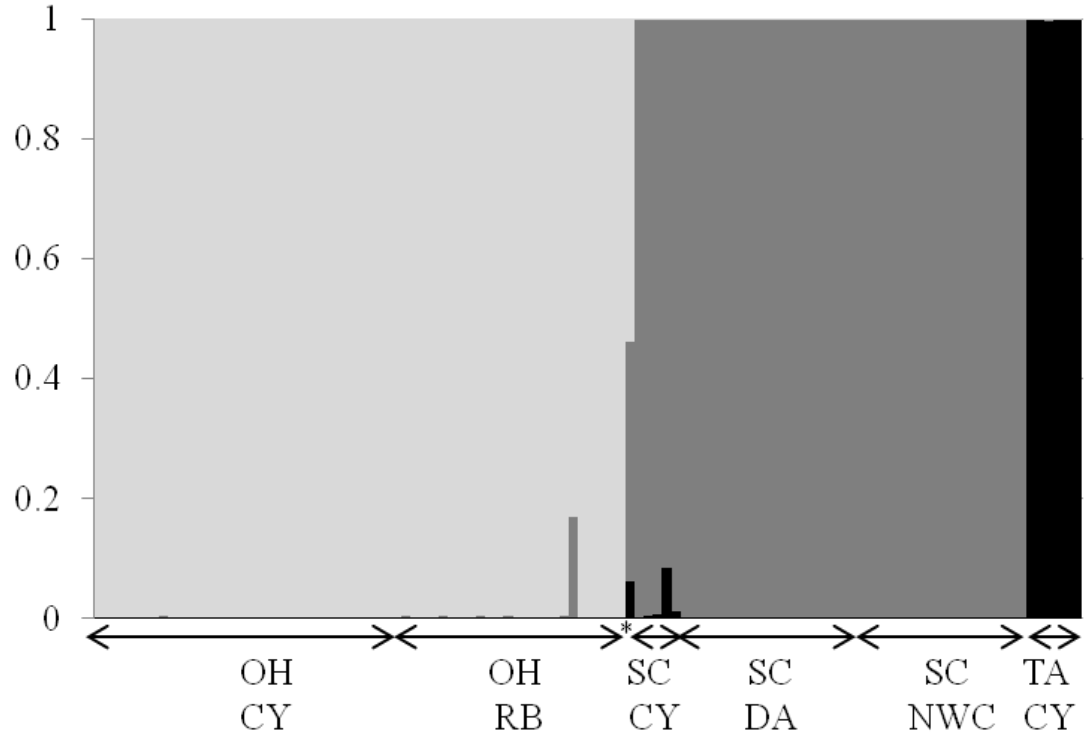


Figure A3.2. Structure plot including all samples used in the study. OH = snubfin dolphin, *suspected hybrid, SC = humpback dolphin, TA = bottlenose dolphin, CY = Cygnet Bay, RB = Roebuck Bay, DA = Dampier Archipelago, NWC = North West Cape.

Table A3.3. *P* values (from Wilcoxon sign-rank test) and presence of mode shifts indicating whether dolphins have recently undergone a bottleneck at sampling locations. Visualisations of potential mode shifts are shown in Figure A3.3.

	Two-tailed *P* values for *H* excess or deficiency			Mode shift[¶]
	IAM	**SMM**	**TPM**	
Snubfin dolphins				
Cygnet Bay (n = 32)	<0.01*	0.79	0.04*	no
Roebuck Bay (n = 25)	<0.01*	0.20	<0.01*	no
Humpback dolphins				
Dampier Archipelago (n = 19)	0.76	<0.01*	0.28	no
North West Cape (n = 18)	1.0	0.03*	0.23	yes

H: heterozygosity; IAM: infinite allele model; SMM: stepwise mutation model; *statistically significant result ($P < 0.05$): [¶]assessed by BOTTLENECK.

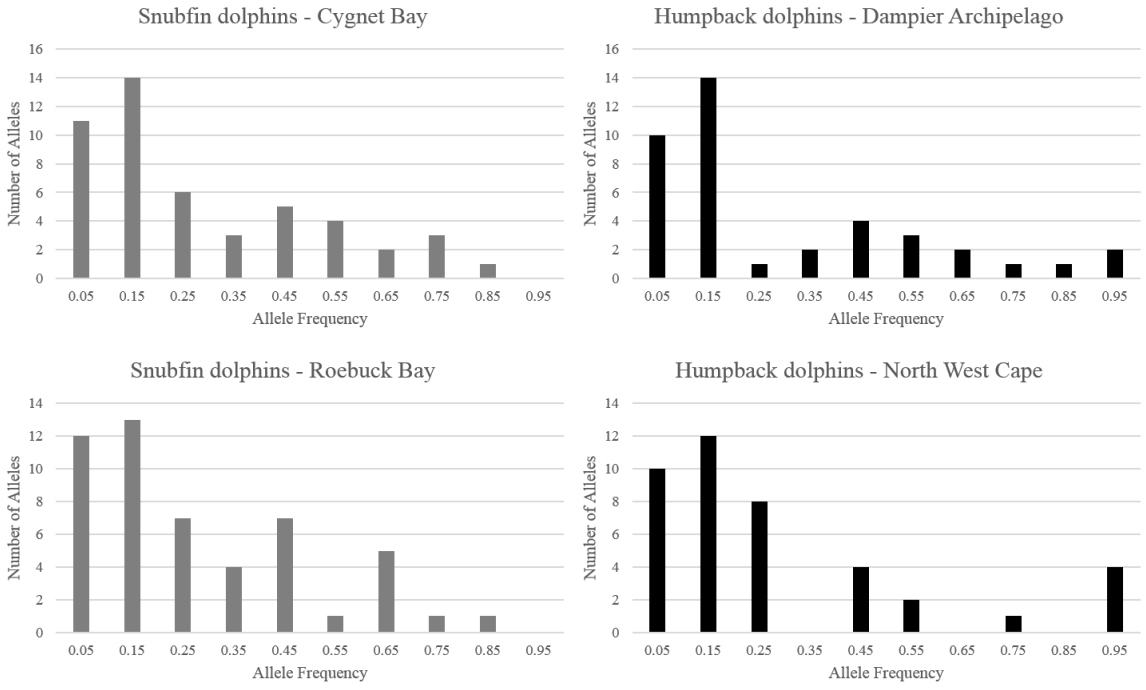


Figure A3.3. Allele frequency distribution visualising potential mode-shift distortion. The figures are based on 12 microsatellite loci for snubfin dolphins and 13 microsatellite loci for humpback dolphins.

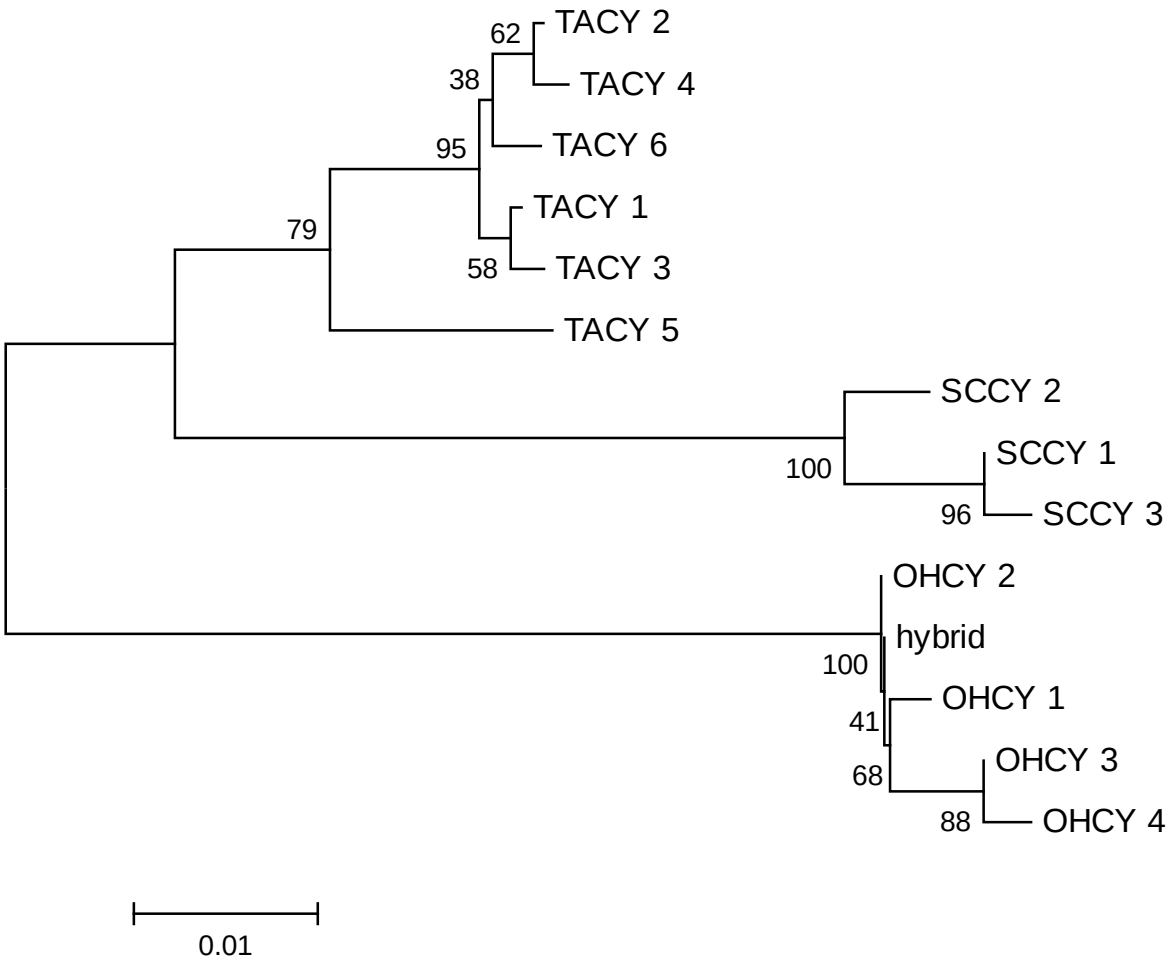


Figure A3.4. Neighbor-Joining tree of all haplotypes (based on 416 bp) identified in the three dolphin species regularly present at Cygnet Bay: TA = bottlenose dolphin, SC = humpback dolphin, OH = snubfin dolphin. The percentage of replicate trees in which the associated taxa clustered together in the bootstrap test (1,000 replicates) is shown next to the branches.

Chapter 4. The social structure of Australian snubfin dolphins: investigating sex-differences in association patterns and correlations with genetic relatedness[13]

4.1 Abstract

Characterising social structure is essential to understanding the behavioural ecology of a population or species. In this study, I describe the social structure of Australian snubfin dolphins (*Orcaella heinsohni*) in a tropical embayment in north-western Australia. Using photo-identification and molecular data, I investigated sex-specific grouping, genetic relatedness and association patterns for 28 males and 15 females within an apparently resident local population of c. 50 animals. While there was evidence of sex-segregation, a minimum of 42% of groups (47 of 111) were of mixed-sex. There were pronounced sex-differences in sociality: males generally formed stronger associations and were far more gregarious than females. There was significant evidence of non-random associations within all sex classes, with the exception of female-female associations. Male-male associations showed long-term temporal stability, whereas female-female associations decayed more rapidly. Overall, males appeared to form a single large network of frequently associating individuals, some of which associated more frequently than others, while most females were relatively solitary. Associations were not correlated with genetic relatedness, and individuals which associated more frequently were no more related than expected by chance. There was a considerable male-bias in both the frequency of sightings and number of biopsy samples obtained, suggesting that female snubfin dolphin may be underrepresented in studies that use boat-based observation and biopsy sampling techniques. This likely reflected the greater detectability and approachability of larger, male-dominated groups, and may have implications for common assumptions of capture-recapture studies of abundance and demographic parameters. These results further our understanding of the behavioural ecology of snubfin dolphins, and illustrate that their social systems depart from several patterns observed in coastal bottlenose dolphins. Future studies should seek to characterise the social structure of larger populations of snubfin dolphins, and investigate the behavioural context of their patterns of association.

[13] Chapter publication status: in prep.

4.2 Introduction

The social structure of a population or species describes the characteristics of interactions between individuals (Hinde 1976). These social behaviours reflect individuals' attempts to maximise survival and reproductive success (Wilson 1975), and can be influenced by a range of ecological, demographic and life history factors (Alexander 1974, Wilson 1975, Bertram 1978). Social structure influences key population processes, including reproductive fitness (e.g. Silk et al. 2003, 2009, McDonald 2007, Frère et al. 2010a), the flow of genetic material (Chepko-Sade and Halpin 1987), the spread of pathogens (Hamede et al. 2009, Fenner et al. 2011), and the transmission of information or behaviours between conspecifics (Weilgart and Whitehead 1997, Allen et al. 2013). Social structure is, therefore, an important element of species' population biology (Slooten et al. 1993, Whitehead 1997), and often has important implications for conservation and management (Caro 1999, Berger-Tal et al. 2011).

Characterising interactions between pairs of individuals (dyads) is the basis of describing the social organisation of a population (Hinde 1976). However, detailed data on interactions (e.g. grooming or antagonistic events) are often difficult to observe in wild animals; for example, individuals are underwater or in dense vegetation. As individuals generally need to be in close proximity in order to interact, associations between individuals, defined by spatial proximity, can provide a proxy for interactions (Whitehead 1997). Patterns of association have been used to infer social structure in a range of taxa, including reptiles (e.g. Strickland et al. 2014), terrestrial mammals (e.g. Festa-Bianchet 1991, Vonhof et al. 2004, Archie et al. 2006), and cetaceans (e.g. Connor et al. 1992a, Ottensmeyer and Whitehead 2003, Wells 2003, Gero et al. 2008).

Dolphins are a diverse family of cetaceans which show considerable interspecific variation in their ecology (LeDuc 2009). Many species live in complex social systems which exhibit a variety of social strategies (Connor et al. 1998, Gowans et al. 2007). As has been well-documented in many terrestrial mammals [e.g. elephants (Wittemyer et al. 2005); primates (Ren et al. 2012) and ungulates (Festa-Bianchet 1991, Sundaresan et al. 2007)], coastal dolphin social systems, in particular, are typically characterised by fission-fusion grouping dynamics (e.g. Wells et al. 1987, Bräger 1999, Karczmarski 1999, Connor et al. 2000). In fission-fusion societies, groups of variable size and composition form, break up, and reform

at frequent intervals in response to ecological influences and shifts in behaviour (Conradt and Roper 2005). Such a grouping pattern allows individuals to balance the costs (e.g. increased competition for resources) and benefits (e.g. reduced predation risk) of group living (Bertram 1978, Aureli et al. 2008).

Within dolphin fission-fusion societies, there is considerable variability in the number, strength, and temporal stability of associations between individuals (Connor et al. 2000, Gowans et al. 2007). Patterns of non-random associations are common, wherein pairs of individuals may associate more or less frequently than expected by chance (e.g. bottlenose dolphins, Tursiops spp., Wells et al. 1987, Smolker et al. 1992). Associations between individuals range from 'casual', short-term (e.g. Hector's dolphins, Cephalorynchus hectori, Slooten et al. 1993, Bräger 1999, humpback dolphins, Sousa spp., Karczmarski 1999, Parra et al. 2011) to strong bonds which may persist over several years (e.g. spotted dolphins, Stenella frontalis, Elliser and Herzing 2014), or even decades (e.g. bottlenose dolphins, T. aduncus, Connor and Krützen 2015). Patterns of association in bottlenose dolphins have been related to a variety of factors, including: age and sex class, behavioural state, female reproductive state, matriline, genetic relatedness, and home range overlap, and these relationships vary between populations (Wells 1991, Smolker et al. 1992, Herzing and Brunnick 1997, Krützen et al. 2003, Gero et al. 2005, Gibson and Mann 2008, Frère et al. 2010b).

Some of the most pronounced differences in the number, strength and temporal stability of associations observed among adult dolphins are those between the sexes (e.g. Smolker et al. 1992, Elliser and Herzing 2014). Such patterns are common within social mammals, where differences in the life histories of male and female mammals drive pronounced sex-differences in many elements of their behaviour, including their patterns of association (Ruckstuhl and Neuhaus 2005). For example, female distribution is largely influenced by food resources; by contrast, the distribution of males is expected to be highly influenced by both the distribution of females, and the presence and behaviour of other males (Rubenstein and Wrangham 1986). Far greater female parental investment negatively biases the number of sexually receptive females to sexually mature males, generating intensive competition between males for access to mates (Emlen and Oring 1977, Clutton-Brock and Parker 1992).

While sex-specific analyses of social structure are the norm among terrestrial mammals, they are less common among small cetaceans. Dolphins rarely exhibit sufficient dimorphism and/or readily-observable genitalia for sex to be reliably inferred from visual observations, and molecular sexing may be beyond the logistical or ethical constraints of some studies (Chapter 5). Consequently, investigations of sex-specific social structure are largely restricted to a limited number of long-term studies on approachable populations, primarily of coastal bottlenose dolphins, *Tursiops* spp. (e.g. Wells 1991, Smolker et al. 1992, Möller et al. 2001, 2006, Lusseau et al. 2003, Connor and Krützen 2015), and also spotted dolphins, *S. frontalis* (Elliser and Herzing 2014). Generally, these studies have revealed that, while mixed sex groups are common, there is segregation of males and females. Both sexes show preferred associations with individuals of the same sex, some of which may be long-lasting. However, males typically form strong, long-lasting bonds with one or two other males, whereas females exhibit a larger network of more casual bonds with other females, with some stronger bonds between females of similar reproductive state (Wells 1991, Smolker et al. 1992, Rogers et al. 2004, Möller and Harcourt 2008, Elliser and Herzing 2014). Male-female associations are dependent, to some extent, on the reproductive status of females (Smolker et al. 1992), where males will associate more with females which are reproductively receptive in an attempt to maximize mating opportunities (Connor et al. 1996a).

In many mammalian groups, social relationships associated with cooperative behaviour and coalition formation are often observed between kin (review in Smith 2014). However, studies of relatedness patterns in dolphins are limited, with most information available for a few coastal populations of bottlenose dolphins (review in Möller 2012). Generally, females appear to associate preferentially with other females who are more genetically related than expected by chance (Duffield and Wells 1991, Möller et al. 2006, Frère et al. 2010b, Wiszniewski et al. 2010), but may also associate closely with unrelated females. In one population, some strongly associated 'allied' male bottlenose dolphins (who have been observed cooperatively coercing females) were more closely related than expected by chance, whereas other allied males were not (Krützen et al. 2003). In two other populations, allied males were no more closely related than expected by chance (Möller et al. 2001, Owen 2003). As social bonds among both male and female bottlenose dolphins have been shown to influence reproductive success (Frère et al. 2010a, Wiszniewski et al. 2011), there

is much interest in the extent to which these relationships may be associated with kin selection (e.g. Krützen et al. 2003).

Little is known of the social behaviour of the Australian snubfin dolphin (*Orcaella heinsohni*, hereafter 'snubfin dolphin'). A single study of snubfin dolphin social structure on the east coast of Australia revealed a fission-fusion grouping pattern with numerous strong associations, including some which were long-lasting (Parra et al. 2011). However, sex-specific patterns of association, or how these might correlate with genetic relatedness between individuals, have yet to be explored. The species does not exhibit any readily discernible sexual dimorphism, so sex-determination is largely dependent on the collection and analysis of skin tissue samples, which can be difficult to obtain from this often shy species. Snubfin dolphins occur in shallow, coastal and estuarine waters of northern Australia and likely southern New Guinea (Beasley et al. 2005). Their ecology in general is poorly understood, and data deficiencies preclude assessment of their conservation status and the management of anthropogenic impacts to local populations (Parra et al. 2006a, Allen et al. 2012, Beasley et al. 2012, Bejder et al. 2012, Woinarski et al. 2014). Available evidence suggests that they occur as small, somewhat isolated, local populations with restricted ranges and are, therefore, vulnerable to localised declines (Parra et al. 2006a, Cagnazzi et al. 2013b, Brown et al. 2014; Chapters 2 and 3). Snubfin dolphins are a species of conservation concern, and there is a considerable management need for further information on their behavioural ecology (Department of the Environment 2013b, Woinarski et al. 2014).

In this chapter, I investigate the social structure of a small, apparently resident local population of approximately 50 snubfin dolphins in a tropical embayment in north-western Australia (Chapters 2 and 3). Using group composition and genetic data, I investigate community structure and sex-specific grouping and association patterns, including the temporal structure of associations and correlations with genetic relatedness.

4.3 Materials and methods

4.3.1 Data collection

Boat-based surveys were conducted in approximately 130 km^2 of near-shore waters in Cygnet Bay, Kimberley region, between April 2012 and September 2014 (Fig. 4.1). Data

collection was focused around two periods each year: Apr/May and Sep/Oct. In 2012 and 2013, survey effort included both stratified and opportunistic surveys. Only opportunistic surveys were conducted in 2014. Stratified surveys comprised multiple repeats of pre-determined transects, providing even coverage of the study area. Further details of data collection methods are provided in Chapter 2.

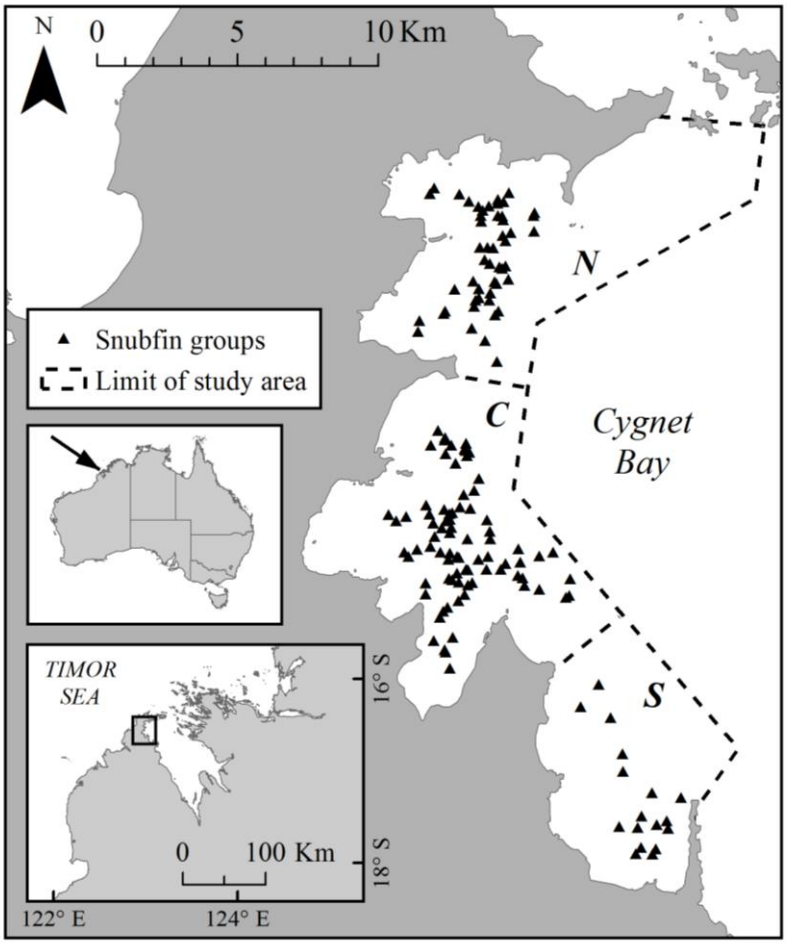


Figure 4.1. Location of Cygnet Bay, Western Australia, showing approximate extent of study area (c. 130 km^2) and locations of snubfin dolphin groups. The study area is partitioned into northern (N), central (C) and southern (S) zones. Insets show Australian and regional (western Kimberley) contexts.

A group was defined as all dolphins exhibiting relatively close spatial cohesion, where each member was within 100 m of any other member and involved in the same or similar behavioural activity (Bräger 1999, Parra et al. 2011). However, spatial cohesion was usually much closer, i.e. ≤ 10 m separation between individuals within a group. Upon sighting a group of dolphins, the vessel approached to within 30 m to: record date, time, and location; estimate group size; assess predominant behaviour and age composition; and

obtain photographs for photo-identification of individual animals. Individuals were assigned one of three mutually exclusive age-classes (adult, subadult, or calf): adults appeared fully grown relative to others in the population; subadults were independent animals up to two thirds the size of adults; calves were ≤ 2/3 the size of adults and consistently observed in infant position alongside the same adult individual (Mann and Smuts 1998, Parra et al. 2006a).

Two photographers captured photographs of the dorsal fins of dolphins, with the objective of obtaining multiple photographs of all individuals within a group to ensure that group composition could be accurately determined during subsequent image analysis. Photographs were subsequently examined to identify distinctive individuals present in each group using permanent nicks, notches and distinctive dorsal fin shape visible from either side of the dorsal fin (Würsig and Jefferson 1990). An individual was only considered identified if captured in an image of sufficient photographic quality (i.e. focus, contrast, angle, resolution) to identify the least distinctive individual included in the analyses (Nicholson et al. 2012, Urian et al. 2015). These individual distinctiveness and image quality control measures ensured that individuals were not misidentified. The sexes of individuals were determined either by molecular analysis of skin tissue samples (see below), or adults were inferred as females through consistent observations with a dependent calf (Mann and Smuts 1998).

Skin tissue samples were obtained using a biopsy darting system (Krützen et al. 2002) once sighting and photo-identification data had been collected. Biopsy darting required close proximity to an individual (i.e. five to 15 metres), a predictable surfacing pattern, and calm sea conditions. As such, darting was conducted opportunistically in suitable conditions only.

4.3.2 Ethical note

Boat-based observations and photo-identification have been extensively applied to small cetaceans for several decades (review in Urian et al. 2015) and do not require any physical contact with the animals. Dolphins were approached in such a manner as to minimise potential disturbance, and encounters were aborted where animals fled or repeatedly showed avoidance of the boat (Parra et al. 2011). Biopsy darting typically produces a startle

response from the sampled animal and a small wound which heals within approximately three weeks (Krützen et al. 2002). While studies reviewing responses of small cetaceans to biopsy darting are often of limited duration, no evidence of long-term effects has been reported to date (Noren and Mocklin 2012). Biopsy darting was only conducted by trained and experienced operators. No attempt was made to sample calves or adults with neonate calves.

4.3.3 Group sizes

Group size was estimated in the field, and subsequently validated with photo-identification data where available. There was occasionally uncertainty over the exact group size, and in such cases a minimum and maximum estimated group size was recorded. Summary statistics presented on group sizes correspond to the minimum estimated size and exclude groups where uncertainty was > two dolphins. For summary statistics on the sex-composition of groups, I excluded those where uncertainty in group size was > one dolphin.

4.3.4 Association patterns

Analyses of association patterns were performed on individuals of known sex using SOCPROG 2.6 (Whitehead 2009). Dolphins were considered associated when identified within the same group at the same time during a single day (the sampling period). Key assumptions of this 'gambit of the group' approach are: (1) all individuals within a group are associated; (2) interactions occur within groups; and (3) all individuals within group interact at a similar rate (Whitehead and Dufault 1999). The strength of associations between dyads was quantified using the half weight association index (HWI):

$$HWI_{ab} = \frac{x}{x + y_{ab} + \frac{1}{2}(y_a + y_b)}$$

where x is the number of sampling periods that individuals a and b were associated, y_{ab} is the number of sampling periods where both a and b were identified but not associated, and y_a and y_b are the total number of sampling periods in which only a and b were observed, respectively (Cairns and Schwager 1987). HWI is an estimate of the proportion of time two individuals spend together, with values ranging from 0 (never associated) to 1 (always associated). The HWI is considered the most appropriate where the assumption of

identification of all individuals within a group cannot be met (Ginsberg and Young 1992). To further reduce potential bias associated with imperfect identification, groups with < 50 % of individuals identified were excluded from the analysis of association patterns (Parra et al. 2011).

When analyzing association data, it is important to strike a balance between representative data (inclusion of as many individuals as possible) and reliable data (maximum sighting frequencies) (Bejder et al. 1998, Chilvers and Corkeron 2002). Consequently, only individuals sighted five or more times (i.e. within ≥ five single day sampling periods) were included in association analyses. This sighting threshold is comparable to other studies of cetacean social structure [e.g. ≥ 3 sightings, Fedutin et al. (2014); ≥ 4, Bräger et al. (1994), Parra et al. (2011); ≥ 5, Rossbach & Herzing (1999), Chabanne et al. (2012)], albeit lower than those which utilize long-term data sets [e.g. ≥ 30 sightings, Frère et al. (2010b)].

Estimated association indices may differ from the true association indices (the proportion of time dyads spend together), and therefore provide a poor representation of real social structures (Whitehead 2008a). To test the power of the observed association data to detect the true social system, the correlation coefficient between the true and estimated association indices (r) was calculated. Values of r range from 0 (no power) to 1 (perfect power), with $r \sim 0.8$ indicating good power and $r \sim 0.4$ moderate power. To provide a measure of how varied associations were between individuals within the population, the coefficient of variation (CV) of the true association indices (S) was calculated. Values of $S < 0.3$ indicate low levels of differentiation (fairly homogenous societies); greater than ~ 0.5 indicate well differentiated societies; and greater than ~ 2 extremely differentiated societies (Whitehead 2008b). Both r and S were calculated using maximum likelihood procedures.

Patterns of association were summarized for females (with all other individuals), males (with all other individuals), and for associations within each of the following sex classes: female-female, male-male, male-female, and female-male. For each category, I provide the mean and maximum HWI, in addition to the sum of all HWI values – which is indicative of the 'typical group size' (i.e. size of group in which the average individual found itself) (Jarman 1974, Whitehead 2008b). A Mantel test (Mantel 1967, Schnell et al. 1985) with

1,000 permutations was used to test the hypothesis that association rates between and within classes were similar.

4.3.5 Non-random associations

Non-random patterns of association were tested by calculating random permutations of associations within sampling periods, using a modification of the Bejder et al. (1998) procedure, which accounts for differences in gregariousness and situations where not all individuals are present in each sampling period (Whitehead et al. 2005, Whitehead 2008b). Permutations shuffle the raw data (i.e. dyad membership) by randomly assigning dyad membership within a sampling period and calculating a specified number of random HWI matrices. The test statistic was the CV of the mean association indexes. If some dyads show preferred associations over several sampling periods, then the CV of the observed association indexes will be significantly higher than that of the random data (Whitehead 2008b). Here, the sampling period was set as one day. Permutation tests were performed on all individuals of known sex, in addition to sex-specific pairwise classes. A total of 1,000 permutations were used per test; increasing the number of permutations did not alter the significance of *p*-values.

4.3.6 Temporal patterns of association

To investigate the temporal persistence of associations, I estimated lagged association rates (LARs) and compared these to the null association rates for each sex class. The LAR provides an estimate of the likelihood that two associated individuals at time zero will still be associated at a given time lag, whereas the null association rate represents the expected LAR if individuals are associating at random (Whitehead 1995). I calculated standardised lagged association rates (SLARs), which give the probability that, given individual *A* is an associate of *B*, if a randomly chosen associate of *B* is identified after a given time lag, then that associate is *A* (Whitehead 2008b). The SLAR considers the number of associates observed with an individual at specific time-lags, and is preferable where not all associates of an individual may be observed within a sampling period (Whitehead 1995, 2008b).

For the estimation of SLARs, all sexed individuals were included, regardless of their total number of sightings. This resulted in the inclusion of one additional adult female observed

in three sampling periods. Restricting SLARs to the most frequently observed individuals is likely to cause a positive bias in the estimates (Baird and Whitehead 2000).

Plots of lagged and null association rates were visually interpreted in relation to published theoretical models (Whitehead 2008b). Additionally, four pre-determined model structures of exponential decay specified in SOCPROG (Whitehead 2008b, 2009) were fitted to SLARs to quantitatively assess the temporal structure of associations. Model fit was assessed using the quasi-Akaike information criterion (QAIC) (Whitehead 2007).

4.3.7 Spatial overlap of individuals

Individuals must occur in the same space in order to associate. The degree to which two individuals' home ranges overlap will influence their opportunities to associate, and therefore their observed patterns of association (Whitehead 2008b). Where the study area is large relative to the home range of individuals within the study population, some individuals may rarely, if at all, have the opportunity to overlap (e.g. Urian et al. 2009, Titcomb et al. 2015). However, accurate estimation of and individuals' home range estimation requires considerable data; a minimum of 30 sightings, but preferably ≥ 50, has been recommended (Seaman et al. 1999).

As the current study site was small, and numbers of sightings for individuals were below recommended minimums for accurate home range estimation (Section 4.4.1), I did not attempt to quantitatively estimate home ranges and their degree of overlap between individuals. As an alternative, I examined the distribution of sightings of each individual, and approximately defined their space use according to their occurrence in each of three zones within the study area, defined here as northern (N), central (C) and southern (S) zones (Fig. 4.1). These zones corresponded to three apparently discrete clusters of sightings within the study area. Using ArcGIS (v10.2, ESRI 2014), individuals' sighting locations were plotted, including only the first sighting within each day. For each individual, I recorded which of the three zones they had been sighted in at least once over the total study period. This provided a crude measure of each individuals' space-use, and a means by which to qualitatively assess the spatial overlap between individuals.

4.3.8 Community division

I explored the potential for the population to be divided into clusters based on their association patterns, where HWI values were general higher among individuals within a cluster, and lower among individuals of different clusters. These analyses estimated modularity (*Q*): a measure of the difference between the proportion of the total association within clusters and the expected proportion when the individuals associate randomly (Newman 2004, Whitehead 2008b). Values of $Q > 0.3$ indicate useful division of the population (Newman 2004). Two methods were implemented in SOCPROG 2.6. The first performs a hierarchical cluster analysis (HCA) to display association data as a dendrogram, with modularity estimated iteratively at different levels of branching to determine the association index which maximizes *Q*. The cophenetic correlation coefficient (CCC) provides a measure of how well the dendrogram matches the matrix of association indices, with values of CCC > 0.8 indicating a good match (Bridge 1993). The second method was an eigenvector-based algorithm for assigning clusters to maximise *Q* (Newman 2006).

4.3.9 Molecular sexing and pairwise relatedness measures

Skin tissue samples were obtained from 40 individuals using a biopsy darting system (Krützen et al. 2002). Sex was determined using sex chromosome-specific primers, and genotypes were successfully determined at 14 microsatellite loci, following previously published protocols (Frère et al. 2010c, Brown et al. 2014; Chapter 3).

Pairwise relatedness (*R*) was estimated from genotypes using program COANCESTRY (Wang 2011). The moment estimator approach of Queller & Goodnight (1989) was used, which provides a mean value of zero for the sampled population and a continuous scale of pairwise relatedness ranging from -1 to 1. Mantel tests with 5,000 permutations were implemented in SOCPROG 2.6 to investigate relationships between a matrix of pairwise *R* estimates and the HWI matrix within each sex class.

I also tested whether dyads which frequently associated were more or less related than expected by chance using a Monte Carlo randomization method (Manly 2007) implemented in the computing program R (R Core Team 2014). I conservatively defined frequent associates as dyads in the top 10% of HWI association indices within each sex class (cf. Möller et al. 2006). Within each sex class, all pairwise relatedness estimates were randomly

resampled with replacement to generate randomized mean pairwise relatedness estimates. Significance was then assessed as the proportion of 1,000 resampling events where the randomized mean relatedness was greater than the observed mean relatedness of frequent associates.

4.4 Results

A total of 162 groups of snubfin dolphins were observed across 72 of the 100 days (or part thereof) of effort during the study. Group size varied from one to 26, with a mean of 5.6 ± 0.4 SE (n = 150) (Fig. 4.2). The mean group size from which one or more individuals were successfully biopsy sampled for molecular sex-determination was 10.2 ± 1.3 SE (n = 22). Calves were present in 36 groups, of which 32 included a single calf and four included two calves. Mean group size where one or more calves were present was 5.2 ± 0.7 SE (range 2-17).

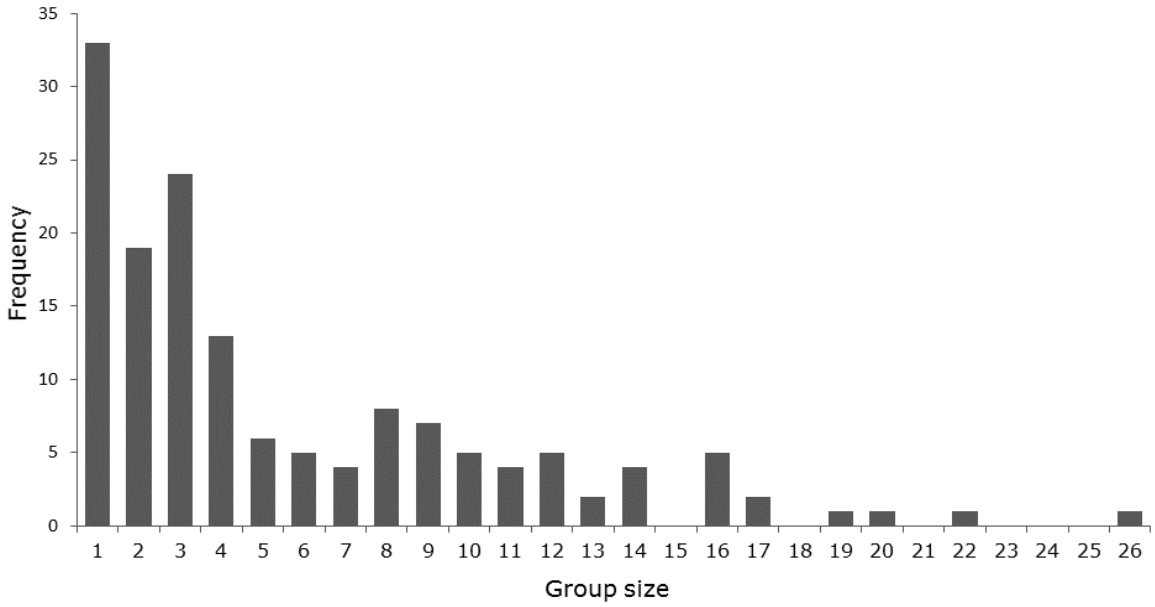


Figure 4.2. Estimated group sizes of snubfin dolphins in Cygnet Bay. Group sizes include dependent calves.

Fifty-four distinctive snubfin dolphins were photo-identified: 49 were assessed as adults and five as subadults. Skin tissue samples were obtained from 40 individuals (39 adults and one subadult); 28 were molecularly sexed as male, and 12 as female. A further four females were identified through consistent observations with a dependent calf, so the proportion of known-sex individuals in the population was c. 80% (44 of 54 distinctive individuals).

Sex-specific group sizes of non-calves were assessed for 111 groups where the uncertainty of the group size estimate was not greater than one (e.g. a group size estimate of 6-7 dolphins would be included; an estimate of 6-8 dolphins would be excluded). Based on these criteria, forty-three single-sex groups were identified, which were small in size for both sexes (mean = 1.5 dolphins) (Table 4.1). Male-only groups were dominated by single individuals (n = 15/17). A total of 42.3% (n = 47) of groups were known to be of mixed sex; this represents a minimum estimate, as it is reasonable to expect that a proportion of the male-unknown sex and female-unknown sex groups also represent mixed-sex groups.

Table 4.1. Sex-specific group frequency and size for snubfin dolphins at Cygnet Bay.

Group composition	Mean group size* (Min-Max)	Number of groups (%)
Male only	1.5 (1-8)	17 (15.3)
Female only	1.5 (1-3)	26 (23.4)
Male and unknown sex	6.8 (3-16)	11 (9.9)
Female and unknown sex	2.9 (1-6)	7 (6.3)
Male and female	6.1 (2-16)	18 (16.2)
Male, female and unknown sex	10.7 (3-22)	29 (26.1)
Unknown sex only	1.0 (1-1)	3 (2.7)
Total / overall	**5.2 (1-22)**	**111 (100)**

*minimum estimated group size; excluding dependent calves

4.4.1 Association patterns

Association indices were calculated for 43 individuals of known sex (28 male; 15 female) which were sighted on five or more occasions. Of these, 42 were classed as adults, and one (female A56) was classed as a subadult. One adult female individual (HYB) was known to be a hybrid, with Australian humpback dolphin (*Sousa sahulensis*) paternity, but is included here due to its consistent associations with other snubfin dolphins (Brown et al. 2014; Chapter 3). The number of sightings per individual varied between 5-24, and was significantly higher for males (mean = 14.2 ± 0.8 SE) than females (mean = 10.2 ± 1.2 SE, randomization test $p = 0.005$) (Table 4.2).

Table 4.2. Sighting frequency (number of day sampling periods sighted), time lag between first and last sighting, average time lag between sightings, study area zones sighted and mean HWI for 43 male and female snubfin dolphin individuals sighted on ≥ five occasions in Cygnet Bay. *Continued overleaf.*

ID*	Sighting frequency	Lag between first and last sighting (days)[$]	Mean / median lag between sightings (days)	Study area zones sighted[†]	Mean HWI
Females					
A02	5	595	189 / 202	C, S	0.05
A09	10	752	84 / 10	N, C	0.03
A10	14	875	67 / 10	N, C, S	0.17
A11	9	505	63 / 11	N, C	0.05
A13	6	873	175 / 138	N, C	0.08
A18	9	384	48 / 9	N, C, S	0.11
A20	10	606	67 / 7	N, C, S	0.12
A29	5	740	185 / 188	N, C	0.02
A31	14	610	47 / 8	N, C, S	0.24
A37	20	621	33 / 5	N, C, S	0.21
A38	13	734	61 / 17	N, C, S	0.23
A49	5	726	182 / 183	N, C	0.04
A53	10	727	81 / 47	N, C	0.13
A56	5	411	103 / 76	N, C	0.08
HYB	18	875	51 / 7	N, C	0.09
Mean ± SE	*10.2 ± 1.2*	*669 ± 40*	*96 ± 15 / 61 ± 20*	-	*0.11 (± SD 0.07)*
Males					
A03	18	613	45 / 8	N, C, S	0.28
A04	8	221	53 / 4	N, C, S	0.12
A05	12	743	81 / 31	N, C, S	0.13
A06	19	607	42 / 6	N, C, S	0.23
A07	21	609	38 / 6	N, C, S	0.27
A08	14	610	59 / 12	N, C, S	0.24
A15	10	366	41 / 6	N, C, S	0.15
A16	10	733	81 / 12	N, C, S	0.13
A19	11	606	61 / 9	N, C, S	0.13
A22	20	618	33 / 8	N, C, S	0.25
A23	24	608	26 / 3	N, C, S	0.29
A24	15	740	53 / 5	N, C, S	0.19
A25	8	740	106 / 8	N, C, S	0.16
A26	12	740	67 / 11	N, C, S	0.20
A27	9	615	77 / 11	N, C, S	0.19
A28	8	618	88 / 15	N, C, S	0.16
A32	15	613	44 / 5	N, C, S	0.22
A33	18	613	36 / 6	N, C, S	0.27
A34	12	610	55 / 7	N, C, S	0.22
A35	16	613	41 / 6	N, C	0.20
A36	14	613	47 / 7	N, C, S	0.24

Continued overleaf.

ID*	Sighting frequency	Lag between first and last sighting (days)[$]	Mean / median lag between sightings (days)	Study area zones sighted[†]	Mean HWI
A39	18	602	35 / 6	N, C, S	0.27
A40	18	734	43 / 6	N, C, S	0.27
A41	14	612	47 / 7	N, C, S	0.22
A43	12	604	55 / 4	N, C, S	0.17
A44	13	602	50 / 8	N, C, S	0.20
A46	18	589	35 / 3	N, C, S	0.27
A54	11	392	39 / 2	N, C, S	0.22
Mean ± SE	*14.2 ± 0.8*	*607 ± 22*	*53 ± 4 / 8 ± 1*	-	*0.21 (± SD 0.05)*

*Includes the total 43 male and female individuals sighted on a minimum of five occasions. [$]The maximum possible lag between first and last sighting was 887 days (total study period duration). [†]Indicates if the individual was observed at least once in the northern (N), central (C) and/or or southern (S) zone of the study area; refer to Figure 4.1 and methods for further information.

The CV of the true association indices (social differentiation, *S*) indicated a well-differentiated society at 0.67. An estimated correlation coefficient of 0.73 between the true and calculated association indices indicated good power to detect the true social system.

Associations within sex classes were significantly higher than those between sex classes (Mantel test, $t = 6.23$, matrix correlation = 0.31, $p < 0.001$). Mean male-male associations were almost three times higher than that of female-female associations (Table 4.3). Males were far more gregarious than females, with the sum of associations indicating that males exhibited a typical group size (9.8) almost twice that of females (5.6) (Table 4.3). The proportion of non-zero associations also varied considerably between sex class (male-male = 94.1%; female-female = 59.0%; male-female = 66.9%). Visual representation of these associations highlighted the general pattern of a greater number and strength of associations between males than females (Fig. 4.3). It was noted that the three females which were observed with a dependent calf at each sighting (IDs: A09, A11 and A29) were among those with the lowest mean association indices (Table 4.2). By contrast, no female with a mean HWI greater than the female average (0.11) was observed with a dependent calf during the study.

Table 4.3. Summary of HWI associations by sex class of snubfin dolphins at Cygnet Bay.

Class	Mean (± sd)	Sum (± sd)	Max (± sd)
Male	0.21 (0.05)	9.80 (2.20)	0.60 (0.14)
Female	0.11 (0.07)	5.64 (3.08)	0.35 (0.14)
Male-male	0.26 (0.07)	7.97 (1.87)	0.59 (0.15)
Female-female	0.09 (0.04)	2.23 (0.49)	0.29 (0.10)
Male-female	0.12 (0.03)	1.83 (0.39)	0.41 (0.12)
Female-male	0.12 (0.10)	3.41 (2.67)	0.31 (0.15)
Within classes	0.20 (0.10)	5.97 (3.16)	0.49 (0.20)
Between classes	0.12 (0.06)	2.38 (1.75)	0.38 (0.14)
Overall	0.17 (0.08)	8.35 (3.21)	0.51 (0.18)

Values (± sd) correspond to the mean value per sex class of the following: Mean = for each individual, the mean HWI with all other individuals (excluding with itself); Sum = for each individual, the sum of all HWIs (excluding with itself); Max = for each individual, the maximum HWI (excluding with itself). Mantel test for differences in associations between/within sex classes: $t = 6.23$, $p < 0.001$, matrix correlation = 0.31.

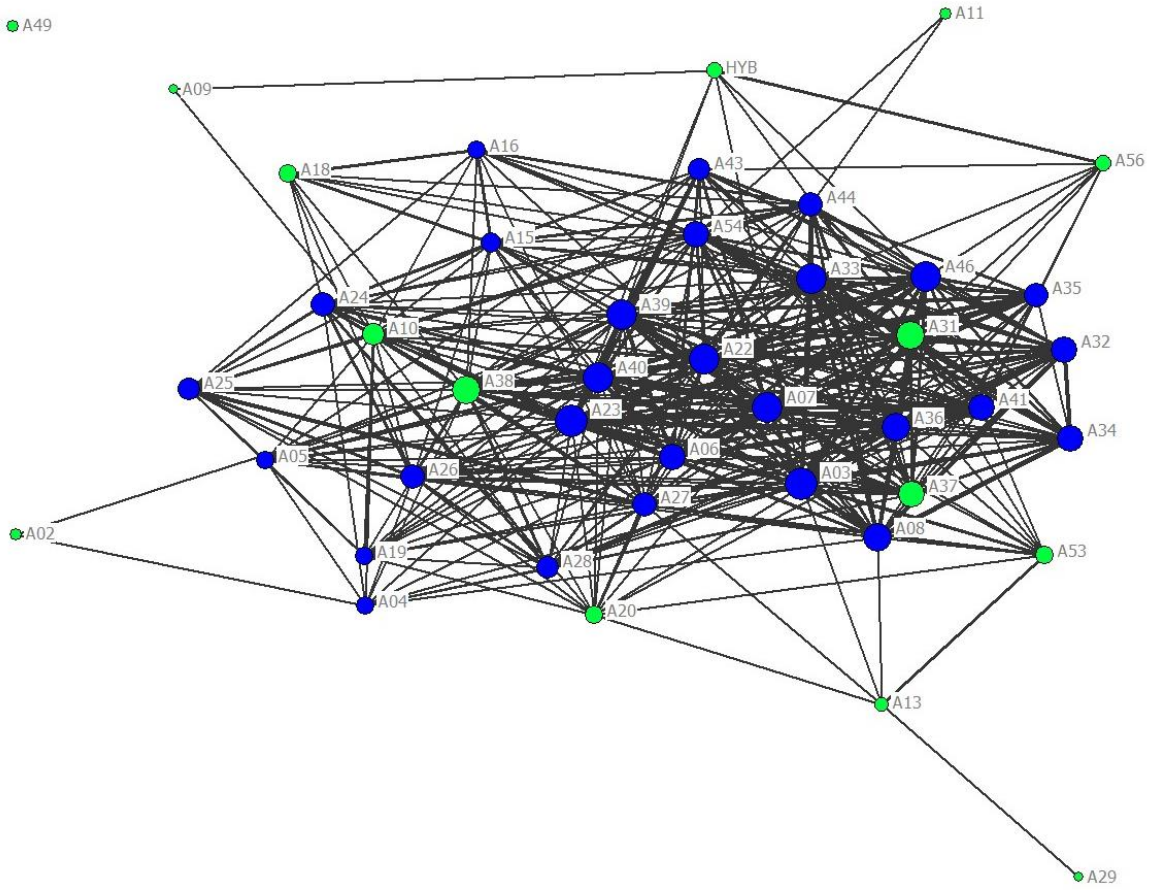


Figure 4.3. Network diagram of associations (HWI) between male (blue nodes) and female (green nodes) snubfin dolphins within Cygnet Bay. Nodes correspond to individuals (named with ID) and are scaled according to the gregariousness (sum of HWIs) of the individual. Edges illustrate associations ≥ the mean HWI of 0.17, with edge thickness and distance (approximate) to other individuals scaled by each dyadic HWI. Female individual A49 did not show any associations of HWI ≥ 0.17.

4.4.2 Non-random associations

Based on Whitehead's (2008a) suggestion of $S^2 \times H > 5$, where H is the mean number of associations per individual, the data showed adequate power to detect non-random patterns of association between dyads ($0.67^2 \times 106.23 = 47.69$). There was significant evidence of non-random associations when tested within all individuals combined (Table 4.4). A higher CV of observed vs random mean HWI indicated that individuals of all sex classes showed preferred associations, with the exception of female-female associations ($p = 0.606$).

Table 4.4. CV of observed vs random mean HWI association indices from permutation tests for non-random associations by sex class within snubfin dolphins at Cygnet Bay.

Sex class	Observed	Random	*p*-value*
All individuals	0.916	0.876	0.000
Male-male	0.651	0.605	0.000
Female-female	1.103	1.111	0.606
Male-female	1.057	1.037	0.010
Female-male	1.057	1.040	0.012

**p*-values represent the proportion of 1,000 randomized matrix permutations where the random value was greater than the observed value.

4.4.3 Temporal patterns of associations

Standardised lagged association rates (SLARs) revealed clear differences in the temporal persistence of male-male and female-female associations (Fig. 4.4). Despite showing a slow and fairly constant decline over time, male-male SLAR remained significantly above the null association rate to the maximum lag of 600 days. By contrast, female-female associations showed a more rapid rate of decline, with SLAR not significantly above the null association rate at a lag of c. 250 days. For both sexes, the best fitting model was one of continuous exponential decay, suggesting disassociation of male-male associations after c. 6 years and female-female associations after c. 1.5 years. Model fit was poor; therefore these model-estimated rates of disassociation should be interpreted with caution. However, they reflect the overall pattern in SLARs of greater temporal stability of associations between males than females.

4.4.4 Spatial overlap of individuals

The distribution of sightings indicated that almost all males (n = 27, 96%) were observed at least once in all three zones within the study area (N, C, S), while a single male was only observed in the northern two zones (N, C) (Table 4.2). By contrast, only 40% (n = 6) of females were observed in all three zones; 53% (n = 8) were only observed in zones N and C, and a single female was only observed in the southern two zones (C, S).

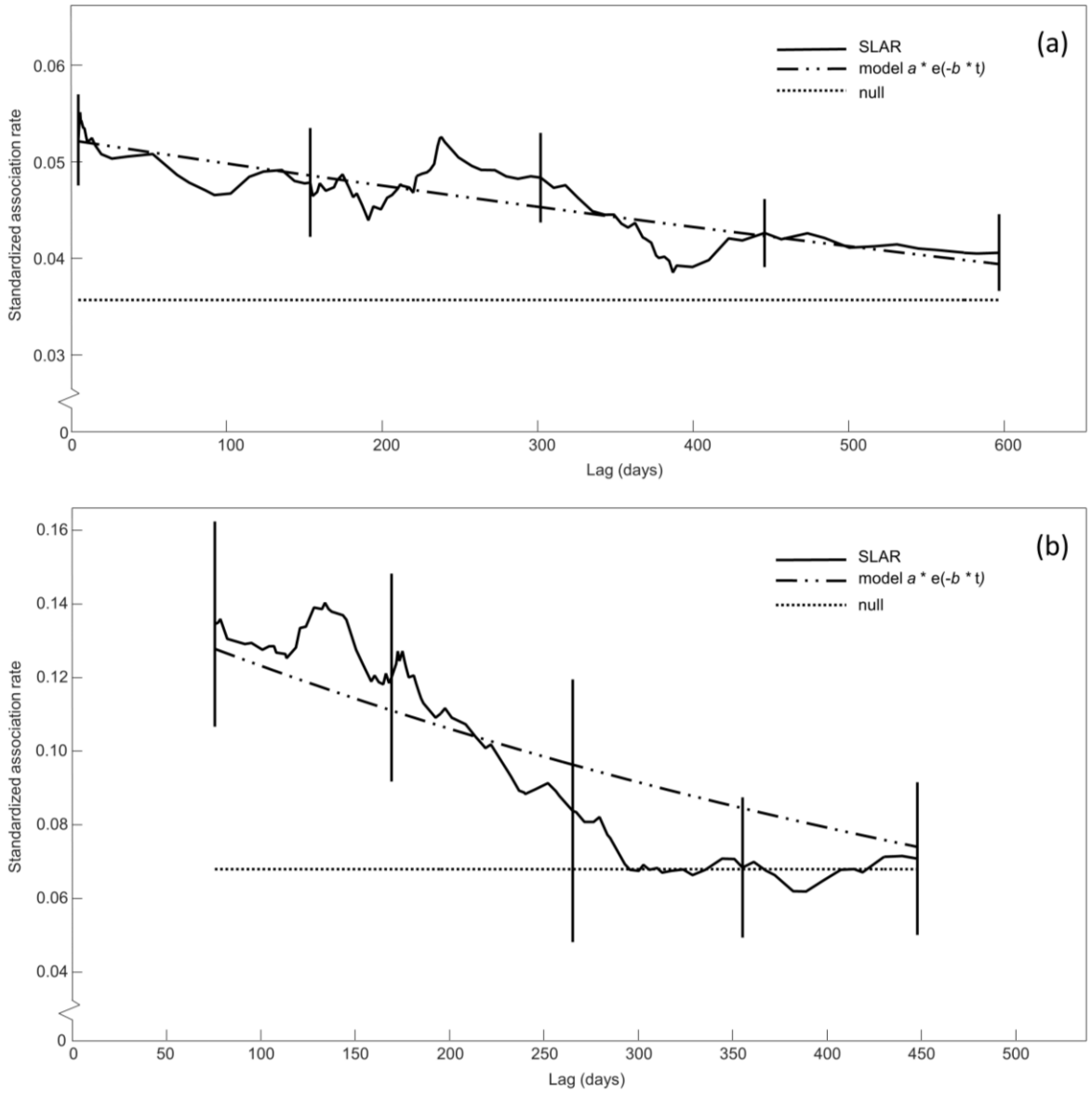


Figure 4.4. Standardised lagged association rate (LAR), null association rate and best-fitting models for (a) male-male and (b) female-female associations between snubfin dolphins within Cygnet Bay. Vertical bars provide estimates of precision via a temporal jackknife procedure. Model parameter estimates (± SE) for (a) include a = 0.0522 (±0.0034) and b = 0.0005 (±0.0002); and, (b) include a = 0.1414 (±0.0.0284), b = 0.0016 (± 0.0005). Moving averages of 20,000 (male-male) and 600 (female-female) associations were used to smooth the curves, resulting in different x-axis limits. Due to standardisation of lagged association rates, the absolute values of the y-axis cannot be directly compared between (a) and (b).

4.4.5 Community division

The HCA produced a dendrogram with a good match to the matrix of association indices (CCC = 0.85); individuals were assigned to eight clusters plus five singletons (all of which

were females). The eigenvector method assigned individuals to four different clusters. For both methods, maximum modularity (Q) was below 0.3, suggesting that the clusters did not represent meaningful community divisions (Q_{HCA} = 0.12, $Q_{eigenvector}$ = 0.16) (Newman 2004). Additionally, visual representation did not suggest any obvious clustering (Fig. 4.3).

4.4.6 Analysis of correlations between associations and relatedness

Pairwise genetic relatedness (R) was estimated for 39 individuals for which genetic samples were obtained. I excluded the hybrid individual (Chapter 3) from analyses of relatedness due to its mixed-species ancestry introducing a downward bias in R. Values of R ranged from -0.57 to 0.71, with a mean of 0.02 ± 0.24 sd. Correlation coefficients (r) between the R matrix and HWI were low and non-significant within each sex class (Table 4.5; Fig. 4.5). Additionally, I did not find that frequent associates (top 10% HWI values) were more closely related to each other than expected by chance for any sex class (Table 4.6). Caution is required when interpreting these results for the female-female class due to small sample size (frequent associates: n = 7).

Table 4.5. Correlation coefficients (r) between pairwise relatedness (R) matrix and HWI matrix for snubfin dolphins in Cygnet Bay

Sex class	***n***	***r***	***p*-value***
Male-male	28	0.014	0.393
Female-female	11	0.054	0.364
Male-female	28-11	0.102	0.175
Female-male	11-28	0.146	0.202

*Mantel test with 5,000 permutations. A square root transform was applied to HWI to reduce the influence of extreme values.

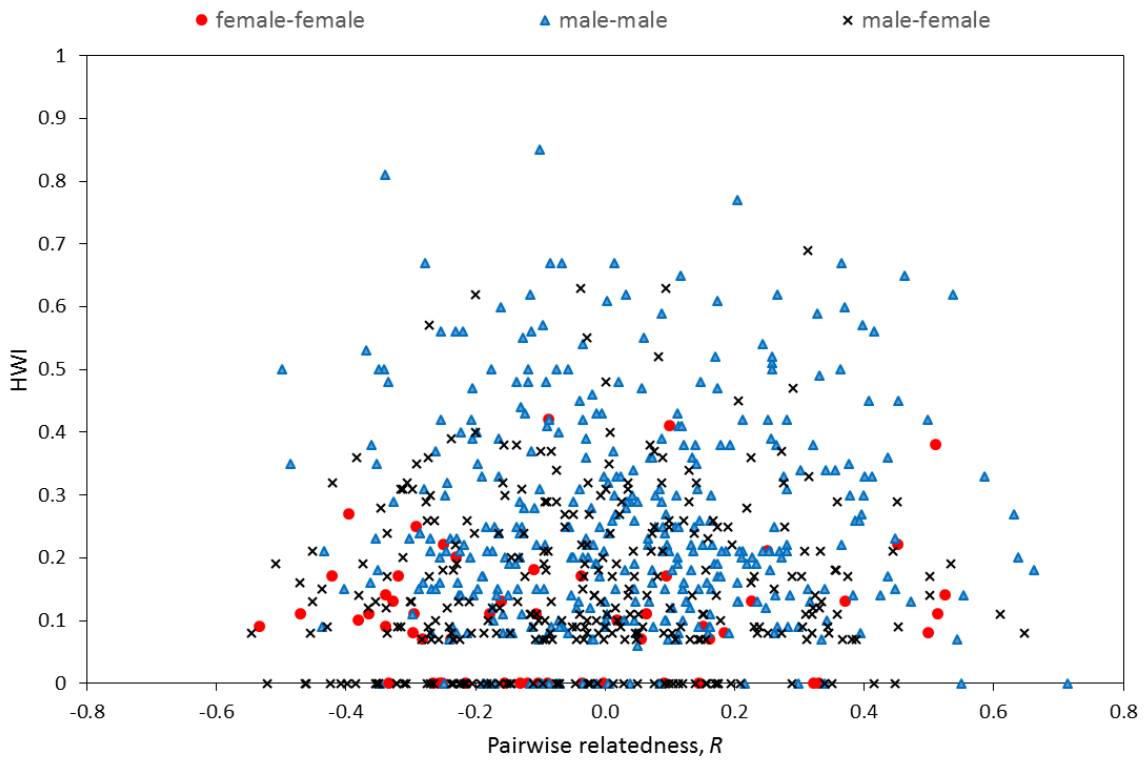


Figure 4.5. HWI vs pairwise genetic relatedness (*R*) for snubfin dolphins in Cygnet Bay, showing male-male dyads (blue triangle), female-female dyads (red circles) and male-female dyads (black crosses).

Table 4.6. Mean pairwise relatedness (*R*) among frequent associates (top 10% of HWI values) by sex class of snubfin dolphins at Cygnet Bay.

Sex class	Frequent associate threshold (≥ HWI)	*n*	mean *R* (± SD)	*p*-value*
Male-male	0.50	44	0.0055 (± 0.2632)	0.599
Female-female	0.22	7	-0.0185 (± 0.3735)	0.225
Male-female	0.32	37	-0.0438 (± 0.2045)	0.469

* Significance level compared to 1,000 Monte Carlo randomised mean *R* values for each sex class.

4.5 Discussion

This study presents an investigation of the social structure of a small population of Australian snubfin dolphins, a data deficient species of conservation concern (Beasley et al. 2012, Woinarski et al. 2014). I present the first data on sex-specific grouping and association patterns for snubfin dolphins, and investigate correlations between genetic relatedness and association patterns.

Overall, the population of snubfin dolphins in Cygnet Bay exhibited: variable group sizes; evidence of non-random associations with many strong associations; and patterns of associations which, to some extent, decayed over time. These results are broadly comparable to those of Parra et al. (2011) for a population of c. 67 snubfin dolphins in Cleveland Bay, on the east coast of Australia. Such characteristics suggest that snubfin dolphins interact in a relatively fluid fission–fusion social system with some degree of social preferences driving the underlying structure, as has been reported in other small delphinids (e.g. Connor et al. 2000, Gowans et al. 2007, Parra et al. 2011). However, examination of sex-specific patterns of association in snubfin dolphins has revealed considerable differences in the degree of sociality between males and females.

4.5.1 Group composition

Both mixed and single sex groups of various sizes were observed. Single sex groups appeared to be generally small for males and females, although these may be biased low by the higher likelihood of knowing the sex of all individuals present within smaller groups (Wells et al. 1987). The minimum estimate of 42.3% of mixed sex groups is comparable to the 49% mixed sex groups observed for bottlenose dolphins in Shark Bay, Western Australia (Smolker et al. 1992). This indicates that, while mixed sex groups of snubfin dolphins were common, there was a degree of social segregation between the sexes within the study population.

4.5.2 Sex-specific patterns of association

There were pronounced sex-differences in the extent of sociality of snubfin dolphins: males typically associated with a larger number of individuals and formed stronger associations than did females. In particular, mean male-male associations were approximately three times those between pairs of females. Non-random associations were observed within all sex classes, with the exception of female-female associations. Associations between males showed greater temporal stability, with a slow rate of disassociation. By contrast, associations between females decayed more quickly.

Male-male associations

Associations between adult males are stronger and more temporally stable than those between adult females in several populations of bottlenose dolphins (Wells et al. 1987,

Wells 1991, Smolker et al. 1992, Möller et al. 2001, 2006, Rogers et al. 2004) and one population of Atlantic spotted dolphins (Elliser and Herzing 2014). In a population of Hector's dolphins, males had significantly more associates than females, although associations were similarly weak and short-term in both sexes (Slooten et al. 1993). The nature of male-male associations in bottlenose dolphins varies between populations (e.g. Connor et al. 2000, Lusseau et al. 2003, Lusseau 2007). Several studies have reported the presence of allied pairs and trios of males, which cooperate in the context of agonistic interactions with other alliances, and in securing access to breeding females (Connor et al. 1992a, 2001, Möller et al. 2001).

Male-male associations within snubfin dolphins at Cygnet Bay were among the strongest reported of any sex class; however, the analyses did not reveal distinct clusters of pairs or trios akin to those reported in some bottlenose dolphin populations (Fig. 4.3). While there was significant evidence of non-random associations between males, almost all potential dyads (94%) associated at least once. Overall, males appeared to form a single, large network of frequently associating individuals, some of which associated more frequently than others. This contrasts with the patterns observed in most populations of bottlenose dolphins (e.g. Wells et al. 1987, Smolker et al. 1992, Möller et al. 2001) and indeed many social mammals, where, with the exception of cooperative male alliances, associations are typically greater between females (Harcourt 1992, Ruckstuhl and Neuhaus 2005).

Sex-specific group size data (Table 4.1) suggests that groups of mixed sex were larger than those which only included males, the latter being dominated by lone individuals. As such, and considering the results above, I hypothesise that the high rates of association between male snubfin dolphins are driven, to some extent, by males aggregating in the presence of females. With the group composition data presented here, it is not possible to determine the nature of interactions within these mixed sex groups; for example, if there were patterns of agonistic or cooperative behaviour between males. Field observations noted frequent body contact among multiple individuals in tight groups; while apparently agonistic interactions were occasionally observed, their context was difficult to ascertain. I also note one observation (during conditions of exceptional water clarity) of a group of nine adults (seven males, one female, one of unknown sex): the apparently receptive female engaged in multiple mating events with at least three different male individuals during one hour of observations. Future studies which define the behavioural context of these patterns of

associations are required to better understand factors influencing this high degree of sociality among male snubfin dolphins.

Female-female associations

In contrast to males, associations between females were characterised by a high proportion (40%) of zero elements and low mean association index. This was the only sex class which did not show significant evidence of non-random associations. The relatively solitary behaviour of most female snubfin dolphins observed in this study shows similarities and differences to patterns of female-female associations reported for coastal bottlenose dolphin populations. For example, some female bottlenose dolphins tend to be largely solitary, while others are usually found in groups (Wells et al. 1987, Smolker et al. 1992). Within large networks of fairly fluid associations, stable 'bands' of c. 10 females have been reported in several populations (Wells et al. 1987; Smolker et al. 1992; Möller et al. 2006). However, both sexes tend to separate when foraging (Connor et al. 2000). Living in groups can offer fitness benefits to females. For example, reproductive success has been related to the presence of social bonds in bottlenose dolphins (Wells 1993, Frère et al. 2010a), in addition to birds and other mammals (e.g. Rubenstein and Wrangham 1986, Silk et al. 2003, Cameron et al. 2009), and strong, long-term bonds between female baboons have been shown to enhance longevity (Silk et al. 2010).

I did not find any evidence of stable groupings of female snubfin dolphins, and only a small number of dyads (n = 16, 15%) showed association indices greater than the population mean. This suggests that group living for female snubfin dolphins may not provide the benefits which appear to arise from the formation of groups in bottlenose dolphins, such as defence against male harassment or reduced predation risk (Connor et al. 2000, Gowans et al. 2007). However, it is important to note the small sample size for female snubfin dolphins in this study, both in terms of the number of individuals and the sighting frequencies. At low sighting frequencies, it is unlikely that all associates of an individual were observed. For example, Frère et al. (2010b) found that the proportion of zero associations between female bottlenose dolphins did not reach an asymptote until 30 sightings of each individual were included in their analyses. As such, the association indices presented here may be biased low for individuals with a low number of sightings, many of which were females. Further research should strive to incorporate a larger number of female individuals with higher numbers of sightings in order to confirm, or otherwise, the patterns observed here.

Male-female associations

The reproductive state of females appears to be a key driver of male-female associations in both bottlenose (Connor et al. 2000, Owen et al. 2002) and spotted dolphins (Elliser and Herzing 2014), where males will associate more with females that are reproductively receptive in an attempt to maximize mating opportunities (Connor et al. 1996a). There was some evidence that male-female associations between snubfin dolphins at Cygnet Bay were associated with the reproductive state of females. For example, those females with dependent calves throughout the study (A09, A11, A29), which may not have been reproductively receptive, showed weak associations with males, as did the one subadult female (A56) and the hybrid female. By contrast, those females whose associations with males were the highest (e.g. A10, A31, A37, A38) were all without calves throughout the study, and mating attempts were observed on three of these females (A10, A37, A38).

4.5.3 Correlations between associations and genetic relatedness

There was no evidence that association patterns of snubfin dolphins were correlated with genetic relatedness for any sex class. Due to small sample sizes for females, results involving this sex should be considered preliminary. Investigations of relatedness in coastal dolphins are limited; however, given the results of such studies on bottlenose dolphins, my results are not unexpected. Within some populations of bottlenose dolphins, there appears to be a tendency for females to form moderate social bonds with related females (Duffield and Wells 1991, Möller et al. 2006, Frère et al. 2010b), and some cooperating males are more related than expected by chance (Krützen et al. 2003). However, both sexes, including cooperating males, also preferentially associate with both related and unrelated individuals of the same sex (Möller et al. 2001, 2006, Krützen et al. 2003, Owen 2003, Frère et al. 2010b).

Among mammals, there is a general trend of individuals preferring kin over non-kin as social partners, although such associations are typically in the context of cooperative behaviour and coalition formation, where there may be inclusive net fitness benefits to individuals (review in Smith 2014). As such, future studies of genetic relatedness and social structure in snubfin dolphins should seek to determine the behavioural context of associations.

4.5.4 Considerations of individuals' space use

The degree of home range overlap between individuals has shown to be correlated with association patterns in several taxa (e.g. delphinids, Frère et al. 2010b, marsupials, Best et al. 2014, reptiles, Strickland et al. 2014). Due to the low number of sightings of most individuals in this study, I did not attempt to quantify the degree of home range overlap of snubfin dolphins in this study. However, I showed that all individuals were observed at least once in the same zone within the study area (central zone), with most occurring in ≥ two of the three zones, suggesting that all individuals had the opportunity to associate to some extent. Given this inferred pattern of space use, the small size of the study area, and the lack of community division, the influence of home-range overlap on the association indices between most individuals within this study population seems likely to be small. However, future investigations of association patterns in snubfin dolphins should seek to quantify the degree of home range overlap and its relationship with association patterns, particularly where the study area is large.

4.5.5 Lack of community division

The 43 snubfin dolphin individuals included in the study did not appear to form distinctive clusters within which associations were uniformly higher than those between clusters. Many studies of coastal dolphins have identified distinct communities within the study population (e.g. Möller et al. 2006, Wiszniewski et al. 2009a, Dungan et al. 2012, Titcomb et al. 2015), including snubfin dolphins at Cleveland Bay (Parra et al. 2011). Possible explanations for the lack of community division observed among snubfin dolphins within Cygnet Bay include: the low abundance of this apparently resident population; and, the high rates of association between males and some male-female dyads. For example, no clear community division was observed in a small (65 dolphins), isolated population of bottlenose dolphins in Doubtful Sound, New Zealand (Lusseau et al. 2003), nor within an isolated population of 74 Indo-Pacific humpback dolphins *S. chinensis* off the coast of Taiwan (Dungan et al. 2015), both of which were characterised by well-connected social networks with long-term stability of associations.

4.5.6 Representativeness of study population and study period

At approximately 50 individuals (excluding calves), the population of snubfin dolphins within Cygnet Bay is small (Chapter 2), but comparable in size to some populations reported elsewhere in northern Australia (Parra et al. 2006a, Cagnazzi et al. 2013b, Brooks and Pollock 2015). However, larger populations of approximately 100-200 have also been reported (Palmer et al. 2014; Chapter 2). Demographic factors, such as population dynamics, may represent an important influence on the social structure of a population. For example, increased social fluidity was observed with a decline in abundance among a resident population of killer whales (Parsons et al. 2009). Also, differences in relative density, and therefore encounter rates between individuals, has been suggested as a likely driver of inter-population differences in the complexity of male bottlenose dolphin social behaviour (Connor et al. 2000, Connor and Krützen 2015). As such, analyses of social structure among larger populations of snubfin dolphins are encouraged, to investigate how their social strategies may differ in the presence of a larger number of conspecifics.

While the current study spanned three years, data collection was intermittent, with periods of intensive data collection of 3-5 weeks interspersed among longer periods where no data were collected. Intermittent sampling across multiple years is common in studies of cetacean social structure (Dungan et al. 2015, e.g. Fedutin et al. 2015), where factors such as seasonal weather patterns, resources and accessibility may temporally restrict data collection. Consequently, results may have limited ability to capture variability in the nature and strength of association patterns, such as those associated with seasonal peaks in breeding activity (Connor and Smolker 1995, Smith et al. 2016) or changes in female reproductive state (Connor et al. 1996b, Herzing and Brunnick 1997). My results are biased to the dry season months of April-May and September-October. While previous studies have not revealed clear evidence of seasonality in behaviour, grouping patterns or calving rates of snubfin dolphins (Parra 2005, Cagnazzi 2011), data are limited, and no studies to date have investigated temporal variability in association patterns. Further research, collecting data that are longer and more continuous in temporal extent, is required to investigate temporal variations in grouping and association patterns in snubfin dolphins. Such studies may help to identify periods of higher or lower sensitivity to disturbance and inform the development of appropriate management measures (e.g. Smith et al. 2016).

4.5.7 Male-bias in data collection

My analyses included approximately twice as many male snubfin dolphins as females, which was largely due to a male-bias in genetic sampling (male = 28; female = 12). Additionally, the number of sightings per individual was, on average, higher for males. I consider the most likely explanation for this pattern to be that data collection was biased towards the more visible and approachable larger groups, which were dominated in composition by males: the more gregarious sex. This species often exhibits cryptic behaviour (small group size; inconspicuous surfacing pattern; boat avoidance) (e.g. Parra et al. 2002, Cagnazzi 2011). Single individuals or smaller groups of the more solitary females are more likely to be missed by observers, or may be insufficiently approachable for photo-identification and genetic sampling. Field observations suggested that the most difficult groups to approach for photo-identification data were typically single individuals and smaller groups; genetic samples were generally only obtained from larger groups.

A male-bias in genetic sampling has also been observed for snubfin dolphins at other study sites in this region (e.g. Cone Bay: male = 8, female = 1; Roebuck Bay: male = 20, female = 8; Brown et al. unpublished data). Quérouil et al. (2009a) noted a male-bias in biopsy samples taken from several species of oceanic dolphins in the Atlantic, particularly bottlenose and spotted dolphins. They suggested that avoidance of boats by females and/or curiosity of males towards boats were likely contributing factors, and noted an increasing bias towards males when successive samples were obtained from a single group (Quérouil et al. 2009a).

My results suggest that female snubfin dolphins may be underrepresented in studies which use boat-based observation and biopsy sampling techniques. Capture-recapture models, based on photo-identification data collected from small vessels, are the most commonly used method for estimating demographic parameters of snubfin dolphins (e.g. Parra et al. 2006a, Cagnazzi et al. 2013b, Palmer et al. 2014; Chapter 2). Such models assume that all individuals have an equal probability of being photographed (‘captured’); violation of this assumption results in a downward bias in estimates of abundance and survival probabilities (Pollock et al. 1990; Chapter 2). The results presented here suggest that female snubfin dolphins may exhibit a lower capture probability than males. As such, models which incorporate heterogeneity of capture probabilities should be used, where possible, to

produce unbiased estimates of demographic parameters. Additionally, these findings highlight the importance of conducting data collection in sea conditions which maximise the probability of detecting small, inconspicuous groups of snubfin dolphins.

4.5.8 Concluding remarks

Group composition and dynamics can be markedly different both within and between the sexes, and can have profound influences on the social structure of a population. However, sex-specific investigations of social structure within small cetaceans are few, and largely limited to bottlenose dolphins. Here, I have described the social structure of a small population of Australian snubfin dolphins, and revealed considerable sex-differences in patterns of associations. Most females were relatively solitary, whereas males appeared to form a single large network of frequently associating individuals, some of which associated more frequently than others. These results further our understanding of the behavioural ecology of snubfin dolphins, a data deficient species of conservation concern. My results illustrate that their social systems depart from several patterns commonly observed in coastal bottlenose dolphins. Future studies should seek to characterise the social structure of larger populations of snubfin dolphins, and investigate the behavioural context of their patterns of association.

Chapter 5. Sexual dimorphism and geographic variation in dorsal fin features of Australian humpback dolphins, *Sousa sahulensis*[14]

5.1 Abstract

Determining the sex of free-ranging cetaceans can be challenging. Sexual dimorphism among external features may allow inferences on sex, but such patterns may be difficult to detect and are often confounded by age and geographic variation. Dorsal fin images of 107 female and 54 male Australian humpback dolphins, *Sousa sahulensis*, from Western Australia and Queensland were used to investigate sex-, age- and geographic-differences in colouration, height/length quotient, and number of notches. Adult males exhibited more dorsal fin notches ($p < 0.001$) and a significantly greater loss of pigmentation on the upper half of their dorsal fins ($p < 0.001$) than did adult females. These differences likely reflect that males experience a higher frequency and/or intensity of intraspecific aggression than females. In Queensland, heavily spotted dorsal fins were more frequent among females than males ($p < 0.001$). Logistic regression analyses revealed that dorsal fin spotting and loss of pigmentation on the upper half of the dorsal fin provided the best model parameters for predicting the sex of sampled adults, with 97% accuracy. This technique offers a rapid, non-invasive method for predicting sex in Australian humpback dolphins, which could potentially be applied to populations throughout their range. In contrast to adults, presumed immature animals showed little or no loss of pigmentation or spotting; however, the rate of development of these features remains unknown. There were pronounced differences between Queensland and Western Australia in the intensity of spotting on dorsal fins and the extent of pigmentation loss around the posterior insertion and trailing edge of the dorsal fin. While based on a limited sample size, these geographic differences may have conservation implications in terms of population subdivision, and should be investigated further.

[14] Chapter publication status: published 2016.

5.1 Introduction

Sex determination is a critical component of wildlife ecology; the sex of individuals or social groups can have profound influences on distribution, social structure, population dynamics, and reproductive biology (Begon et al. 2006). This is particularly important when studying taxa that exhibit complex and sexually variable social structures, such as cetaceans (Pryor and Norris 1991, Connor 2000, Whitehead and Rendell 2015). Determining the sex of free-ranging cetaceans is often challenging. Direct visual observations of the genital area require the ventral surface of the animals to be visible, and for sufficient time to allow inspection or for photographs to be obtained. The genital area may also be observed via underwater video, given water of sufficient clarity and animals that are approachable to within a few metres (e.g. Herzing and Brunnick 1997). Additionally, consistent close associations between an adult and calf can be used to infer the sex of mature females (e.g. Smolker et al. 1992).

Molecular methods of sex determination are well-established for multiple taxa, and have been shown to be accurate and reliable across a wide range of cetacean species (Palsbøll et al. 1992, Gowans et al. 2000, Shaw et al. 2003, Jayasankar et al. 2008). Molecular sexing of cetaceans, from the collection of biological material by remote biopsy sampling (Krützen et al. 2002, Bilgmann et al. 2007), skin-swabbing (Harlin et al. 1999), blow sampling (Frère et al. 2010c), or faeces (Parsons et al. 1999), provide reliable alternatives to visual observations. However, these techniques present their own challenges, including more intensive field efforts and the need for additional equipment and analyses. For example, tissue collection is typically restricted to the most approachable individuals within a population and may introduce an age- or sex-bias (Quérouil et al. 2009b). Tissue sampling techniques, while generally considered minimally invasive (Noren and Mocklin, 2012), require study-specific risk assessments (Bearzi 2000, Wang et al. 2008), and may present ethical issues that are incompatible with strictly non-invasive research programs. Therefore, there is great value in developing reliable yet non-invasive and logistically simple techniques for determining the sex of free-ranging cetaceans, particularly those species that are difficult to sample.

For adults of some cetacean species, pronounced sexual dimorphism permits reliable determination of sex by visual observations alone (Ralls and Mesnick 2009). Examples

include body size in sperm whales, *Physeter macrocephalus* (Rice 1989a), dorsal fin size and shape in killer whales, *Orcinus orca* (Olesiuk et al. 1990), head shape and colour in northern bottlenose whales, *Hyperoodon ampullatus* (Gowans et al. 2000), and tooth protrusions in several beaked whale species, *Mesoplodon* spp. (Mead 1989). Adult males of some dolphin and porpoise species develop a distinct post-anal hump (e.g. Jefferson 1990, Perrin et al. 1991, Murphy and Rogan 2006), although these ventral features are less readily observed.

Some cetacean species also exhibit sexually dimorphic colouration patterns, and these may be used to infer sex (Perrin 2009b). For example, white colouration on the head of adult male Cuvier's beaked whales, *Ziphius cavirostris* (Heyning 1989), pink colouration on the bodies of adult male river dolphins (botos), *Inia geoffrensis* (Martin and Da Silva 2006), and the presence/absence or shape of genital patches among some delphinids (e.g. Robineau 1984, Slooten 1991). The accumulation of intraspecific scars lacking pigment may result in the appearance of a lighter colouration, particularly among adult males of some species, such as Risso's dolphins, *Grampus griseus* (Baird 2009) and narwhals, *Monodon monoceros* (Gerson and Hickie 1985).

In addition to variation with sex, colouration can vary with age and geographic region (Perrin 2009b). Colouration typically varies from birth to adulthood, with changes often developing from the onset of maturity, e.g. loss of pigment in Indo-Pacific humpback dolphins, *Sousa chinensis* (Jefferson 2000), development of spots in pantropical spotted dolphins, *Stenella attenuata* (Perrin 2009c), development of ventral speckling in Indo-Pacific bottlenose dolphins, *Tursiops aduncus* (Krzyszczyk and Mann 2012). The extent of visible scarring can also increase with age (Gerson and Hickie 1985, Martin and Da Silva 2006, Baird 2009). While colouration and some characteristics of external morphology can vary among individuals, consistent geographic variation may also be observed within species. This geographic variation reflects a lack of gene flow and/or ecological divergence between populations (Perrin 2009a). With sufficient evidence, different geographic forms may be recognised as distinct populations, ecotypes, or even sub-species (Baker et al. 2002, Pitman and Ensor 2003, Pitman et al. 2011, Wang et al. 2015). Characterising populations and their subdivisions is an integral step in assessing a species' conservation status and developing appropriate management strategies. As such, examinations of external

morphology should consider geographic variation and the important information it may provide, particularly for data deficient species and those of conservation concern.

The surfacing behaviour of cetaceans dictates that the dorsal region is one of the most readily observed and photographed features. High quality dorsal fin images are targeted for individual identification purposes, and are readily available for numerous species. Dorsal fin images, therefore, present the most standardised and widely available visual observation tool for most cetaceans, and can provide a valuable data source for investigating sexual dimorphism (Rowe and Dawson 2009), age estimation (Webster et al. 2010), geographic variation and taxonomy (Wang et al. 2015).

Humpback dolphins (*Sousa* spp.) are small cetaceans occurring in coastal waters of the eastern Atlantic, Indian and western Pacific Oceans (Ross et al. 1994, Parra and Ross 2009, Jefferson and Rosenbaum 2014). The Australian humpback dolphin, (*Sousa sahulensis*, 'humpback dolphin' hereafter), is the most recently described species of the *Sousa* genus, and occupies tropical and sub-tropical coastal shelf waters of northern Australia and southern New Guinea (Parra et al. 2004, Jefferson and Rosenbaum 2014). Little is known of its ecology, although available data suggest that it is vulnerable to numerous threatening processes (Beasley et al., 2012). Challenges in studying humpback dolphins are presented by the remoteness of much of their range, the often turbid waters they occupy, and their tendency towards cryptic behaviour (Parra et al. 2004, 2011, Cagnazzi 2011). Opportunities for visual observations of the genital region are rare, and the success of biopsy darting for tissue samples is often limited to chance encounters with larger, more approachable groups or those individuals somewhat habituated to vessel traffic.

Despite the aforementioned challenges, photo-identification techniques have proven effective for humpback dolphins at most locations of study, resulting in high-quality dorsal fin images of individuals of both sexes from multiple geographic areas (e.g. Brown et al., 2012; Cagnazzi et al., 2011; Parra et al., 2011). Humpback dolphins exhibit extensive intraspecific variation in colouration, some of which may be related to age (Ross et al. 1994, Parra et al. 2004). Young animals are typically a uniform dark grey across the dorsal surface. While adult humpback dolphins are primarily grey on the dorsal surface, they exhibit variable amounts of white scarring, blotches of white/pink and dark or light spotting on numerous parts of the body, including the dorsal fin region (Ross et al. 1994, Jefferson

and Rosenbaum 2014). However, age-related patterns in colouration and other external features have not yet been adequately studied, and nothing is known of sex-differences or geographic variation (Jefferson and Rosenbaum 2014).

My own field observations, along with those of my colleagues, resulted in the hypothesis that patterns of colouration on the dorsal fins of Australian humpback dolphins may be sexually dimorphic, particularly among adults. In this chapter, I explore this hypothesis. Using dorsal fin images of humpback dolphins of known sex (determined using molecular techniques, visual observations or calf associations) from existing catalogues at several study sites, I investigated potential sex-differences in several characteristics of the dorsal fin. I then examined the reliability of those characteristics for predicting the sex of individuals using images alone (cf. Rowe and Dawson 2009). Additionally, dorsal fin characteristics were compared between approximate age classes, and between the east and west parts of the species' range (Fig. 5.1).

5.3 Materials and methods

5.3.1 Data collection

Images of 161 humpback dolphins were compiled from photo-identification catalogues representing three study areas in Western Australia (WA) and three in Queensland (QLD) (Fig. 5.1). Images were collected between 1999 and 2014 during multiple studies using photo-identification techniques (Parra et al. 2006a, Cagnazzi et al. 2011, 2013b, Allen et al. 2012, Brown et al. 2012; Chapter 2).

For the majority of individuals whose images were analysed, sex was determined by molecular analysis of tissue samples (n = 117). Samples were obtained using the PAXARMS biopsy darting technique (Krützen et al., 2002; and see Chapter 3) from small research vessels concurrent with the collection of photo-identification data (Table 5.1). Both biopsy darting and photo-identification were performed by trained, experienced personnel. Photographers aimed to capture a series of images illustrating the biopsy darting event, and only sampled individuals of which the identity (i.e. corresponding images) were included in the analysis. Samples were stored in a freezer in either 100% ethanol or saturated NaCl/20% dimethyl sulfoxide (Amos and Hoelzel 1991). Genomic DNA was extracted using the DNeasy Blood & Tissue Kit (Qiagen). Sex was determined genetically

using sex chromosome-specific primers; loci ZFX and SRY (Gilson et al. 1998) were co-amplified in a single polymerase chain reaction (PCR). The PCR products were run on a 1.5% agarose gel and sex was determined based on the different fragments amplified. The sexes of the remaining 44 individuals were determined by inspection of images of the genital region (n = 3; revealing presence/absence of mammary slits), examination of the stranded individual (n = 2), or by observation of repeated association (over multiple days) with a dependent calf (n = 39) (see Table 5.1). A dependent calf was defined as an animal ≤ 2/3 adult body size, that was routinely observed in 'infant position' (Connor and Smolker 1985, Parra et al. 2006a).

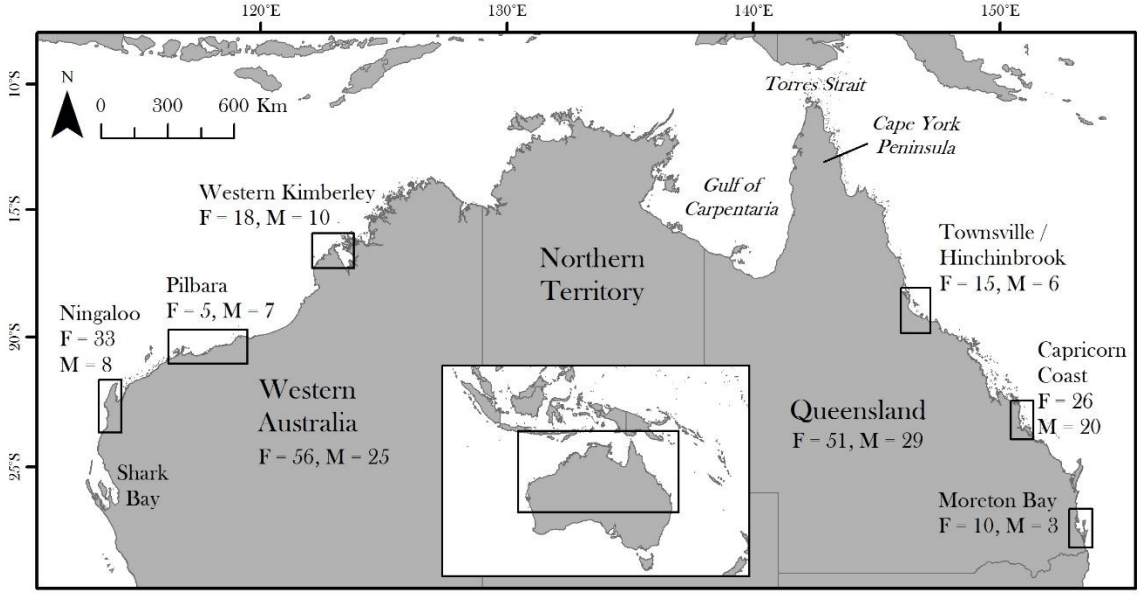


Figure 5.1. Northern Australia, showing study area locations and sample sizes. Sample sizes include all Australian humpback dolphin individuals of known sex (see Table 5.1) available for a minimum of analysis of colouration characteristics; totals for each geographic area are also shown. The range of Australian humpback dolphins in Australian waters is assumed to be coastal waters from Shark Bay in the west to Moreton Bay in the east.

The highest quality images available for each individual were compiled, striving for images that were in sharp focus, well-lit, at an angle perpendicular to the camera lens, and which showed sufficient body of the animal to delineate the dorsal fin. For each individual dolphin, I compiled information on the location, sex, method of sex determination, estimated age class, and, for females, if they had been observed with a dependent calf. To optimise the available sample size, images were assessed for quality and each individual was identified as suitable/unsuitable for two levels of analysis: (1) colouration

characteristics, and (2) proportions (including height/length quotient of dorsal fin, and proportion of upper dorsal fin with loss of pigmentation) and number of notches.

Table 5.1. Method of sex determination of individual Australian humpback dolphins by study area.

	Method of sex determination*		
Study area	**Molecular analysis**	**Visual inspection**	**Dependent calf**
Western Australia			
Ningaloo	F=13, M=8	F=1, M=0	F=19
Pilbara	F=5, M=7	0	0
Western Kimberley	F=4, M=9	F=0, M=1	F=14
Total	*F=22, M=24*	*F=1, M=1*	*F=33*
Queensland			
Townsville/Hinchinbrook	F=11, M=6	0	F=4
Capricorn Coast	F=24, M=17	F=0, M=3**	F=2
Moreton Bay	F=10, M=3	0	0
Total	*F=45, M=26*	*F=0, M=3*	*F=6*
Overall total	**F=67, M=50**	**F=1, M=4**	**F=39**

* See Section 5.3.1 for details of methods of sex determination. ** Includes visual examination of two stranded males.

5.3.2 Colouration characteristics

For analysis of colouration characteristics, the minimum requirement for each individual was an image of one side of the dorsal fin of sufficient resolution, lighting and focus for the colouration to be scored according to several criteria. For all individuals, the single best image (left and/or right side) was selected for analysis. Where images of both left and right sides of an individual of comparable quality were available, these were both included to investigate the symmetry of characteristics between sides and, therefore, the reliability of including individuals with images of only one side available. To minimise the influence of changes in colouration over time, only left and right side images of the same individual taken within consecutive years of data collection were included.

Field observations and a preliminary assessment of the compiled images suggested that dorsal fin colouration could be grouped into three main characteristics: ‘upper LOP (loss of pigment)’, ‘posterior LOP’, and ‘spotting’ (Table 5.2; Fig. 5.2). For each characteristic, a progressive list of categories was defined, beginning at one (characteristic not visible)

and increasing incrementally in the extent/intensity of the characteristic (Table 5.2 and Appendix A5.1).

Table 5.2. Descriptions of dorsal fin colouration characteristics for Australian humpback dolphins, and their corresponding categories. Reference images are provided in Figure 5.2 and Appendix A5.1.

Upper LOP
Description: Loss of pigmentation (LOP) focussed on the upper half of the dorsal fin; varies 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.
Categories:
1 – Small spot(s) of LOP, covering < 1 % of fin, or no discernible LOP
2 – Small patch or multiple small spots of LOP, totalling approximately 1 – 5 % of fin
3 – Larger patch of LOP, totalling approximately 5 – 10 % of fin
4 – Larger patch of LOP, totalling approximately 10 – 20 % of fin
5 – Extensive LOP, totalling > 20 % of fin; may extend **only partially** down the leading edge of the dorsal fin
6 - Extensive LOP, totalling > 20 % and extending down the **full length** of the leading edge of the dorsal fin
Posterior LOP
Description: Loss of pigmentation focussed around the posterior insertion point; varies in density from faint spotting to a distinct region of LOP; may extend partially or completely up the trailing edge of the dorsal fin.
Categories:
1 – Nothing visible; uniform grey colour around posterior insertion
2 – Faint spotting/lighter colour around posterior insertion
3 – Well-defined light spotting around posterior insertion
4 – Well-defined light spotting around posterior insertion with obvious LOP patch
5 – As 4, with larger area of LOP extending **only partially** up trailing edge of dorsal fin
6 – As 4, with larger area of LOP extending up the **full length** of the trailing edge of dorsal fin (merging with 'Upper LOP' if present)
Spotting
Description: Even spotting across the dorsal fin (where LOP absent); varies from low-density small spots (either light or dark in colour) to a completely mottled appearance.
Categories:
1 – Unspotted: uniform grey colour across dorsal fin
2 – Faintly spotted: low-density light or dark small spots
3 – Heavily spotted: higher density light or dark spots of larger size; mottled appearance

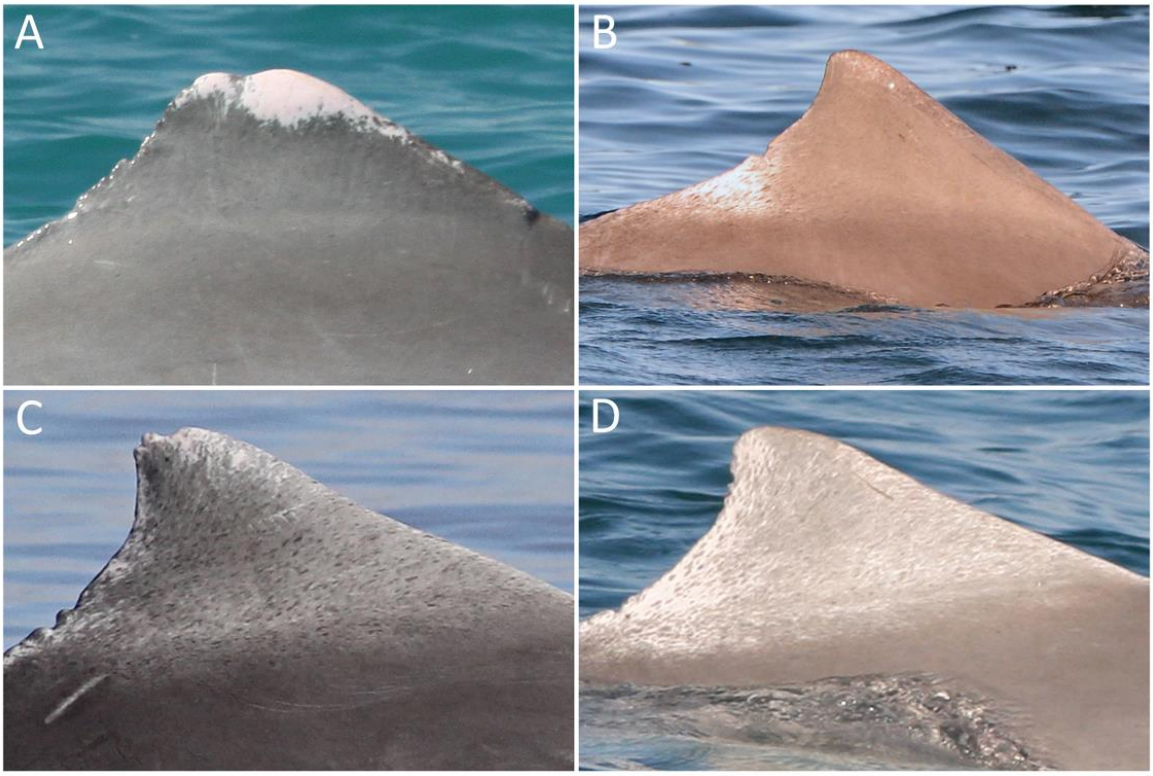


Figure 5.2. Examples images illustrating the three dorsal fin colouration characteristics of Australian humpback dolphins, as defined in Table 5.2. (A) adult male (WA) showing moderate (category 4) upper LOP; (B) adult female (WA) showing moderate (category 4) posterior LOP; (C) and (D) adult females (QLD) showing dark and light, respectively, heavy (category 3) spotting.

Each image was renamed and sorted according to a unique, randomly generated number before being scored independently by ten different scorers. Five of the scorers had extensive experience in photo-identification of humpback dolphins and were familiar with some of the individuals in the analyses. The other five scorers had experience in photo-identification of small cetaceans, but not specifically with humpback dolphins, and were unfamiliar with the individuals included in the analyses (cf. Wang et al. 2008). Scorers were provided with instructions, including a description of the dorsal fin characteristics, their associated categories, and reference examples of each category (see Appendix A5.1). If scorers could not reliably score an image for a particular characteristic, 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 location, sex, or age class of individuals was provided to the scorers, and left and right side images were not consecutively ordered.

For each characteristic, the mode score across all scorers was taken as the assigned category for that image. Where an image was tied (e.g. five scorers scored a '3', while the other five scored '2'), the lead author had the casting vote. Where an image was scored as 'unknown' for a particular characteristic by two or more scorers, an overall category was not assigned. A permutation-based modification of Fleiss' Kappa statistic, *K* (Fleiss 1971, Falotico and Quatto 2014), was calculated to determine the level of agreement among scores for specific images. Values of *K* can range from zero to one, with low values indicating poor inter-scorer agreement and one being perfect agreement.

5.3.3 Proportions and number of notches

The image quality requirements for analysis of proportions (i.e. height/length quotient of dorsal fin and proportion of upper dorsal fin with LOP) and number of notches were more stringent. These parameters are sensitive to bias from inconsistent delineation of the dorsal fin and parallax error where the angle of the fin deviates from perpendicular to the camera lens (Durban and Parsons 2006). Therefore, individuals analysed for proportions and notches required at least one image where the dorsal fin appeared to be completely perpendicular to the photographer, with sufficient body visible above the water to draw lines for accurate and consistent delineation of the fin (see below), and of sufficient clarity to identify small notches on the fin.

For consistency, a single person (A.M. Brown) performed all image processing and analysis, using Adobe Photoshop (version 7.0, Adobe Systems Inc.). To determine the anterior insertion point, a straight line was drawn between the body and the lower leading edge of the dorsal fin, creating a boundary over this concave region (Line 1, Fig. 5.3a). The anterior insertion point was then defined as the deepest point of the concave region (Line 2, Fig. 5.3a). The posterior insertion point was defined as the point at which the straight line of the back (Line 3, Fig. 5.3a) deviated into the curve of the trailing edge of the dorsal fin (Rowe and Dawson 2009, Augusto et al. 2013). A straight line between the two insertion points defined the lower boundary of the dorsal fin. Images were rotated so that the base of the fin was horizontal, and the image was cropped from the base of the fin to the tip, and between the insertion points (Fig. 5.3b). Dividing the height of the image by the length of the image (in pixels) provided the dorsal fin height/length quotient, *H/L* (Fig. 5.3b).

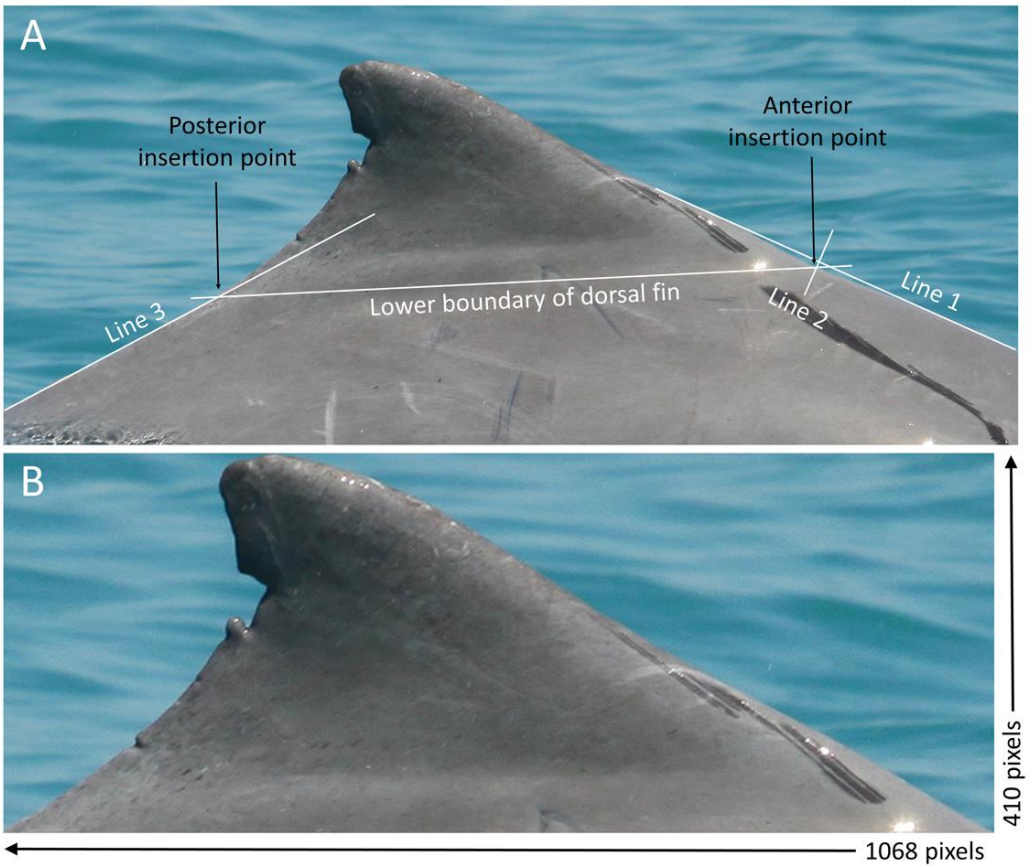


Figure 5.3. (A) Reference lines used to delineate the anterior (Lines 1 and 2) and posterior (Line 3) insertion points of the dorsal fin, and consequently the lower boundary of the dorsal fin. (B) Rotated and cropped dorsal fin image, showing pixel relative height and length (*H/L* of 410/1068 = 0.384). Image shows an adult female Australian humpback dolphin (WA).

The dorsal fin of humpback dolphins slopes smoothly into the dorsal surface of the body (Ross et al. 1994); therefore, anterior and posterior insertion points are less distinct relative to many other small cetaceans with more erect dorsal fins. To address the issue of accurately delineating the dorsal fin from the body, I compared the variability of within-individual *H/L* measurements to the variability between different individuals. For the 53 individuals where two or more suitable images were available, a mean *H/L* and CV was calculated for each individual; within-individual CVs ranged from < 0.1 % to 3.7 %, with a mean of 1.8 %. By contrast, the between-individual CV of mean *H/L* (across the same 53 individuals) was 8.5 %. The greater variability in *H/L* between-individuals than within-individuals suggested that measurement errors would not introduce undue bias, and that including *H/L* values derived from a single image was justified. I did not calculate *H/L* for individuals

where a severe modification to the tip of the fin had resulted in a pronounced (c. ≥ 20%) reduction in relative height (n = 2).

Notches along the edges of dorsal fins are common in small cetaceans and have been widely used to identify individuals of various species (see Würsig and Jefferson 1990). Here, notches were defined as either small nicks, the internal corners of larger notches (Augusto et al. 2013), or noticeable concave deviations from the normal edge of the fin. From the cropped image, the total numbers of notches along the leading and trailing edges of the dorsal fin were counted.

The colouration analyses provided a categorical measure of the level of LOP on the upper half of the dorsal fin. Additionally, a more precise measure of the proportion of upper LOP could be calculated from the delineated and cropped dorsal fin images. The outline of the dorsal fin was selected from the background to count the number of pixels occupied by the dorsal fin. Areas of upper LOP were then traced in bright red, allowing them to be readily selected and their pixel coverage counted (Fig. 5.4). Dividing the number of pixels occupied by upper LOP by the number occupied by the dorsal fin gave the proportion of upper LOP. In order to isolate this measurement from the extension of posterior LOP up the trailing edge of the dorsal fin, LOP along the trailing edge in the bottom half of the frame was ignored in the calculation of % upper LOP (Fig. 5.4).

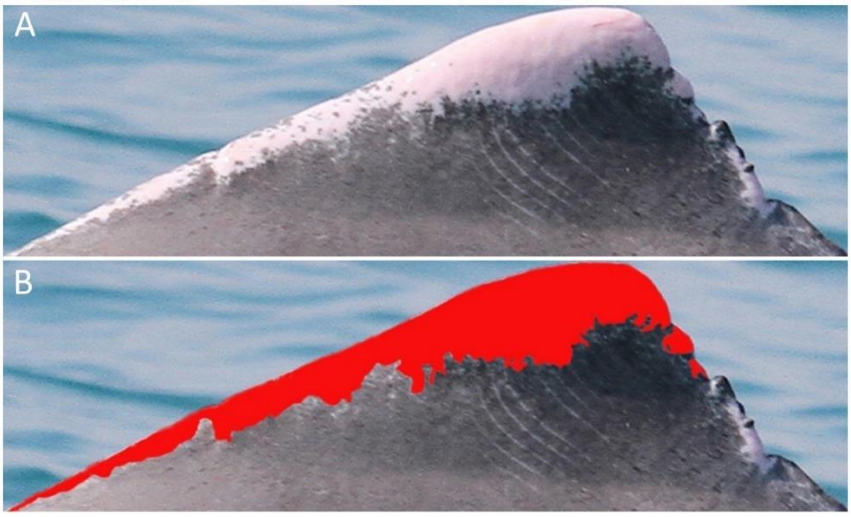


Figure 5.4. (A) Delineated and cropped dorsal fin image, (B) with upper loss of pigmentation (LOP) traced and selected. Note the omission of LOP in the bottom half of the frame along the trailing edge of the fin. Image shows an adult male Australian humpback dolphin (WA).

5.3.4 Determining age classes

All individuals in the dataset were independent juveniles or older, although little information on age was available beyond that. A total of 71 female individuals were routinely observed with a dependent calf (see Section 5.3.1), indicating sexual maturity, and were therefore classified as 'adult'. A total of eight individuals (representing two study areas) had been defined as 'juveniles/sub-adults' based on field observations of the animals' apparent size and appearance, being smaller in body length and typically characterised by a uniform grey dorsal region (Ross et al. 1994, Parra et al. 2004). Using images of these eight individuals as a reference point, a further 14 individuals were defined as 'suspected juveniles/sub-adults'. Preliminary analyses revealed very similar colouration characteristics, proportions and number of notches between the two classes of juveniles/sub-adults, so these were pooled for further analyses. In the absence of information on age class beyond a visual appearance not resembling a juvenile/sub-adult, the remaining 68 individuals were all classified as 'adults'.

5.3.5 Data analysis

Statistical analyses for identifying differences in dorsal fin features between age, sex and geographic groups (WA vs QLD) were performed using the computing programme R (R Core Team 2014). Differences between groups for the scored colouration characteristics were tested using Chi-squared analyses; in cases of small sample sizes where expected values were < 5, Fisher's exact probability tests were performed (GNU R package "gmodels", Warnes 2013). Differences in the means and distributions of the variables % upper LOP and *H/L* were tested using permutation tests employing 5,000 Monte Carlo simulations, which randomly assigned pooled observations between the two groups of data being tested (GNU R package "perm", Fay and Shaw 2010). Wilcoxon rank sum tests were used to test for differences in the distributions of number of notches.

Binomial logistic regression was used to test the effectiveness of the six dorsal fin features (upper LOP, lower LOP, spotting, % upper LOP, *H/L* and number of notches) as predictors of sex. Binomial logistic regression is a form of multiple regression which allows for both continuous and categorical predictor variables that are not assumed to fit any specific distribution, nor to share a linear relationship with the response variable (Field et al. 2012).

Models were developed for: (1) all adult individuals for which a complete set of six measured features were available; (2) all adult individuals for which a complete set of scored colouration characteristics were available; and, (3) as in (2), but separated by geographic location. Stepwise model selection was used to identify significant predictors of sex, and model fit was assessed using Akaike's Information Criterion (AIC). The efficacy of each model in predicting sex was assessed as the percentage of humpback dolphins whose model-predicted sex (based on dorsal fin features) matched their known sex (as determined by the methods provided in Section 5.3.1).

The continuous % upper LOP and categorical upper LOP variables were strongly correlated (r^2 = 0.9), so only % upper LOP was used where available. When models comprised colouration characteristics alone, they experienced issues of complete separation. This was indicated by unreasonably large SE values for each coefficient and resulted from having limited intermediate values for predictor variables, which hindered the identification of a suitable slope for the model within that region (see Field et al. 2012). Complete separation was addressed using Firth's bias-reduced logistic regression approach, which employs penalized profile likelihood-based confidence intervals for its parameter estimates (GNU R package "logistf", Heinze et al. 2013).

5.4 Validation of methods

5.4.1 Inter-scorer agreement and pooling of categories

The number of scorers that scored an image in the same colouration characteristic category varied from three to ten (the maximum possible), with mean values of 7.8 (upper LOP), 6.7 (posterior LOP) and 7.1 (spotting). Based upon the interpretation of Landis and Koch (1977), there was 'moderate' agreement between all ten scorers for each characteristic overall (range of K = 0.45-0.61). This suggested that categories were too numerous, insufficiently discrete, not adequately described or a combination of those factors. In the case of spotting, scorers reported that image quality was often insufficient to make a reliable distinction between unspotted and faintly spotted dorsal fins. Consequently, adjacent categories were pooled *post-hoc* as follows:

- Upper LOP: limited (categories 1-2); moderate (3-4), extensive (5-6)
- Posterior LOP: limited (categories 1-2); moderate (3-4); extensive (5-6)
- Spotting: none/faint spotting (categories 1-2); heavy spotting (3)

The *post-hoc* pooling of categories increased inter-scorer agreement by 22-32%, to a 'substantial' level (Landis and Koch 1977), with *K* values of 0.78 (upper LOP), 0.68 (posterior LOP) and 0.73 (spotting). Future application of this method may benefit from pooling categories and reference images (Appendix A5.1), as described here, prior to scoring images.

5.4.2 Consistency of colouration between left and right side images

Images of comparable quality of the left and right sides were scored for 75 individuals. Using the pooled categories (see Section 5.4.1), there was no change in category between left and right side images for 93% of individuals for upper LOP, 87% for posterior LOP and 100% for spotting. No differences between sides were > ± 1 pooled category, suggesting that colouration characteristics of specific individuals were largely symmetrical between left and right sides. Therefore, undue bias should not be introduced by using the single best image of an individual for analysis, irrespective of the side.

5.5 Results

5.5.1 Sample sizes

The number of individuals available for the two levels of analysis varied between study areas, sex and age class (Table 5.3). Due to a small sample size for the juveniles/sub-adults (n = 22), I did not investigate sex- or geographic-differences within this age class. More females were biopsy sampled and molecularly sexed than males, and additional adult females were sexed based upon associations with a dependent calf (see Table 5.1). Thus, there were approximately twice as many adult females as there were adult males available for analysis. Sample sizes were similar between the two geographic areas, with the exception of a greater number of adult females available for the assessment of proportions and notches from WA (n = 45) compared to QLD (n = 24).

Table 5.3. Sample sizes for Australian humpback dolphins used for examination of dorsal fin features by geographic area, age class, level of analyses (see Sections 5.3.2 and 5.3.3) and sex.

	WA	**QLD**	**Total**
Colouration characteristics			
All age classes	81 (F=56, M=25)	80 (F=51, M=29)	161 (F=107, M=54)
Adult	72 (F=53, M=19)	67 (F=42, M=25)	139 (F=95, M=44)
Juvenile/sub-adult	9 (F=3, M=6)	13 (F=9, M=4)	22 (F=12, M=10)
Proportions and number of notches			
All age classes	66 (F=48, M=18)	44 (F=30, M=14)	110 (F=78, M=32)
Adult	62 (F=45, M=15)	34 (F=24, M=10)	96 (F=69, M=25)
Juvenile/sub-adult	7 (F=3, M=4)	10 (F=6, M=4)	17 (F=9, M=8)

WA = Western Australia; QLD = Queensland

5.5.2 Differences between adult females and adult males

Analyses of sex differences in dorsal fin characteristics were restricted to the 139 individuals classified as adults, which included 95 females and 44 males. The majority of females (81 of 95, 85%) showed only limited upper LOP coverage, whereas all males showed moderate or extensive upper LOP coverage (X^2 = 91.4, df = 2, $p < 0.001$) (Fig. 5.5). Of note, 15 of 16 individuals with upper LOP extending down the entire leading edge of the dorsal fin were male. Conversely, more females (28 of 92, 25%) showed heavy spotting than males (4 of 38, 11%; X^2, df = 1, p = 0.006). Females and males were represented in all posterior LOP categories, with no significant sex-difference observed for this characteristic (X^2 = 4.7, df = 2, p = 0.096).

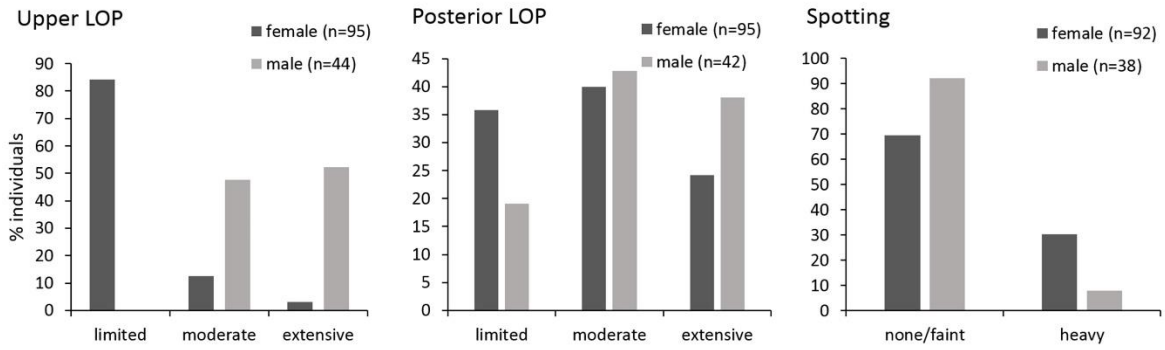


Figure 5.5. Colouration characteristics (upper LOP, posterior LOP and spotting) for adult female vs adult male Australian humpback dolphins. Sample sizes are provided in the legends.

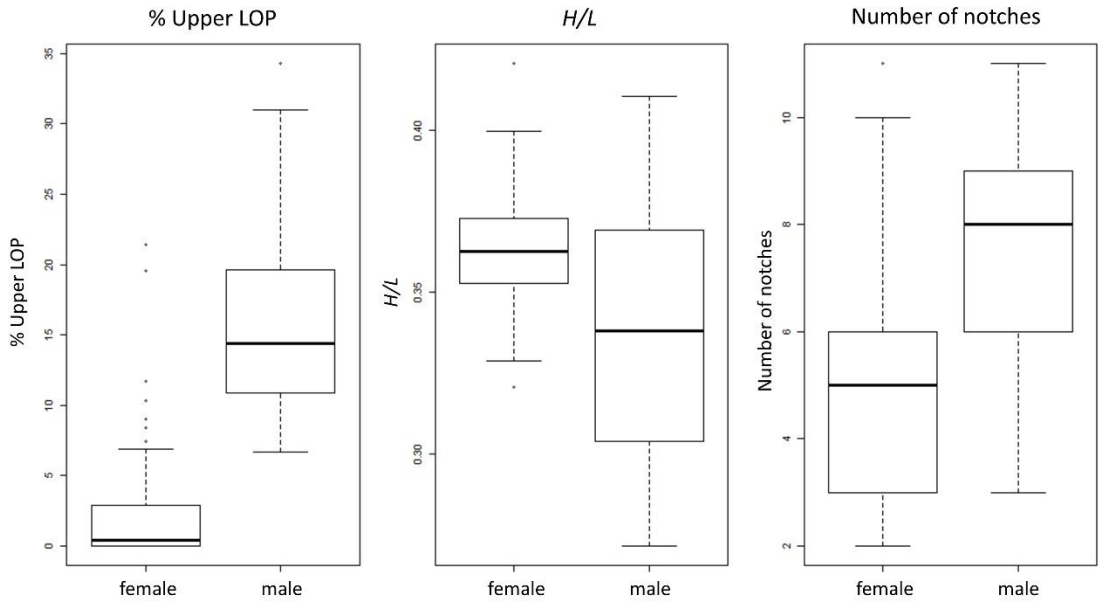


Figure 5.6. Proportion of upper LOP, height-to-length quotient (*H/L*) and number of notches for female (n = 69) vs male (n = 25) Australian humpback dolphins. Thicker horizontal lines show medians; boxes show lower and upper quartile; whiskers show minimum and maximum values (excluding outliers); dots show outliers.

Males exhibited a higher % upper LOP (mean = 16.0 ± 1.7 SE) than females (mean = 2.3 ± 0.04 SE; permutation test $p < 0.001$), with values for females highly skewed towards zero (Fig. 5.6). Excluding outliers, the ranges of values for % upper LOP were almost non-overlapping between sexes. The outliers were seven females with high % upper LOP, including two notably high values of 20 and 21% upper LOP. The most extreme value overall was a male with 34% upper LOP. *H/L* was lower for males (mean = 0.338 ± 0.007 SE) than females (mean = 0.364 ± 0.003 SE; permutation test $p = 0.002$). Males exhibited a greater number of notches (median = 8) than females (median = 5; Wilcoxon rank sum test, Z = -4.3, $r = -0.46$, $p < 0.001$), despite considerable overlaps in the values of both characteristics.

5.5.3 Predicting the sex of adult humpback dolphins based on dorsal fin features

Logistic regression was applied to 87 adult humpback dolphins (67 females, 20 males) for which the complete set of variables was available. Results indicated that % upper LOP ($X^2 = 54.7$, df = 1, $p < 0.001$), *H/L* ($X^2 = 26.8$, df = 1, $p < 0.001$), number of notches ($X^2 = 15.8$, df = 1, $p < 0.001$) and spotting ($X^2 = 4.3$, df = 1, $p = 0.037$) were all individually significant predictors of sex. Stepwise model selection revealed three competitive models within two

delta AIC of each other; all three models included % upper LOP and spotting as significant predictors of sex. The most parsimonious model was selected, with just two predictors – % upper LOP and spotting (X^2 = 70.4, df = 2, $p < 0.001$) – which correctly predicted the sex of 84 of 87 (97%) individuals, misclassifying one female and two males. When the number of notches or *H/L* were added as covariates to a model, they were not significant and both resulted in an additional female (an outlier with high number of notches) being misclassified.

The discriminant function, which can be used to predict the probability that a particular individual is male, is:

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

where π_i is the probability that the individual is a male, *a* is % upper LOP and *b* is spotting. 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.

Logistic regression was also applied to 128 adult humpback dolphins (92 females, 36 males) for which only a complete set of scored colouration characteristics was available. Upper LOP ($p < 0.001$) and spotting ($p < 0.001$) were the only significant variables and constituted the best predictive model, which correctly predicted the sex of 119 out of 128 (93%) individuals, misclassifying six females and three males. The discriminant function using scored colouration characteristics, which can be used to predict the probability that a particular individual is male, is:

$$\pi_i = \frac{e^{[-4.770 + a_i + b_i]}}{1 + e^{[-4.770 + a_i + b_i]}}$$

where π_i is the probability that the individual is a male, *a* is upper LOP and *b* is spotting. Where upper LOP is limited, *a* = 0; for moderate, *a* = 5.750; for extensive, *a* = 7.856. For none/faint spotting, *b* = 0, while *b* = -3.0944 for heavy spotting. Where $\pi_i > 0.5$, the individual is predicted to be male, while < 0.5 is female.

Using WA individuals only (51 females, 16 males), upper LOP was the only significant variable ($p < 0.001$) and, when modelled alone, correctly predicted the sex of 61 of 67 (91%) individuals, misclassifying six females. The addition of spotting, while not found to be a significant predictor in the model ($p = 0.337$), improved the number of correct sex predictions to 62 of 67 (93%, five females misclassified) and was, therefore, considered a worthwhile addition to the model. Using QLD individuals only (41 females, 20 males), both upper LOP ($p < 0.001$) and spotting ($p < 0.001$) were significant. These features collectively constituted the best predictive model, correctly predicting the sex of 57 of 61 (93%) individuals and misclassifying one female and three males. These geographic area-specific models offered no improvement on the accuracy of the overall models, and so no corresponding discriminant functions are provided.

5.5.4 Differences between age classes

A total of 22 individuals (12 female, 10 male) were classified as juvenile/sub-adult (see Section 5.3.4). While adults exhibited a range of colouration characteristics, juveniles/sub-adults showed little or no upper LOP, posterior LOP or spotting (Fig. 5.7). Juvenile/sub-adult individuals showed significantly lower categories than adults for all scored characteristics (Fisher's exact probability tests, $p < 0.001$ for all characteristics).

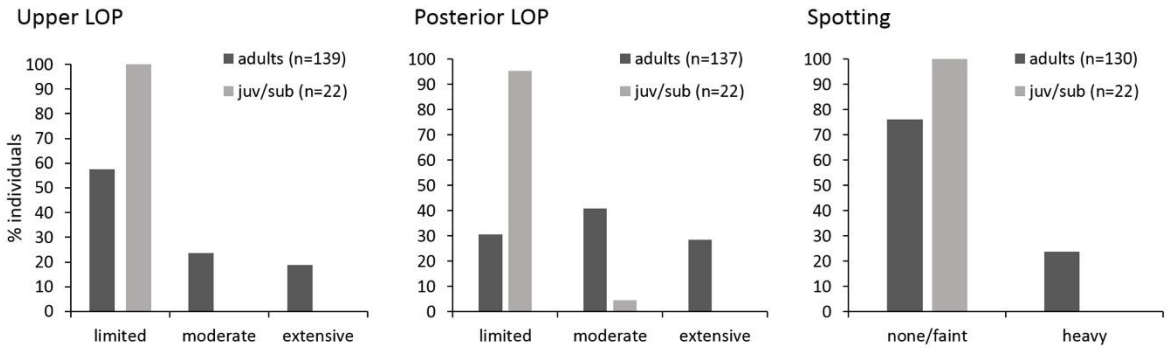


Figure 5.7. Colouration characteristics (upper LOP, posterior LOP and spotting) for adult vs juvenile/sub-adult (juv/sub) Australian humpback dolphins. Sample sizes are provided in the legends.

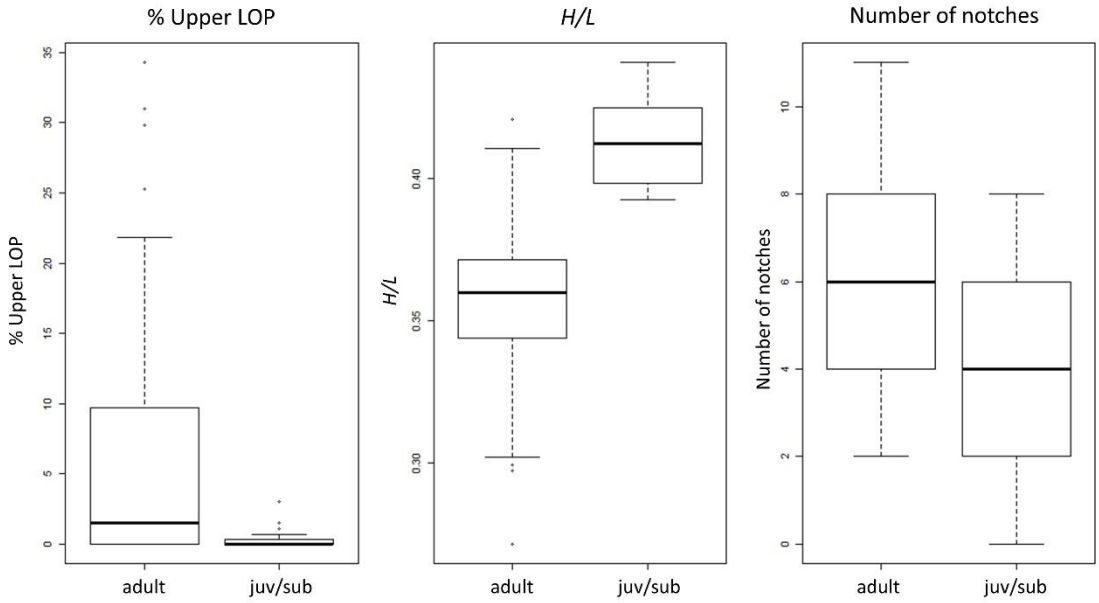


Figure 5.8. Proportion of upper LOP, height-to-length quotient (*H/L*) and number of notches for adult (n = 94) vs juvenile/sub-adult (juv/sub, n = 22) Australian humpback dolphins. Thicker horizontal lines show medians; boxes show lower and upper quartile; whiskers show minimum and maximum values (excluding outliers); dots show outliers.

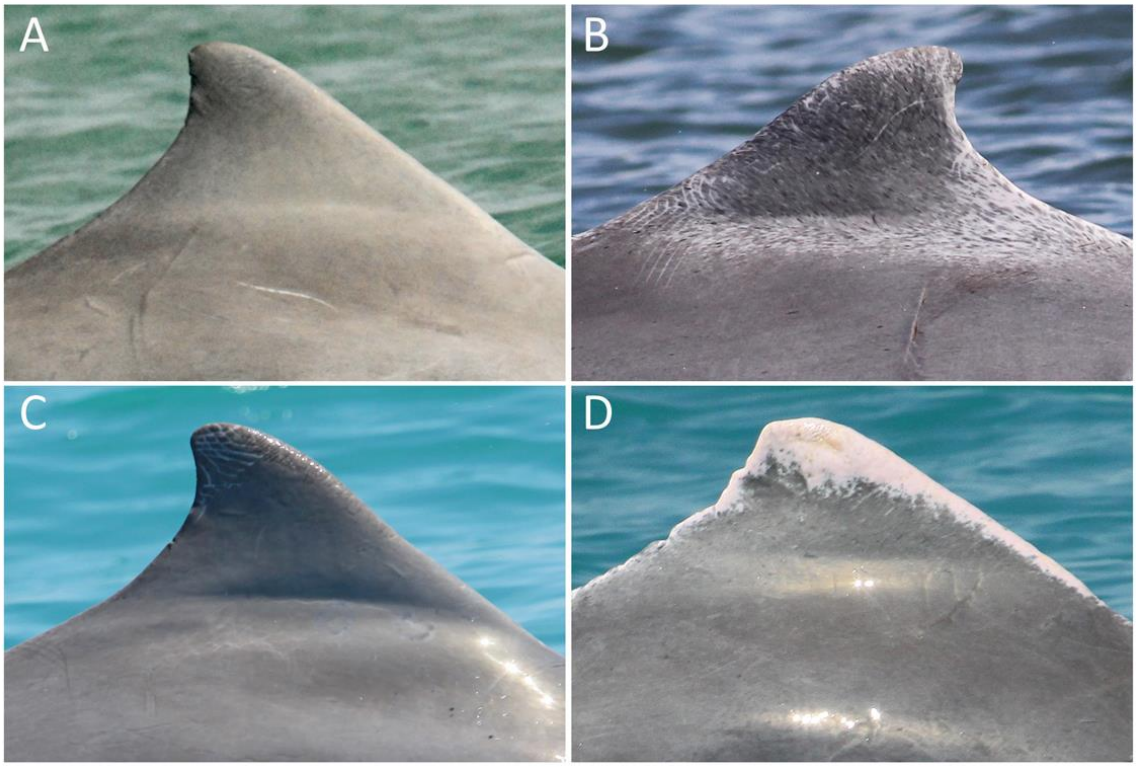


Figure 5.9. Example dorsal fin images of Australian humpback dolphins, illustrating (A) juvenile/sub-adult female, QLD; (B) adult female, QLD; (C) juvenile/sub-adult male, WA; and (D) adult male, WA. Calculated mean *H/L* quotients for these individuals were 0.415 (A), 0.383 (B), 0.426 (C) and 0.316 (D).

The proportion of upper LOP was highly skewed toward zero for both age classes; however, adults showed a much greater range and mean values were significantly lower for juveniles/sub-adults (mean = 0.4 ± 0.2 SE) than adults (mean = 5.9 ± 0.8 SE, permutation test $p < 0.001$) (Fig. 5.8). Values of *H/L* of juveniles/sub-adults (mean = 0.412 ± 0.003 SE) were significantly higher than those of adults (mean = 0.357 ± 0.003 SE; permutation test $p < 0.001$). Compared to adults, juveniles/sub-adults had significantly fewer notches on their dorsal fins (Wilcoxon rank sum test, $Z = -2.8$, $p = 0.005$). Example images of juveniles/sub-adults' dorsal fins alongside those of adults are provided in Fig. 5.9.

5.5.5 Comparing dorsal fin features between WA and QLD

Given the pronounced sex-differences observed in some dorsal fin features of adults, I present comparisons of features between the geographic areas of WA and QLD for each sex separately. Individuals from WA and QLD showed similar within-sex patterns in the extent of upper LOP (Fig. 5.10). For posterior LOP, however, there were significant differences between geographic area for both females (Fisher's exact probability test, $p < 0.001$) and males ($p < 0.001$). Across both sexes, extensive posterior LOP (extending partially or completely up the trailing edge of the dorsal fin) was observed in very few WA individuals (2 of 71, 3%), but this feature was observed in over half of QLD individuals (37 of 66, 56%). While males showed no significant difference in spotting between geographic areas (Fisher's exact probability test, $p = 0.238$), heavily spotted females were far more frequent in QLD (27 of 41; 66%) compared to WA (1 of 51, 2%; $X^2 = 43.8$, df = 1, $p < 0.001$). When only examining individuals from WA, there were no longer significant sex-differences in spotting. All other reported sex-differences in colouration characteristics (see Section 5.5.2) remained significant when tested within each geographic area.

There were no significant differences in % upper LOP or number of notches between WA and QLD, and also no differences in *H/L* among females between the two geographic areas. Adult males, however, showed significantly lower *H*/*L* in WA (mean = 0.320 ± 0.007) compared to QLD (mean = 0.364 ± 0.010; permutation test $p = 0.002$). When considering adults from QLD only, sex-differences in *H*/*L* were insignificant ($p = 0.161$).

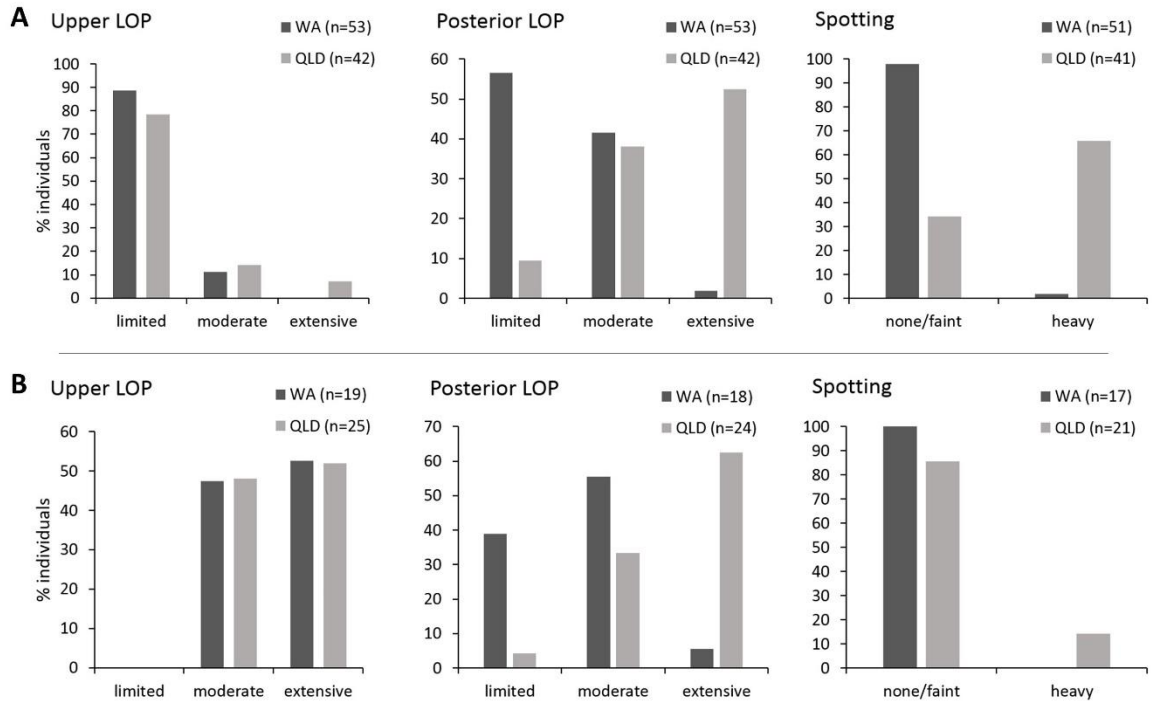


Figure 5.10. Colouration characteristics (upper LOP, posterior LOP and spotting) for Western Australia (WA) vs Queensland (QLD) for (A) adult female and (B) adult male Australian humpback dolphins.

5.6 Discussion

5.6.1 Sexual dimorphism in dorsal fin features

Sex-differences have been reported in several dorsal fin features for various species of delphinids, including size (Tolley et al. 1995), surface area (Rowe and Dawson 2009), indices of shape (Jefferson 1990, Perrin et al. 1991, Jefferson et al. 1997), the severity of epidermal lesions (Rowe and Dawson 2009), and level of scarring and notches (Scott et al. 2005, Rowe and Dawson 2009, Marley et al. 2013, Orbach et al. 2015).

The results reported here revealed significant sexual dimorphism in the dorsal fin features of adult Australian humpback dolphins. Adult male humpback dolphins exhibited a greater loss of pigment (LOP) on the upper half and leading edge of the dorsal fin than was observed on most females. This was the feature that showed the most pronounced dimorphism between adults, irrespective of location. As sexual dimorphism develops with age (Read et al. 1993, Ralls and Mesnick 2009), the presence of young, sexually immature animals in a dataset may obscure potential sex-differences in morphology. The strong sex-

differences observed in these results suggest that relatively few immature animals were erroneously classified as adults.

The exact origin of the LOP on the upper half of humpback dolphin dorsal fins is unclear. However, the greater prevalence of this feature among males suggests that it is likely related to a male-bias in the frequency and/or intensity of intraspecific aggression. Among mammals, far greater parental investment by females produces a bias in the ratio of sexually receptive females to sexually mature males (Emlen and Oring 1977, Clutton-Brock and Parker 1992). This bias can generate intense competition between males for access to mates, which may manifest as considerable inter-male aggression within some dolphin populations (e.g. Connor et al. 1992b, Parsons et al. 2003, Martin and Da Silva 2006). The dorsal fin of male humpback dolphins appears to be regularly targeted in intraspecific physical aggression, often exhibiting multiple tooth-rakes that may penetrate the dermis (Fig. 5.11). Furthermore, the greater number of dorsal fin notches observed among males than for female humpback dolphins is consistent with a sex-difference in intraspecific aggression (Scott et al. 2005, Orbach et al. 2015).

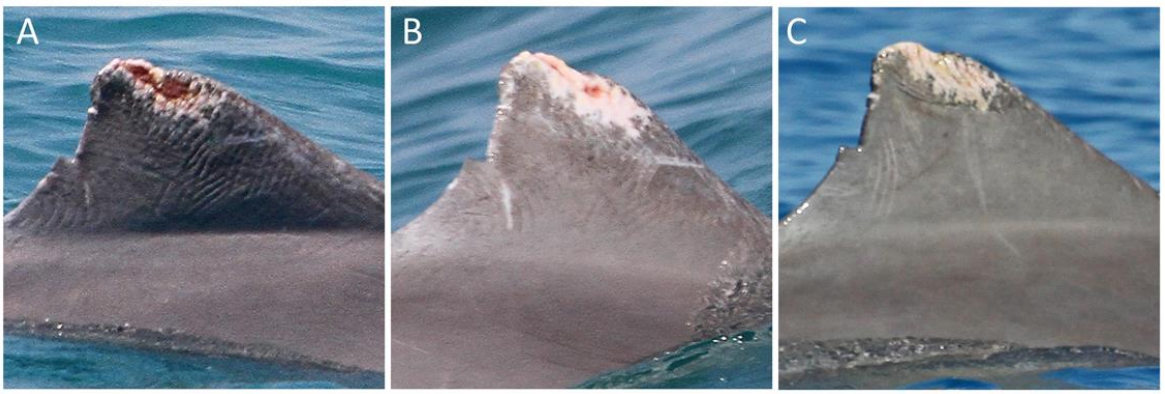


Figure 5.11. Multiple tooth-rake injuries on the dorsal fin of an adult Australian humpback dolphin (WA) and its progression from open wound to healed area without pigment. (A) t = 0, (B) t + two weeks, (C) t + one year.

Across several odontocete species, intraspecific scarring is more prevalent among adult males than females (e.g. MacLeod 1998, Scott et al. 2005, Martin and Da Silva 2006, Rowe and Dawson 2009, Orbach et al. 2015). As these scars heal, they are initially lacking in pigment and take on a white appearance. In some species, such as common bottlenose dolphins, *T. truncatus*, scars are not cumulative and will re-pigment within 5-20 months (Lockyer and Morris 1990). In other species, such as Risso's dolphins and narwhals, scars

appear to remain unpigmented and accumulate with age (Gerson and Hickie 1985, Baird 2009). I hypothesise that the upper LOP observed on male humpback dolphin dorsal fins represents an accumulation of unpigmented scar tissue from multiple healed tooth-rake and other injuries resulting from aggressive inter-male interactions.

Figure 5.12. Adult male Australian humpback dolphin (WA) exhibiting extensive loss of pigment on the upper dorsal fin, along with loss of pigment along the dorsal ridge of the peduncle and edges of flukes. A large, healed shark bite is visible mid-way along the peduncle.

Similar unpigmented areas have been observed on the tips of the flukes and peduncle of adult male humpback dolphins (Fig. 5.12). These body areas are known to be targeted in inter-male aggression in other dolphin species (Scott et al. 2005, Martin and Da Silva 2006) and, along with the dorsal fin, may frequently be subject to abrasions and injuries. It is noted that similar white areas, interpreted as scarring, have been observed on the dorsal fin and tail stock of larger adult Indian Ocean Humpback dolphins, *Sousa plumbea,* off South Africa (Jefferson and Karczmarski 2001, Best 2007). However, in many cases, tooth-rakes (including those on the dorsal fin) and other bodily injuries do apparently heal and re-pigment in humpback dolphins (see shark bite in Figure 5.12).

Alternatively, the LOP on the upper half of the dorsal fins of humpback dolphins may develop independently of, or in conjunction with, intraspecific interactions. Humpback dolphins of both sexes also exhibited LOP around the posterior insertion point and trailing edge of the dorsal fin. Additionally, many females (particularly those in QLD) showed light or dark spotting across the entire dorsal fin. The mottled appearance of these features

suggests that they develop from a gradual fading of pigment, independent of intraspecific interactions. As such, posterior LOP and spotting in humpback dolphins may be primarily age-dependent, comparable to the progressive pigmentation loss observed in Indo-Pacific humpback dolphins (Jefferson and Leatherwood 1997, Jefferson 2000). Age-effects are also likely to be present in the development of upper LOP, as older individuals would be expected to show a greater extent of cumulative scarring (Gerson and Hickie 1985, Baird 2009).

Despite females generally showing limited upper LOP extent, there were seven outliers with up to 21% dorsal fin upper LOP (see Appendix A5.1, Upper LOP, category 5, left image). All these female outliers for upper LOP were genetically sexed, of which three were also observed with a dependent calf. Errors can occur during molecular sexing procedures (Robertson and Gemmell 2006, Lanyon et al. 2009), and the potential remains for a small number of individuals in this study to have been sexed incorrectly. However, the existence of several female dolphins with a high % of dorsal fin upper LOP is likely to reflect the large inter-individual variation observed in dorsal fin features, along with a lack of understanding of age effects on these features. Females exhibiting extensive upper LOP may be older individuals. Aggressive intraspecific interactions may also result in scarring on the dorsal fins of female humpback dolphins (Scott et al. 2005), and interactions with predators (i.e. large sharks) (Heithaus 2001) or anthropogenic activities (Wells et al. 2008, i.e. vessel strikes or fishing gear entanglement, Slooten et al. 2013) may result in dorsal fin scarring to individuals of either sex.

5.6.2 Predicting sex from dorsal fin images

Models were presented that were able to predict the sex of this sample of adult humpback dolphins with a high degree of accuracy using dorsal fin images alone. The accuracy of sex predictions was higher (97%) when optimum quality images were available. Nonetheless, the comparable performance (93% accuracy) of the model based on categorical predictors alone suggests that accurate predictions of sex may be achievable even in the absence of optimum quality images. Misclassified individuals included males and females from both geographic areas, suggesting no pronounced sex- or geographical-bias. However, the lack of heavy spotting on females in WA resulted in those individuals being more susceptible to misclassification when their dorsal fins showed moderate upper LOP extent. Future

studies might improve visual discrimination between male and female humpback dolphins by either refining colouration characteristic categories or quantifying additional features, such as more detailed measures of shape (Rowe and Dawson 2009, Augusto et al. 2013). However, image quality may be a limiting factor when attempting to examine more fine-scale differences in dorsal fin colouration.

The photo-identification technique presented here provides a rapid, non-invasive method of determining the sex of humpback dolphins, offering an alternative to more logistically demanding, costly, and invasive methods of sex determination for free-ranging cetaceans. Applying this technique to individuals of unknown sex within the populations sampled here may enhance the study of many elements of humpback dolphin biology.

The greater potential value of the discriminant function identified by this study will be revealed by its application to populations beyond those represented in the current dataset. Geographic variation in external morphology and associated sexual dimorphism may reduce the effectiveness of discriminant functions when they are applied to different populations and geographic areas. Rowe and Dawson (2009) used dorsal fin images to develop a discriminant function which correctly predicted the sex of 93% (40 of 43) of a sample of common bottlenose dolphins within one population, but accuracy was lower (75%, 18 of 24) when applied to an adjacent population (Currey et al. 2008). By contrast, the discriminant function presented here was based on a larger sample size representing a wide geographic range, including both western and eastern extremes of the species' range. The most influential predictor of sex in both WA and QLD humpback dolphins was the extent of upper LOP, suggesting that this feature may be an effective predictor of sex within other parts of the species' range.

The colour pattern of Australian humpback dolphins is different from that of other species in the genus *Sousa* (Jefferson and Rosenbaum 2014) and, therefore, the discriminant functions presented here are not directly applicable to other *Sousa* species. However, I encourage those studying other *Sousa* species, and other species of cetaceans in general, to use their existing photo-identification data and perform comparable image-based investigations of dorsal fin and other morphological features. In particular, the observations of white scarring on the dorsal fins of some larger adult Indian Ocean humpback dolphins (Best 2007) draw comparisons to the current results, and should be investigated further.

The current study analysed data which were not collected for the specific purpose of investigating sex-differences in external features. As such, there was no inclusion of a photogrammetric control (i.e. laser dots at a known distance apart) and, therefore, no measurements of the absolute size of dorsal fin features could be made. Laser-photogrammetry represents a low-cost (relative to the camera equipment) and simple addition to photo-identification methods, and has been successfully used to produce morphological measurements in bottlenose dolphins (Rowe and Dawson 2009, Cheney et al. 2015). Future photo-identification studies of humpback dolphins should consider the addition of laser-photogrammetry; this would allow accurate and reliable measurements of external features and morphology, potentially improving methods of sex-determination and facilitating additional investigations of morphology.

5.6.3 Age effects

Some species of delphinids exhibit profound age-related changes in colouration, which enable inferences to be made on the relative maturity of individuals (Perrin 2009c, Jefferson et al. 2012). For example, Indo-Pacific humpback dolphins in Hong Kong waters are born a uniform grey before progressively losing pigment with age; some adults, primarily females, are completely unpigmented (Jefferson 2000, Jefferson et al. 2012).

As specific age data on individuals was lacking, the current analysis was only able to investigate age-differences between two approximate age classes of Australian humpback dolphins: (1) juveniles/sub-adults; and (2) adults. As has been previously reported, the dorsal fins of juveniles/sub-adults showed little or no colour deviation from a uniform dark grey (Ross et al. 1994, Parra et al. 2004). Their dorsal fins were also proportionally taller and had fewer notches than those of adults, likely reflecting incomplete body growth and only limited exposure to intraspecific aggression.

These results show that spotting and loss of pigmentation on the dorsal fins of humpback dolphins develops with the progression into adulthood, as do colour changes among several other delphinids (Jefferson 2000, Baird 2009, Perrin 2009c, Krzyszczyk and Mann 2012). However, the rate of development, and individual variability, of these features remains unknown. The current dataset was compiled from studies of limited duration (intermittent sampling over < 5 years), so it was not possible to monitor changes in features over any

length of time. Long-term studies that follow individuals from birth to adulthood will be essential to understanding the relationship between age and the development of dorsal fin features in humpback dolphins.

5.6.4 Geographic variation in external morphology

Among odontocetes, geographic variation in morphology has been reported wherever adequate samples have been available (Perrin 2009a). For most species, it is not possible to collect a sufficient number of samples for detailed morphological analysis (Wang 2009). However, image-based analyses of free-ranging animals can reveal pronounced geographic variation in external features, which may provide insight into population structure. Geographic variation has been observed in the fluke pigment of humpback whales, *Megaptera novaeangliae*, (Rosenbaum 1995), dorsal spotting in Indo-Pacific humpback dolphins (Wang et al. 2015), eye patch and dorsal cape variations in killer whales (Pitman and Ensor 2003, LeDuc et al. 2008), and body colouration of spinner dolphins, *Stenella longirostris*, in the eastern Pacific Ocean (Perrin et al. 1991). In each of these examples, colouration patterns were used to infer limited gene flow and inform population subdivision and the identification of management units.

Delineating populations is critical to the conservation of marine mammals (Taylor 1997, Wang 2009) and, in some countries, is a legal requirement of wildlife managers/decision-makers (e.g. the United States' *Marine Mammal Protection Act 1972*). Different populations exhibit local adaptations and genetic differences, which increase the ability of a species to persist through stochastic events (Frankham et al. 2010). Additionally, the nature and severity of threatening processes vary geographically (Halpern et al. 2007), as do populations' vulnerability to such processes, making it essential to implement conservation efforts at an appropriate biogeographic scale (Wang 2009).

Significantly greater posterior loss of pigmentation and spotting was observed on the dorsal fins of humpback dolphins in QLD than for those in WA. The data presented here represent only a subset of the individuals for which dorsal fin images are available (irrespective of the availability of information on sex). Additionally, the current data did not include individuals from large portions of the species' range, including the Northern Territory, the Gulf of Carpentaria, the Cape York Peninsula and New Guinea (see Fig. 5.1). Nonetheless,

these results provide preliminary evidence of geographic variation in dorsal fin colouration of humpback dolphins between WA and QLD, suggesting some level of population structure between the two regions.

No investigation of population genetic structure in Australian humpback dolphins throughout their entire range has been conducted to date. However, regional investigations of genetic connectivity within WA (Brown et al. 2014) and QLD (Cagnazzi 2011) have revealed limited gene flow between putative populations over distances of < 350 km of coastline. Given the thousands of kilometres of coastline between the WA and QLD study areas, it seems highly likely that the observed differences in pigmentation patterns of Australian humpback dolphins reflect population genetic structure. Additionally, between the two geographic areas lies the shallow Torres Strait, which has intermittently presented a land bridge between Australia and New Guinea during periods of lower sea levels through much of the late Pleistocene (Voris, 2000). The isolating influence of this biogeographic barrier has been identified in molecular studies of mobile marine taxa such as the dugong (Blair et al. 2014), and may have facilitated the evolution of different geographic forms of humpback dolphins (Lin et al. 2010, Jefferson and Rosenbaum 2014).

An expanded image-based analysis of dorsal fin features, incorporating a larger number of animals from a wider geographic scope, is recommended for future studies of geographic variation in humpback dolphin external morphology. Such investigations, augmented by molecular analyses, are required to further describe the population structure of humpback dolphins throughout their range and to identify appropriate geographic scales for conservation management.

Appendix A5.1 Reference images

The following reference images were provided to scorers as a guide for the scoring of colouration characteristics of Australian humpback dolphins (see Section 4.3.2). All pictured individuals were considered adults. The sex of individuals pictured is provided here for the benefit of the reader. To avoid potential bias, sex information was not provided to scorers, and it is recommended that this information be omitted in future scoring exercises.

Terminology

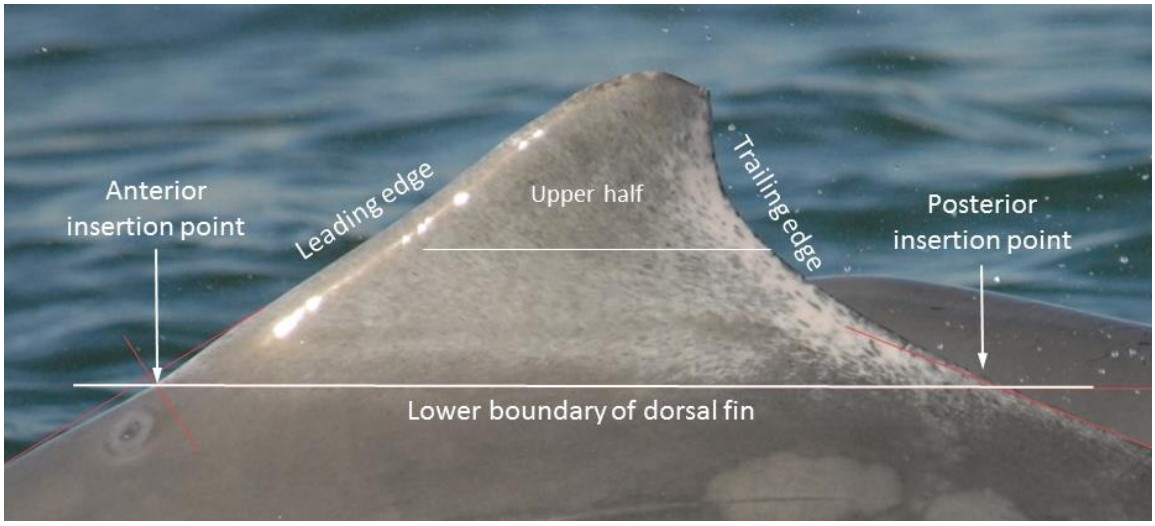


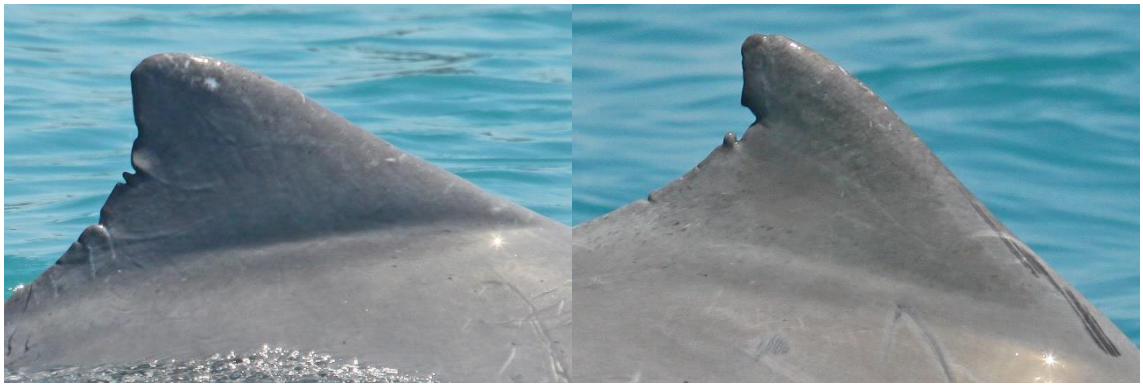
Image shows an adult female (QLD).

Upper LOP

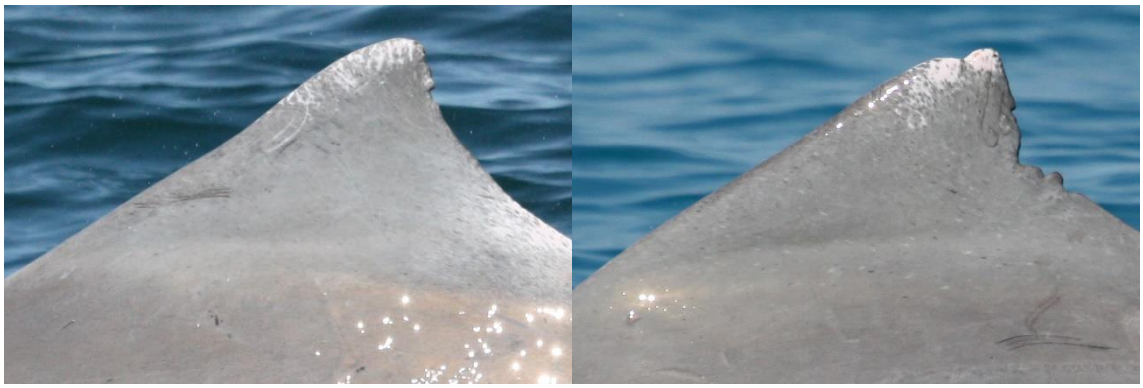
Description: loss of pigmentation focussed on the upper half of the dorsal fin (*but including the entire leading edge of the fin*); varies in density from sparse spots of white to a continuous region of white/pink covering over a third of the dorsal fin; may extend partially or completely down the leading 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.

Categories:

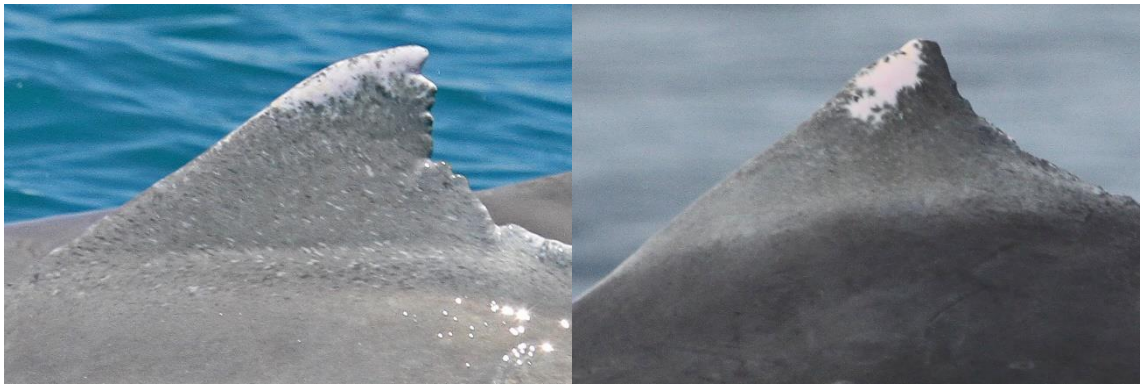
1 – Small spots of LOP, covering < 1 % of fin (left, female, WA), or no discernible LOP (right, female, WA)



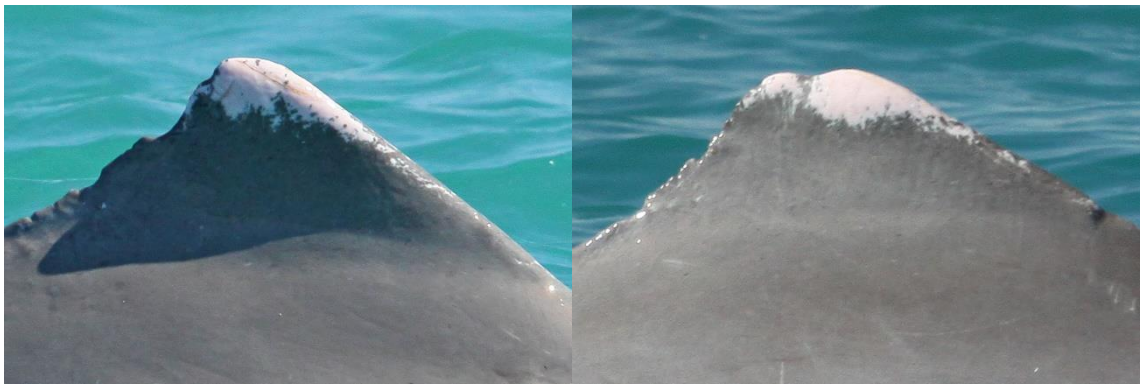
2 – Small patch or multiple small spots of LOP, totalling approximately 1 – 5 % of fin (both female, WA)



3 – Larger patch of LOP, totalling approximately 5 – 10 % of fin (both female, WA)



4 – Larger patch of LOP, totalling approximately 10 – 20 % of fin (both male, WA)



5 – Extensive LOP, totalling > 20 % of fin; may extend only partially down the leading edge of the dorsal fin (left, female, QLD; right, male, QLD)

6 - Extensive LOP, totalling > 20 % and extending down the full length of the leading edge of the dorsal fin (both male, WA)

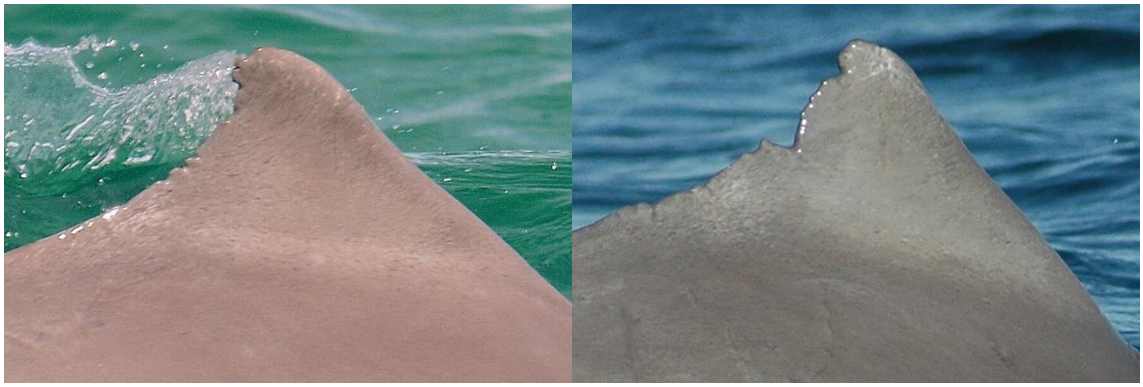
Posterior LOP

Description: loss of pigmentation focussed around the posterior insertion point; varies in density from faint spotting to a distinct region of LOP; may extend partially or completely up the trailing edge of the dorsal fin.

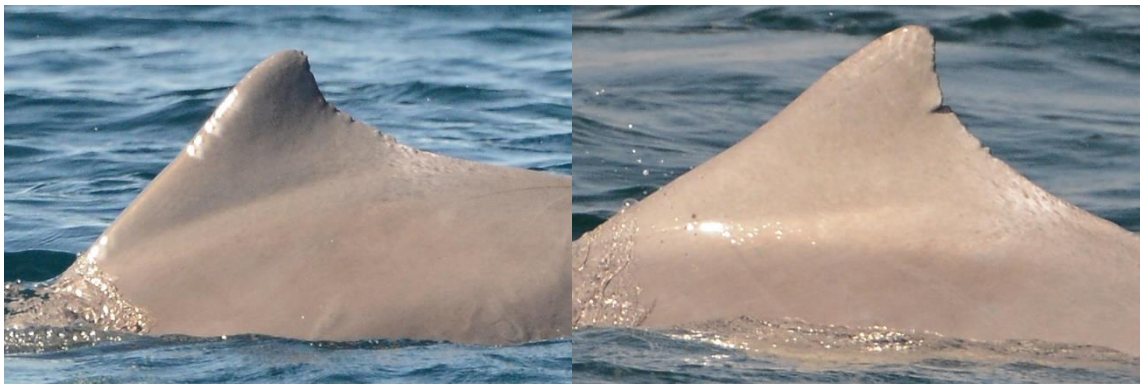
Categories:

1 – Nothing visible; uniform grey colour around posterior insertion (both female, WA)

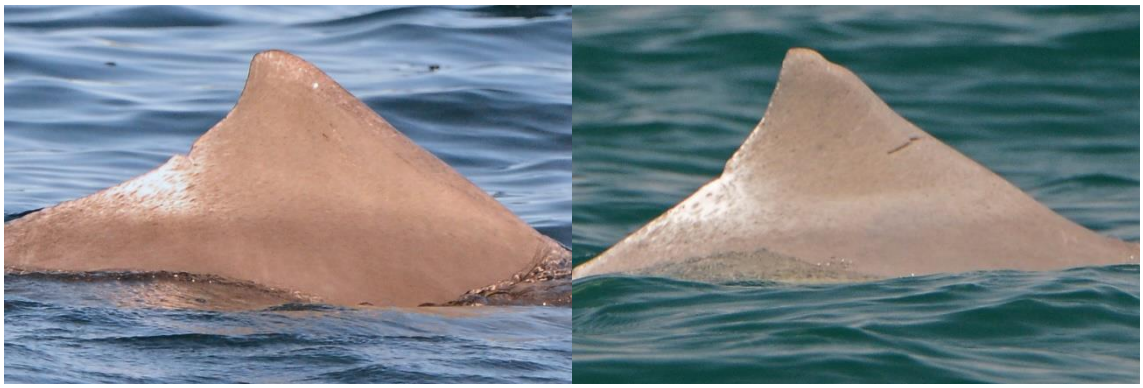
2 – Faint spotting/lighter colour around posterior insertion (both female, WA)



3 – Well-defined light spotting around posterior insertion (both female, WA)

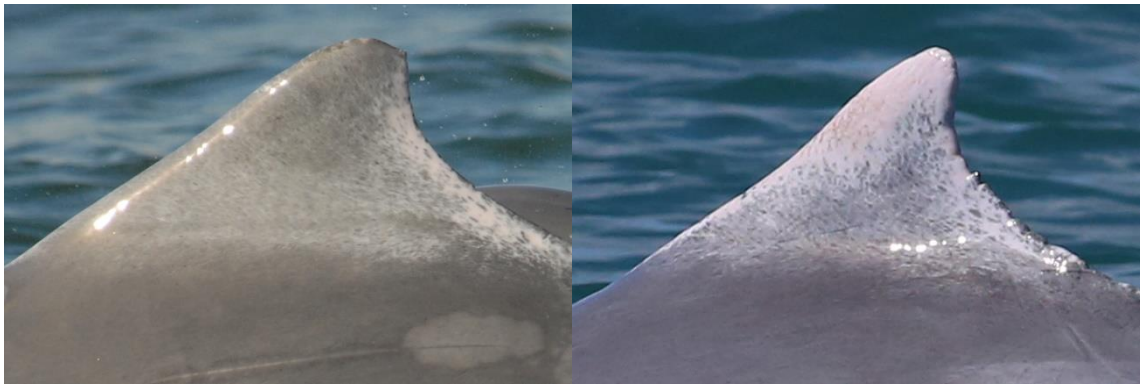


4 – Well-defined light spotting around posterior insertion with obvious LOP patch (both female, WA)



5 – As 4, with larger area of LOP extending only partially up trailing edge of dorsal fin (left, female, WA; right, female, QLD)

6 – As 4, with larger area of LOP extending up the entire trailing edge of dorsal fin (merging with ‘Upper LOP’ if present) (left, female, QLD; right, male, QLD)



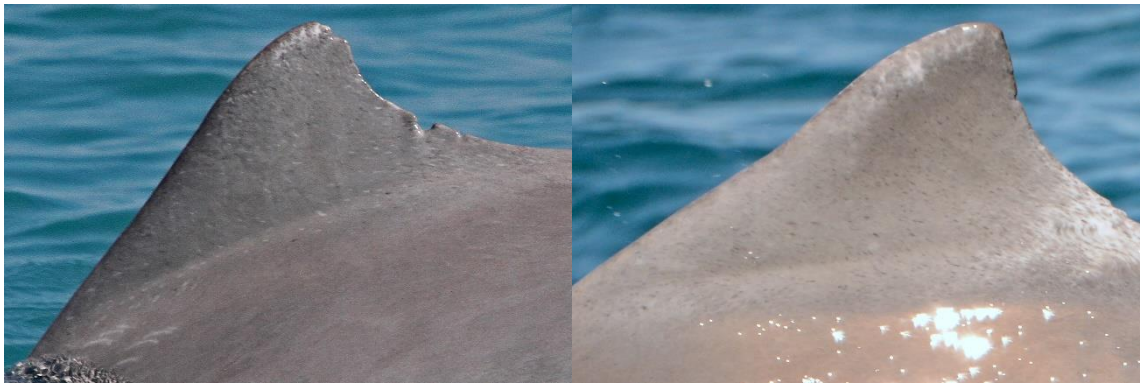
Spotting

Description: even spotting across the dorsal fin (where LOP absent); varies between 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.

Categories:

1 – Unspotted: uniform grey colour across dorsal fin (both female, WA)

2 – Faintly spotted: low-density light or dark small spots (both female, WA)



3 – Heavily spotted: higher density light (right) or dark (left) spots of larger size; mottled appearance (both female, QLD)

Chapter 6. General discussion and recommendations

The overarching aim of this thesis was to improve the scientific basis for the conservation and management of the three species of dolphins occurring in the inshore waters of tropical northern Australia: the Australian snubfin dolphin (*Orcaella heinsohni*), Australian humpback dolphin (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*). This research was motivated by the lack of data on these species, particularly in north-western Australia, which has precluded comprehensive assessment of their vulnerability (i.e. conservation status) and the management of potential impacts of threatening human activities (Beasley et al. 2012, Bejder et al. 2012, Woinarski et al. 2014). Through the four data chapters, I have presented: estimates of the abundance and site fidelity of these three species across multiple sites in north-western Australia (Chapter 2); an examination of population genetic structure in snubfin and humpback dolphins in this region (Brown et al. 2014; Chapter 3); a sex-specific investigation of the social structure of a population of snubfin dolphins occurring within this region (Chapter 4); and, an analysis of sex- and geographic differences in the dorsal fin features of humpback dolphins, utilising data collected from both north-western and north-eastern Australia (Chapter 5). In so doing, I have extended the geographic scope of quantitative population data on Australia's tropical inshore dolphins into the western third of their distribution, presented new information on the social behaviour of snubfin dolphins, and developed an effective method for determining the sex of adult humpback dolphins. Combined, this research has provided valuable data to inform their conservation and management both within the main region of study and throughout northern Australia. The methodological approach I utilised, including field data collection and analytical techniques, are broadly applicable to coastal and estuarine dolphins in both remote and populated areas where dolphin population data are lacking.

The focus of this research was on the less-studied and more geographically restricted snubfin and humpback dolphins. Data were also presented on the abundance and site fidelity of bottlenose dolphins, which are subject to the same data deficiencies and threatening activities as other inshore dolphin species in this region. The population genetic structure of bottlenose dolphins off north-western Australia, while not a component of this thesis, is presented in Allen (2015), including samples collected concurrent to data

presented in this thesis. I refer the interested reader to Allen (2015) for these complementary findings.

In the following sections I present, for each of the data chapters: the key findings; their implications; to what extent the chapter objectives were fulfilled; and, the limitations of the data. I reiterate and expand upon the recommendations made in each of the data chapters; these provide options for future research to support the conservation and management of inshore dolphins in north-western Australia, many of which are broadly applicable across northern Australia and to other species of inshore dolphins elsewhere. Chapters 2 and 3 are grouped due to their complementary findings and implications. Additionally, I provide a discussion of how these findings contribute to the assessment of the conservation status of snubfin and humpback dolphins under defined criteria, and summarise recent, nationally coordinated efforts to this end.

6.1 Chapters 2, 3: Abundance estimation and population differentiation

Abundance estimates are an important element of wildlife management strategies: they contribute to assessments of the vulnerability and conservation status of populations, and facilitate the management of potential impacts from threatening activities. Using small vessels as cost-effective research platforms, photo-identification surveys and capture-recapture models were applied to provide the first quantitative abundance data for snubfin, humpback and bottlenose dolphins at five sites in the Kimberley region of north-western Australia. Repeated sampling provided information on the fidelity of animals to some sites, while a power analysis tested the utility of a series of abundance estimates for trend detection. There were considerable differences in species' abundance between the sites surveyed, particularly for snubfin and bottlenose dolphins, likely reflecting species-specific habitat preferences. Within the c. 130 km^2 study sites, the estimated abundance of most species was $\leq$ 60 individuals (excluding calves), and fewer than 20 humpback dolphins were identified at each site in any one 3-5 week sampling period. However, larger estimates of c. 130 snubfin and c. 160 bottlenose dolphins were obtained at two different sites. Several local populations showed evidence of high site fidelity, particularly snubfin dolphins. A power analysis indicated that, with the most precise abundance estimates obtained in this study, it would take a minimum of seven years to detect modest rates of

change with high statistical power, by which time populations could be depleted to very low levels.

Understanding the structure of populations is important in determining the appropriate management scale at which to assess potential anthropogenic impacts and inform conservation strategies. The objective of Chapter 3 was to examine the genetic diversity and structure of snubfin and humpback dolphins among selected locations in north-western Australia, including the occurrence of hybridisation between the two species. Skin tissue biopsy samples were collected from free-ranging dolphins at four study sites: snubfin dolphins from Cygnet (n = 32) and Roebuck Bays (n = 25), each separated by 250 km of coastline; and, humpback dolphins from the Dampier Archipelago (n = 19) and the North West Cape (n = 18), each separated by 350 km of coastline. Analyses of nuclear and mitochondrial DNA markers revealed significant genetic differentiation between sampled populations of both species. Estimates of migration rates between sampled populations were either close to, or below, recommended thresholds for considering sampled populations as independent management units (Hastings 1993, Palsbøll et al. 2007). There was preliminary evidence of low effective population size (N_e) within sampled populations of snubfin dolphins. Additionally, strong photographic and genetic evidence was presented for the first documented case of hybridisation between a female snubfin dolphin and a male humpback dolphin. This phenomenon likely represents a low frequency, natural hybridisation, resulting from the propensity of humpback dolphins to initiate aggressive-sexual interactions with snubfin dolphins.

When combined, my estimates of abundance (Chapter 2) and population genetic structure (Chapter 3) add to the limited, but growing, body of evidence to suggest that snubfin and humpback dolphins in northern Australia occur as a metapopulation: a discontinuous distribution of small local populations, with evidence of site fidelity and a low level of connectivity between populations (Parra et al. 2006a, Cagnazzi 2011, Cagnazzi et al. 2011, 2013b, Brown et al. 2014, Palmer et al. 2014, Brooks and Pollock 2015; Chapters 2 and 3). Small, largely isolated populations are at greater risk of local declines than large, stable populations due to limited resilience to mortality resulting from stochastic environmental perturbations and anthropogenic activities (Shaffer 1981). For isolated populations of approximately 100 dolphins, the annual loss of a single individual above natural mortality is unsustainable (e.g. Slooten et al., 2006; Cagnazzi et al., 2013). To maintain the viability

of these local populations, it is essential that: (*i*) threats to local populations are characterised, quantified and mitigated; and, (*ii*) opportunities for dispersal between local populations are maintained.

The results of highly variable abundance of each species between study sites (Chapter 2) highlights the need for site-specific data collection using appropriate survey techniques to quantitatively assess the status of local populations and their vulnerability to potentially threatening activities. In the absence of such data, the assumption of similar relative abundance among these broadly sympatric species may grossly underestimate, or overestimate, the importance of a site to a single species. The value of long-term data to support conservation and adaptive management of wildlife populations is well-recognised (e.g. Clutton-Brock and Sheldon 2010, Cheney et al. 2014), and recent expert-led prioritisation exercises have emphasised the need for long-term studies of population dynamics of inshore dolphins in northern Australia (Department of the Environment 2013b, 2015b). The abundance estimates presented in Chapter 2 for several sites and species can inform the selection of sites for future long-term research, and provide a base from which to investigate trends in abundance. While such data are necessary to provide inferences on population trajectories to inform assessments of species' conservation statuses (see Section 6.4), it is important to consider the challenges involved in detecting trends within populations of the sizes reported here. Power analyses (Chapter 2) reaffirmed the assertion that implementing conservation measures should not be contingent upon statistically robust proof of a decline for small populations of cetaceans (Taylor and Gerrodette 1993, Thompson et al. 2000, Taylor et al. 2007b). Monitoring trends in abundance alone will not ensure the longevity of populations (e.g. Jaramillo-Legorreta et al. 2007, McDonald-Madden et al. 2010), and must fall within an adaptive management framework which seeks to mitigate threats and specifies precautionary trigger points for intervention (e.g. Potential Biological Removal approaches, Wade 1998, Thompson et al. 2000).

6.1.1 Fulfilment of objectives and study limitations

The collection of population data on free-ranging cetaceans is typically time-consuming, costly, and logistically-challenging (Wilson et al. 1999). The data collection presented in this thesis was subject to a variety of challenges, including: the cryptic tendencies of snubfin and humpback dolphins; the remoteness of the study region; the limited prior

knowledge of the species' occurrence; and, limited periods of calm sea conditions appropriate for sighting small cetaceans. These challenges placed constraints on study site selection, study design, often resulted in limited sample sizes, and therefore placed certain limitations on the data analyses and interpretation of results.

In Chapter 2, estimates of absolute abundance were produced for multiple sites and species where such data were previously lacking. Furthermore, repeat sampling periods at three sites provided an indication of the fidelity of individuals to these sites. As such, I consider the objectives of this chapter fulfilled, with the results providing a significant contribution towards knowledge of the abundance of inshore dolphins in the Kimberley region of north-western Australia. The survey design represented a compromise between: obtaining robust estimates of absolute abundance; repeat sampling to investigate site fidelity; covering as many study sites as possible; the accessibility of sites; and, the available resources. Consequently, several relatively small and accessible study sites were selected, from which a subset were surveyed multiple times, therefore providing robust site-specific abundance data complemented by insight into site fidelity and the variability of abundance within the region.

The study design incorporated multiple repeats of a c. 60 km long transect within an area of c. 130 km^2. This represented a level of effort which could be completed within a period of 3-5 weeks on-site (given average weather patterns) and therefore provide capture-recapture abundance estimates of reasonable precision, given the resources available. These methods were based upon those which had been successfully implemented in studies of inshore bottlenose dolphins elsewhere in Australia (Smith et al. 2013, Sprogis et al. 2016), and proved to be effective for study sites in the Kimberley region, where reasonable numbers (i.e. $\geq$ c. 15) of a species were repeatedly observed during a sampling period. However, for several sites/species, apparent low densities of dolphins resulted in insufficient number of captures for capture-recapture methods to be used to estimate absolute abundance. While the use of a standardised survey design ensured that at least a measure of the relative abundance of each species could be produced and compared between sites, future capture-recapture studies may be more successful if they: (*i*) focus on areas where prior knowledge strongly suggests a higher density of animals; and/or (*ii*) increase effort to survey a larger area (e.g. by using multiple vessels, Brooks and Pollock 2015). Alternatively, it may be more appropriate to adopt alternative methods of abundance

estimation, such as broad-scale line-transect surveys from vessel or aerial platforms (see Dawson et al. 2008).

Through study design and selected analytical procedures, the assumptions of the capture-recapture models used to estimate abundance in Chapter 2 were considered to be largely met, and these estimates subject to minimal bias. However, the possibility remains that some estimates may be slightly biased downwards due to potential heterogeneity of capture probabilities, as the findings of Chapter 4 suggest may be occurring for snubfin dolphins at Cygnet Bay. While, in this study, any potential bias would not be sufficient to influence the conclusions drawn from these findings, it may be desirable to use models which account for potential heterogeneity of capture probabilities ('heterogeneity models') in future studies. As it may not be possible to effectively implement heterogeneity models to small data sets using traditional maximum likelihood estimators (as was the case in this study), Bayesian versions of heterogeneity models may offer more suitable alternatives (Rankin et al. 2016).

The results of Chapter 3 present the first estimates of genetic diversity and differentiation for snubfin and humpback dolphins in Western Australia, therefore providing valuable insight into the population genetic structure of these species and fulfilling the objectives of this chapter. However, the low number of samples and sampling sites did restrict some of the analyses and subsequent interpretation of the results. For humpback dolphins, sample sizes were too low to estimate N_e, and estimates of N_e for snubfin dolphins (where sample sizes were slightly larger) exhibited wide confidence intervals. For both species, population genetic structure could only be examined between two sampling locations. Consequently, it was not possible to test for a pattern of isolation-by-distance (e.g. Fontaine et al. 2007), thereby limiting the inferences which could be made as to the likely scale at which populations of these species become differentiated. Incorporating a greater number of sampling locations into future analyses will be essential to provide more detailed examination of the population genetic structure.

Several authors argue that differentiating populations using genetic data alone is unwise (Paetkau 1999, Crandall et al. 2000, Waples and Gaggiotti 2006). An absence of historical gene flow may not correspond to current demographic isolation, yet it is the contemporary movement of animals which may be more pertinent in conservation and management

actions (Palsbøll et al. 2007). Genetic pedigree analysis has been used to identify patterns of contemporary dispersal in another marine mammal, the dugong (Cope et al. 2015), and may prove a useful tool in future studies of inshore dolphins, although sample sizes would need to be considerably larger (i.e. hundreds) than those currently available for such methods to be effective. While a combination of demographic, ecological and genetic data will provide the most robust assessments of population differentiation (e.g. Paetkau 1999, Taylor and Dizon 1999), such inter-disciplinary approaches require considerable resources and lengthy time-frames (Olsen et al. 2014). In the meantime, the findings of genetic differentiation presented in this thesis, combined with the demographic evidence of limited movement (e.g. Parra et al. 2006a, Cagnazzi et al. 2011; Chapter 2), provide a useful indication of the population structure of these species.

6.1.2 Recommendations

The following recommendations are made:

1. *Conduct dedicated, site-specific data collection using appropriate techniques to provide baseline population data on inshore dolphins to inform environmental impact assessments of proposed coastal developments and other potentially threatening activities.* Given the highly variable abundance of different species between sites documented in this Chapter, species-specific abundance data are critical in order to assess the relative importance of sites to each species and the population-level significance of potential impacts. Data collection should include vessel-based surveys of comparable design to those presented here, with a minimum of two sampling periods to add confidence to results and provide preliminary evidence of site fidelity. It is vital that such surveys are conducted in appropriate sea conditions (see Chapter 2: Section 2.4) and extend into shallow, inshore habitats. For major development proposals, the development of longer-term, Before-After-Control-Impact monitoring studies are strongly recommended (e.g. Brooks and Pollock 2015).

2. *At key reference sites of varying levels of impact, establish long-term, individual-based studies of the population dynamics of inshore dolphins to inform conservation and adaptive management* (see Brooks et al. 2014). I identify Roebuck Bay as an ideal candidate for the development of an ongoing monitoring programme on snubfin dolphins, due to the size (c.

130 individuals) and accessibility of this local population, the range of potential threats (see Appendix A1), and the potential compatibility with the proposed Roebuck Bay MPA management plan. An inter-disciplinary approach is recommended, in order to answer a variety of pertinent questions, including trends in abundance and habitat use, the factors influencing these, and a greater understanding of the impacts of threatening activities. Data collection over multiple years will also facilitate the investigation of a variety of behavioural and ecological research questions.

3. *In future capture-recapture studies of inshore dolphins, the use of models which incorporate heterogeneity of capture probabilities is recommended in order to minimise bias in population parameters (see Section 6.2).* Where data are insufficient for these models to be successfully implemented using traditional maximum likelihood estimators, consideration should be given to using Bayesian versions (e.g. Rankin et al. 2016).

4. *Develop a greater understanding of the distribution and habitat preferences of tropical inshore dolphins.* A compilation and spatial analysis of existing sightings data should be undertaken to investigate environmental factors influencing the distribution of each of the three species, and subsequently identify areas of likely occurrence. The results of such an exercise could inform the selection of reference sites for future data collection, which is of particular value to species which appear to be patchily distributed across a large, remote area.

5. *Conduct studies to characterise, quantify and mitigate the potential impacts of threatening activities to inshore dolphins.* In particular, quantitative assessments of the level of interactions between gillnet fisheries and inshore dolphins are urgently required.

6. *Effectively engage local wildlife management agencies and indigenous communities/ranger groups and their capacity (i.e. vessel, logistics base, personnel, knowledge of local area), including the provision of training in inshore dolphin survey techniques, in order to foster collaborations and facilitate the ongoing collection of baseline data from remote locations.*

7. *Collect and analyse a greater number of genetic samples across a broader geographic range in order to gain a more detailed understanding of the population genetic structure of tropical inshore dolphins across northern Australia*[15].

8. The importance of movement corridors between local populations requires greater recognition to ensure sufficient connectivity to maintain the evolutionary potential and viability of these small, somewhat isolated populations. The environmental footprint of coastal developments must be considered in relation to local populations of inshore dolphins, both in the immediate vicinity and adjacent areas, and the influence anthropogenic activities (e.g. prolonged acoustic disturbance through pile driving, increased vessel movements or dredging) may have on the movement of animals between populations.

6.2 Chapter 4: Social structure of snubfin dolphins

In addition to a lack of baseline population data, there is also limited understanding of the social structure of snubfin and humpback dolphins, which represents an important element of a species' population biology (Whitehead 1997). The objective of Chapter 4 was to analyse the social structure of snubfin dolphins within a specific study population: specifically, to investigate sex-specific grouping, association patterns and their correlations with genetic relatedness. Using photo-identification and molecular data collected from a population of c. 50 snubfin dolphins at Cygnet Bay in the Kimberley region of north-western Australia, I revealed pronounced sex-differences in individual sociability: males generally formed stronger associations and were far more gregarious than females. There was evidence of non-random associations within all sex classes, with the exception of female-female associations. Male-male associations showed long-term temporal stability, whereas female-female associations decayed more rapidly. Males appeared to form a single large network of frequently associating individuals, some of which associated more frequently than others, while most females were relatively solitary. While small, single-sex groups were common, a minimum of 42% of groups were of mixed sex, which were

[15] Since the analyses for Chapter 3 were completed, additional genetic samples have been collected of both snubfin and humpback dolphins at existing sites, which will provide more precise estimates of effective population size and gene flow between these sampled populations. Furthermore, samples of both species have been collected at an additional site (Cone Bay), to the east of Cygnet Bay, which will allow preliminary investigation of gene flow across a wider geographic area.

typically much larger. Associations were not correlated to genetic relatedness. These results further our understanding of the behavioural ecology of snubfin dolphins, and illustrate that their social systems depart from several patterns observed in coastal bottlenose dolphin populations (e.g. Connor et al. 2000).

There was a considerable male-bias in both the frequency of sightings and number of biopsy samples obtained, suggesting that female snubfin dolphins may be underrepresented in studies that use boat-based observation and biopsy sampling techniques. This likely reflected the greater detectability and approachability of larger, male-dominated groups, and may have implications for common assumptions of capture-recapture studies of abundance and demographic parameters.

6.2.1 Fulfilment of objectives and study limitations

The chapter objectives were fulfilled, to the extent that the somewhat limited sample size permitted. Of all the sites and species surveyed in the collection of data to support this thesis, snubfin dolphins within Cygnet Bay were the only local population for which sufficient data were collected to perform a meaningful and sex-specific investigation of social structure. Nonetheless, for several individuals, the number of sightings was quite low (i.e. five to ten), particularly for females. The adopted minimum threshold of five sightings is the same or greater than that used in many previous studies of cetacean social structure (e.g. Parra et al. 2011, Chabanne et al. 2012). However, all associations of an individual are unlikely to be captured in five sightings, and therefore association indices of those individuals with a limited number of sightings (i.e. close to the minimum of five) may be biased low. Additionally, there were insufficient sightings of most individuals for accurate estimation of home ranges, which precluded the investigation of the influence of overlap in individual space use on association patterns. However, sighting location data suggested that all individuals had the opportunity to associate to some extent, and that overlap in individuals' space use within the fairly small study area was likely to be high. Lastly, due to the intermittent sampling design (an artefact of the data being primarily collected for demographic purposes), seasonal variations in grouping and association patterns could not be investigated.

6.2.2 Recommendations

The following recommendations are made for future research:

9. *Investigate the social structure of snubfin dolphins within larger populations (i.e. > 50) to determine the representativeness of existing studies, and investigate if patterns of association vary in the presence of a greater number of conspecifics.*

10. *Collect longer-term data on association patterns of snubfin (and humpback) dolphins, including more temporally continuous data collection, in order to obtain larger sample sizes to facilitate investigations of: (i) patterns of association in relation to individual space use (i.e. home ranges); (ii) seasonal variability in grouping, association patterns and behaviour; (iii) long-term stability of associations; and, (iv) behaviour-specific patterns of association and their relationship with genetic relatedness.*

6.3 Chapter 5: Sexual dimorphism and geographic variation in dorsal fin features of humpback dolphins

The sex of individuals or social groups can have profound influences on distribution, social structure (see Chapter 4), population dynamics, and reproductive biology (Begon et al. 2006), and the sex-ratio of a population is an important parameter in population viability analysis (Boyce 1992). Determining the sex of free-ranging cetaceans is challenging (Gowans et al. 2000); however, identifying sexual dimorphism in readily observable external features, such as dorsal fins, may facilitate simple, non-invasive methods of sex-determination (Rowe and Dawson 2009). The objectives of Chapter 5 were to: use dorsal fin images to investigate potential sex-differences and geographic variation in dorsal fin features of humpback dolphins; assess the utility of dorsal fin images to determine sex; and, infer potential population structure between geographic regions.

By performing a quantitative analysis of dorsal fin images of 107 female and 54 male humpback dolphins from several study sites in north-western and north-eastern Australia, I revealed sex-differences in several dorsal fin features of adult humpback dolphins. Adult males exhibited more dorsal fin notches and a significantly greater loss of pigmentation on the upper half of their dorsal fins than did adult females, likely reflecting that males experience a higher frequency and/or intensity of intraspecific aggression than females.

Based on the observed sex-differences in dorsal fin features, I developed discriminant functions that were able to predict the sex of adult individuals with a high level of accuracy (93-97%). The analyses of dorsal fin images also revealed significant differences in the pigmentation patterns observed on dorsal fins of humpback dolphins between north-western and north-eastern Australia. In contrast to adults, presumed immature animals showed little or no loss of pigmentation or spotting; however, the rate of development of these features remains unknown.

The technique presented here offers a rapid, non-invasive method for predicting sex in Australian humpback dolphins, which could potentially be applied to populations throughout their range and further enhance studies of their population dynamics and behavioural ecology. The observed geographic differences in the dorsal fin colouration of humpback dolphins, while based on a limited sample size, suggest some level of population structure between the two regions, and may have conservation implications in terms of population differentiation.

6.3.1 Fulfilment of objectives and study limitations

The objectives of Chapter 5 were fulfilled, although several limitations in the analyses are noted. This study utilised data that were not collected for the specific purpose of investigating sex-differences in external features. As such, there was no inclusion of a photogrammetric control (i.e. laser dots at a known distance apart) and, therefore, no measurements of the absolute size of dorsal fin features could be made. Laser-photogrammetry represents a low-cost (relative to the camera equipment) and simple addition to photo-identification methods, and has been successfully used to produce morphological measurements in bottlenose dolphins (Rowe and Dawson 2009, Cheney et al. 2015). Future photo-identification studies of humpback dolphins should consider the addition of laser-photogrammetry; this would allow accurate and reliable measurements of external features and morphology, potentially improving methods of sex-determination, and facilitating additional investigations of morphology such as growth rates and more accurate age-class categorisation.

Additionally, it was not possible to determine the sex of smaller, presumed immature individuals from dorsal fin features. Due to limited study durations, age data were

unavailable, and individuals (all of which were non-calves) were simply categorised into two age classes: juvenile/subadult and adult. Longer-term data are required to investigate the relationship between age and the development of dorsal fin features in humpback dolphins, the results of which may assist in estimating the proportion of mature individuals within populations.

6.3.2 Recommendations

The following recommendations are made for further research:

11. *Apply the dorsal fin image-based method of sex determination to individuals of known sex within populations not represented in the current data, in order to test the broader efficacy of this technique.*

12. *Apply the dorsal fin image-based method of sex determination to adult individuals of unknown sex within study populations represented in the current data, in order to facilitate sex-specific studies of behavioural ecology and estimate sex ratios.*

13. *Conduct longer-term studies to investigate the relationship between age and the development of dorsal fin features in humpback dolphins.*

14. *Incorporate laser-photogrammetry into the collection of new photo-identification data to allow more accurate investigations of sex-, age- and geographic-differences in external morphology.*

15. *Perform an expanded image-based analysis of dorsal fin features of humpback dolphins, incorporating a larger number of animals from a wider geographic scope, in order to provide further insight into the population structure of humpback dolphins throughout their range.* Where possible, augment such investigations with molecular analyses (as per recommendation 7).

6.4 Assessing conservation status

While a strong motivation for this research was that there were insufficient data available to assess the species' conservation statuses under national and international criteria,

gathering all the necessary data to perform such assessments was not the objective of this thesis research. A task of such magnitude would require a coordinated strategy across northern Australia with considerable resources (see below), and is comfortably beyond the scope of a thesis project. Nonetheless, the research presented in this thesis does provide valuable population data in contribution to future conservation assessments of these species. In particular, the assessments of abundance (Chapter 2) and population differentiation (Chapter 3) will help guide the generation of plausible estimates of total abundance, the degree of fragmentation of their distribution, and the identification of subpopulations and their likely maximum size. Additionally, the abundance estimates presented in Chapter 2 provide a base from which to investigate population trends. While obtaining statistically significant evidence of a decline may be an unrealistic objective (see Chapter 2, Section 2.4.3), repeat surveys at appropriate study sites in the future may allow plausible inferences of population trajectories.

As an example, I consider my findings in the context of Criterion C of the IUCN Categories and Criteria for Species Status Assessment (IUCN 2012) (Table 6.1), which was recently selected as the most appropriate criterion by Parra and Cagnazzi (2016) in their assessment of the Australian humpback dolphin against the IUCN Red List Criteria. Considering the available evidence (which included the findings of Chapters 2 and 3 of this thesis), and following a precautionary approach, the authors suggested that the humpback dolphin qualified as 'vulnerable' under criterion C2a(i) due to: the total number of mature individuals[16] being plausibly $\leq$ 10,000; an inferred continuing decline due to cumulative impacts, particularly ongoing habitat degradation and fragmentation; and, that each local population studied to date (between which there is evidence of limited genetic connectivity) was estimated to contain c. 100 mature individuals – far fewer than the 1,000 subpopulation threshold size (Parra and Cagnazzi 2016) (Table 6.1). An updated assessment of snubfin dolphins against the IUCN Red List Criteria is currently underway (D. Cagnazzi, pers. comm.[17]).

[16] Typically estimated as 50-60% of population size (Taylor et al. 2007a).
[17] Daniele Cagnazzi, Southern Cross University, personal communication, August 2015.

Table 6.1. IUCN Categories and Criteria for Species Status Assessment: Criterion C (Small population size and decline).

	Critically Endangered	**Endangered**	**Vulnerable**
Number of mature individuals	< 250	< 2,500	< 10,000
AND at least one of C1 or C2			
C1. An observed, estimated or projected continuing decline of at least (up to a max. of 100 years in the future):	25 % in 3 years or 1 generation (whichever is longer)	20 % in 5 years or 2 generations (whichever is longer)	10 % in 10 years or 3 generations (whichever is longer)
C2. An observed, estimated, projected or inferred continuing decline AND at least 1 of the following 3 conditions:			
- (a) (i) Number of mature individuals in each subpopulation	≤ 50	≤ 250	≤ 1,000
- (a) (ii) % of mature individuals in one subpopulation =	90-100 %	95-100 %	100 %
- (b) Extreme fluctuations in the number of mature individuals			

(IUCN 2012)

For comprehensive assessment of the conservation status of snubfin and humpback dolphins against national (the *EPBC Act 1999*) listed threatened species criteria (TSSC 2015), data on the overall distribution, abundance, population trends, and impacts of threatening process are required. The acquisition of these data has been subject to considerable attention in recent years, with an expert workshop leading to the production of a "Coordinated research framework to assess the national conservation status of Australian snubfin dolphins (*Orcaella heinsohni*) and other tropical inshore dolphins" (the 2013 Research Framework; Department of the Environment 2013b), including guidance on corresponding research methods (Brooks et al. 2014). However, collecting broad-scale data across a large, remote area such as northern Australia presents many challenges, not least the considerable associated cost; to date, only the Northern Territory has had the resources to begin implementing such surveys (Brooks and Pollock 2014). In light of these ongoing challenges, limited resources, and new information (including the 2014 identification of *S. sahulensis*), the 2013 Research Framework was revised in 2015 to reflect a broader scope of guiding the research required "to inform the conservation and management, rather than the evaluation of the national status *per se*, of all three species of tropical inshore dolphins" occurring in northern Australia (Department of the Environment 2015b).

6.5 Concluding remarks

The research presented in this thesis provides considerable novel information on tropical inshore dolphins of north-western Australia, including important population data to inform conservation and management efforts. These findings are particularly pertinent given the range of threats that local populations of these species may be exposed to, most notably: extensive habitat modification associated with coastal development, and fisheries interactions, including bycatch (Beasley et al. 2012, Bejder et al. 2012, Woinarski et al. 2014). Two important elements of my research lie in the illustration of: (*i*) *what* information is relevant to assess the potential impacts of threatening activities on inshore dolphins, but has *not* been collected in the course of a multitude of environmental impact assessments to support large-scale coastal developments in this region; and, (*ii*) *how* those data can be collected through independent, thoughtfully designed and rigorously conducted research. While our understanding of inshore dolphins in northern Australia has increased considerably in the last decade, immense data gaps remain. Further research is required at both local and national scales in order to: rigorously assess their conservation status against defined criteria (see Brooks et al. 2014); develop a more detailed understanding of their behavioural ecology; and, manage potential and realised impacts to local populations.

As a contribution to the discipline of conservation biology, this thesis represents the application of a diverse suite of field methods and analytical techniques to the study of several cryptic species in a vast, remote region. The approaches taken, findings reported, limitations discussed and recommendations highlighted by this thesis should serve as a guide to future monitoring, research and conservation efforts on inshore and estuarine dolphins, which exemplify megafauna vulnerable to anthropogenic activity throughout the developed and developing world.

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