Dolphins as part of the ecological character of Ramsar-listed wetlands:
a case study of Indo-Pacific bottlenose dolphins in the Peel-Harvey Estuary, Western Australia

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Acknowledgment of Country

We acknowledge the Traditional Owners of the land on which the Mandurah Dolphin Research Project conducts research, the Bindjareb people of the Bibbulmun Nation and pay our respects to Elders past, present and emerging.

Declaration

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

Krista Nicholson

Thesis abstract

Whether dolphins are part of the ecological character of Ramsar-listed wetlands depends on their status as a biological component of the ecosystem (e.g., dolphin biomass, residency) and their involvement in ecosystem processes (e.g., energy and nutrient dynamics, species interactions). The aim of this thesis is to provide the scientific basis for deciding whether Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the Peel-Harvey Estuary (PHE) in Western Australia should be considered part of the ecological character of the Ramsar-listed Peel-Yalgorup wetland system that the PHE is a part of. Dolphin photo-identification and behavioral data, as well as tissue samples, were collected during boat-based surveys in the PHE and adjacent coastal waters between 2016 and 2019. Social, spatial and isotopic ($\delta^{13}C$ and $\delta^{15}N$) niche partitioning were investigated to identify population structure based on biologically meaningful criteria. Social structure, home range and stable isotope analyses confirmed a year-round resident, socially, spatially and isotopically distinct community of ~90 dolphins occupying the PHE. The estuarine community had a slightly negative population growth rate (-0.004, SD 0.062) with a low probability (0.010, SE 0.003) of extinction in 100 years. The community was closed to immigration, with changes in abundance driven by births and deaths and likely permanent emigration of immature males. Social clusters within the community were heterogeneous in their space use and diet. Detritivores, omnivores and herbivores and benthic omnivores and carnivores each contributed approximately a third and water column species 10%, to the annual fish biomass (~200,000 kg) removed by the resident dolphin community. The findings of this thesis provide strong empirical evidence that dolphins are functional biological components of the ecological character of the Peel-Yalgorup Ramsar site.

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List of acronyms

AI	Association Index
CCC	Cophenetic Correlation Coefficient
CEDP	Coastal and Estuarine Dolphin Project
CEPA	Communication, Education and Public Awareness
COP	Conference of the Parties
DEE	Department of the Environment and Energy
DEWHA	Department of the Environment, Water, Heritage and the Arts
DSEWPC	Department of Sustainability, Environment, Water, Population and Communities
DWER	Department of Water and Environmental Regulation
ECD	Ecological Character Description
EGCMA	East Gippsland Catchment Management Authority
GPS	Global Positioning System
HWI	Half Weight Index
IUCN	International Union for the Conservation of Nature
KDE	Kernel Density Estimate
LAC	Limit of Acceptable Change
LAR	Lagged Association Rate
NLAR	Null Lagged Association Rate
PBR	Potential Biological Removal
PCC	Pearson's Correlation Coefficient
PHCC	Peel-Harvey Catchment Council
PHE	Peel-Harvey Estuary
PVA	Population Viability Analysis
PVC	Percent Volume Contour
PYS	Peel-Yalgorup System
QAIC	Quasi Akaike Information Criterion
RIS	Ramsar Information Sheet
SWMRP	South-West Marine Research Program
TAG	Technical Advisory Group
UD	Utilization Distribution

Statement of contributions

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Chapter 2 - Social, spatial and isotopic niche partitioning identify an estuarine community of bottlenose dolphins as a discrete management unit. Krista Nicholson collected, processed and analysed the data and wrote the manuscript. Prof. Lars Bejder, Prof. Neil Loneragan and Dr Hugh Finn critically reviewed the manuscript.

Chapter 3 - Demographics, age structure and viability of an estuarine population of Indo-Pacific bottlenose dolphins. Krista Nicholson collected the data with additional demographic information provided by Mandurah Volunteer Dolphin Rescue Group and Mandurah Cruises. Martin van Aswegen collected the photogrammetry data and estimated the ages of individual dolphins. Krista Nicholson processed and analysed the data and wrote the manuscript. Prof. Lars Bejder, Prof. Neil Loneragan, Dr Hugh Finn and Martin van Aswegen critically reviewed the manuscript.

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Chapter 1

General introduction

Wetlands such as estuaries and rivers are commonly occupied by dolphins and freshwater dolphin species occur only in these habitats (Vidal et al. 1997; Smith et al. 2001; Read et al. 2003; Zhang et al. 2003; Fury and Harrison 2008; Braulik et al. 2014; Urian et al. 2014; Chabanne et al. 2017a). As top predators, dolphins can have an important ecological function through the consumption of large biomass of prey (Bax 1991; Bowen 1997) and by influencing behavior and distribution of prey species (Ohgushi et al. 2012; Morosinotto et al. 2010; Brown and Kotler 2004; Abrams 2000; Lima 1998). Additionally, they may be an important feature of a wetland for cultural (e.g., significance to indigenous people), aesthetic and economic (e.g., tourism) reasons (e.g., Alves and Rose 2008; Lee Long and O'Reilly 2009; RIS 2018).

Given their presence in wetland ecosystems, dolphins may form part of the 'ecological character' of internationally significant wetlands listed under the *Convention on Wetlands of International Importance especially as Waterfowl Habitat* (the Ramsar Convention), e.g., the Indus dolphin (*Platanista gangetica* ssp. *minor*) in the Indus Dolphin Reserve in Pakistan (RIS 2001) and the Tucuxi (*Sotalia fluviatilis*) and Amazon river dolphin (*Inia geoffrensis*) in the Tarapoto Lakes complex in Colombia (RIS 2018). The ecological character of a wetland is defined by the Ramsar Convention as 'the sum of the biological, physical and chemical components of the wetland ecosystem and their interactions, which maintain the wetland and its products, functions and attributes' (COP7, Resolution VII.10, 1999). Whether dolphins are considered part of the ecological character of a wetland will depend on their status as a biological component of the wetland ecosystem (e.g., dolphin biomass, residency), their involvement in ecosystem processes (e.g., energy and nutrient dynamics, species interactions) and their contribution to ecosystem benefits and services (e.g., recreation, tourism and Indigenous culture; DEWHA 2008). If dolphins are recognized as part of the ecological character of a wetland, then they will become a feature of monitoring and reporting of changes in the wetland's ecological character (DEWHA 2008).

The ecological character description for a Ramsar site, usually at the time of listing, provides a baseline against which changes in the ecological character can be measured. The Ramsar Convention provides guidance on describing and maintaining the ecological character of listed sites (COP9, Resolution IX.1 Annex A, 2005). This guidance forms the basis of a national framework applied in Australia, developed by the Commonwealth Department of Agriculture, Water and the Environment (DEWHA 2008)[1]. An important component of this framework is setting a Limit of Acceptable Change (LAC), i.e., a tool for assessing when the character of a wetland may have changed, for ecosystem components, processes and services (COP11, DOC.24, 2012). The LAC concept requires identification of measurable range of natural variation in ecological parameters, with values measured outside of their normal range potentially leading to changes in ecological character of a site (COP6, Resolution VI.1, 1996; DEWHA 2008). A LAC should be set in a way that changes may be monitored and evaluated against it.

The main goal of this thesis is to determine whether dolphins are part of the ecological character of a Ramsar listed Peel-Yalgorup System (PYS) in Western Australia. Following the framework applied in Australia (i.e., DEWHA 2008), their status as biological components of the system (i.e., biomass and site fidelity) and involvement in ecosystem processes (i.e., trophic interactions) will be evaluated. A combination of biological parameters (e.g., population structure and demographic parameters) will be used to provide baseline information for dolphins in the PYS. This baseline will provide the scientific basis for deciding whether dolphins are part of the

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[1] The Commonwealth Department of Agriculture, Water and the Environment (current) is a federal regulatory agency that is currently responsible for developing and implementing national legislation and policy to protect and conserve Australia's environment. This portfolio was previously held in the now dissolved Department of the Environment and Energy – DEE (2016 – 20), Department of the Environment -DE (2013 – 16), Department of Sustainability, Environment, Water, Population and Communities – DSEWPC (2010 – 13) and Department of the Environment, Water, Heritage and the Arts – DEWHA (2007 – 10).

ecological character of the Peel-Yalgorup Ramsar site while also informing the development of an appropriate LAC and a long-term monitoring program. While of equal importance, evaluating how dolphins contribute to the site's ecosystem services and benefits is outside the scope of this thesis. These parameters cannot be fully evaluated under a biological framework used here but require a separate framework that incorporates cultural, social and economic information.

This introductory chapter consists of two main parts. The first part will provide background information to the Ramsar Convention, how it is implemented in Australia and what the description of a site's ecological character entails. The second part will give an overview of how dolphins have been included in the ecological character description of different Ramsar sites, methodology that I suggest could be used to determine whether dolphins are part of the ecological character of a site and finally an introduction to the study area and the structure of this thesis.

1.1. Implementation of Ramsar Convention in Australia

Signatories to the Ramsar convention are committed to conservation and wise use of wetlands and are responsible for describing, maintaining and monitoring the ecological character of listed sites (Ramsar Convention, Article 3). Additionally, contracting parties are required to report if a wetland's ecological character has changed, is changing or is likely to change as the result of technological developments, pollution, or other human interference (Ramsar Convention, Article 3).

The Strategic Plan of the Ramsar Convention provides guidance on how the contracting parties should focus their implementation of the Convention. The goals of the current Strategic Plan (2016-2024) are to address the drivers of wetland loss and degradation, effectively conserve and manage the Ramsar site network, wisely use all wetlands and to enhance the implementation of the Strategic Plan (COP12, Resolution XII.2, 2015). While signatories to the Ramsar Convention work toward meeting these goals, they simultaneously contribute to meeting goals set by other international agreements such as the Convention on Biological Diversity (i.e., the Aichi Biodiversity targets), Paris Agreement on Climate Change and the UN Sustainable Development Goals.

In Australia, although the management of Ramsar listed wetlands rests with the States and Territories, the Commonwealth is ultimately responsible for Australia's compliance with the Ramsar Convention (i.e., maintain the ecological character of Ramsar listed wetlands). The *Environment Protection and Biodiversity Conservation Act 1999* (Cth; the *EPBC Act*) implements the Commonwealth's obligations to the Ramsar Convention. The *EPBC Act* focuses Australia's environmental law and policy on matters of National Environmental Significance, which includes wetlands of international importance (i.e., Ramsar-listed wetlands). The *EPBC Act* prohibits, without an approval from the Minister, action that has, will have or is likely to have a significant impact on the ecological character of a declared Ramsar wetland (*EPBC Act*, Section 17B). It also establishes management principles that require any action that is likely to impact the ecological character of a listed wetland to be subject to impact assessment and approval process and a management plan, inclusive of ecological character description, to be developed for each site (*EPBC Act*, Sections 332-335).

The management goal for Ramsar sites is to maintain the ecological character of each site (COP8, Resolution VIII.14, 2002; COP9, Resolution IX.1, 2005). Although the Commonwealth Government Department of Agriculture, Water and the Environment is the administrative authority on the Ramsar Convention, all levels of government (i.e., Commonwealth, State and Territory) are committed to integrating wetland conservation and wise use into their policies, strategies and plans that relate to the use and management of natural resources (DEE 2019). The required management plans for Ramsar sites are often developed and implemented collaboratively by State government agencies and other stakeholders such as city and shire councils, industry, non-profit organizations, research institutions and community/interest groups. A Technical Advisory Group (TAG) comprising stakeholder representatives is typically established for each Ramsar site. The TAG is involved in collaborative management of a site, assessing its ecological health and reporting on monitoring results against management triggers (i.e., LACs) to the Commonwealth Government (i.e., Wetlands and Aquatic Ecosystems Sub Committee), which reports to the Ramsar Secretariat.

1.2. Ecological character of Ramsar listed wetlands

The Ecological Character Description (ECD) identifies and describes components (i.e., physical, chemical and biological), processes (e.g., species interactions and interactions between organisms and the non-living environment), benefits and services (e.g., benefits to humans) of a wetland while identifying those that are critical to determining the ecological character of a site (DEWHA 2008). At minimum a LAC should be set in the ECD for critical wetland components and processes (DEWHA 2008). A change in ecological character is identified when critical parameters fall outside their normal range (i.e., a LAC is not met) and this resulting in impairment or imbalance in processes which maintain the wetland and its products, attributes and values (COP6, Resolution VI.1. 1996). It is important to note that not meeting, or exceeding, a set LAC for any one component does not necessarily indicate change in ecological character for the whole site but will trigger investigation into whether the ecological character has changed, and management action is required.

The ECD should also identify threats to the ecological character of a site, with a detailed risk assessment included in a site management plan (DEWHA 2008). The Ramsar Convention Wetland Risk Assessment Framework (COP7, Resolution VII.10. 1999) identifies changes to water regime, water pollution, physical modification, exploitation of biological products and introduction of exotic species as categories that may cause adverse change to ecological character of a wetland. Further, the ECD is required to identify knowledge gaps, monitoring needs and important messages to be included in a communication, education and public awareness (CEPA) action plan.

1.3. Dolphins in Ramsar listed wetlands

Dolphins comprise a particularly important aspect of a wetland's ecological character if they contribute to a wetland meeting one or more of the Convention's 'Criteria for Identifying Wetlands of International Importance' (COP6, Resolution VI.2, 1996; COP9 Doc.17, 2005; Ramsar Information Paper no. 5, 2007). The criteria likely to be relevant to dolphins are Criterion 2, 3, 4 and 9 (Table 1.1). For example, the globally endangered status according to the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (hereafter IUCN Red List) of Indus dolphins (*Platanista gangetica* ssp. *minor*; Braulik et al. 2012, see also Braulik et al. 2021) and the ecological significance of the Indus Dolphin Reserve in Pakistan to the species, supports this Ramsar site

Table 1.1. Criteria for identifying Wetlands of International Importance under the Convention on Wetlands of International Importance especially as Waterfowl Habitat (1971) and the fulfillment of each criteria by the Peel-Yalgorup Ramsar site in Western Australia

Criterion	**Description** (COP6, Resolution VI.2, 1996; COP9 Doc.17, 2005; Ramsar Information Paper no. 5, 2007)	**Peel-Yalgorup Ramsar site** (Hale and Butcher 2007)
1	A wetland should be considered internationally important if it contains a representative, rare, or unique example of a natural or near-natural wetland type found within the appropriate biogeographic region.	The site includes the largest and most diverse estuarine complex in south-western Australia and examples of coastal saline lakes and freshwater marshes.
2	A wetland should be considered internationally important if it supports vulnerable, endangered, or critically endangered species or threatened ecological communities.	Supports critically endangered Lake Clifton Thrombolite community and vulnerable (IUCN Red List, BirdLife International 2018) fairy terns (Sternula nereis).
3	A wetland should be considered internationally important if it supports populations of plant and/or animal species important for maintaining the biological diversity of a particular biogeographic region.	The site is one of two locations in south-western Australia and one of very few in the world where living thrombolites occur in inland waters.
4	A wetland should be considered internationally important if it supports plant and/or animal species at a critical stage in their life cycles or provides refuge during adverse conditions.	The site supports >50 species of birds, fish and crustacea at critical life stages (e.g., migration, drought refuge, breeding and moulting).
5	A wetland should be considered internationally important if it regularly supports 20,000 or more waterbirds.	The site comprises the most important area for waterbirds in south-western Australia, supporting >20,000 waterbirds annually, with greater than 150,000 individuals recorded in 1977.
6	A wetland should be considered internationally important if it regularly supports 1% of the individuals in a population of one species or subspecies of waterbird.	The site meets this criterion for 14 species of waterbird species (both international and Australian).
7	A wetland should be considered internationally important if it supports a significant proportion of indigenous fish subspecies, species or families, life-history stages, species interactions and/or populations that are representative of wetland benefits and/or values and thereby contributes to global biological diversity.	n/a
8	A wetland should be considered internationally important if it is an important source of food for fishes, spawning ground, nursery and/or migration path on which fish stocks, either within the wetland or elsewhere, depend.	The site is important as a nursery and/or breeding and/or feeding ground for at least 50 species of fish and the Peel-Harvey Estuary is a migratory route for the Pouched Lamprey *(Geotria australis)*.
9	A wetland should be considered internationally important if it regularly supports 1% of the individuals in a population of one species or subspecies of wetland-dependent non-avian animal species.	n/a

meeting Criterion 2 (on the basis that the site has consistently recorded over 500 dolphins since the declaration of a reserve in 1974, RIS 2001). Similarly, the vulnerable Indo-Pacific finless porpoise (*Neophocaena phocaenoides*; IUCN Red List, Wang and Reeves 2017) in the Dong dongting hu Ramsar site in China (RIS 2013) and the endangered (IUCN Red List, da Silva et al. 2018; 2020) Tucuxi (*Sotalia fluviatilis*) and Amazon river dolphin (*Inia geoffrensis*) in Tarapoto Lakes (RIS 2018) contribute to these sites meeting Criteria 2 and 4. In Australia, a resident population of Australian humpback dolphins (*Sousa sahulensis*), listed as vulnerable (IUCN Red List, Parra et al. 2017), contribute to the Great Sandy Strait Ramsar site meeting Criteria 2, 3 and 4 (Lee Long and O'Reilly 2009; Cagnazzi et al. 2011).

Criterion 9 by which 'a wetland should be considered internationally important if it regularly supports 1% of the individuals in a population of one species or subspecies of wetland-dependent non-avian animal species' was added to the listing criteria at the 9th Meeting of the Conference of the Parties in 2005 (COP9, DOC.17, 2005). In terms of dolphins, it is more likely this criterion will be fulfilled for sites important for freshwater species, which have relatively small global populations and restricted habitat ranges (Reeves et al. 2003). For example, the Río Yata Ramsar site in Bolivia hosts more than 1% of the global population of the endangered (IUCN Red List, da Silva et al. 2018) Bolivian river dolphin (*Inia geoffrensis* ssp. *boliviensis*), contributing to the site meeting Criterion 9 (RIS 2012). In Australia, the Gibbsland Lakes Ramsar Site Management Plan (EGCMA 2015) suggests that based on the site being occupied by a population of Burrunan dolphins (*Tursiops australis*)[2], that are genetically distinct from other known populations (Charlton-Robb et al. 2015), the site should also meet Criterion 9.

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[2] Burrunan dolphin (*Tursiops australis*) is not widely accepted as a separate species (Jedensjö et al. 2017) and is not currently recognized by the Society for Marine Mammalogy (Committee on Taxonomy 2021).

Even if dolphins are not considered as a contributor to as why a wetland is listed under the Ramsar Convention, they may form part of a wetland's ecological character and may be included in the ECD. The available information (e.g., residency patterns, abundance and distribution) on dolphins in wetlands influences the extent to which they are, or can be, included in the nomination of a site or its ECD. Similarly, setting a meaningful LAC for dolphins relies on sufficient information on how they use a Ramsar site, how reliant they are on a wetland and how they may influence its ecological character (e.g., Lee Long and O'Reilly 2009). Some Ramsar sites' ECDs briefly mention dolphins using the area within the boundaries of a site (e.g., Hale and Butcher 2007; BMT WBM 2010; BMT WBM 2011a) but do not further discuss them as part of the site's ecological character. Other sites' ECD describes dolphins as important components that provide benefits and services to humans (e.g., dolphin watching: Lee Long and O'Reilly 2009; Kellogg Brown and Root 2010) and are important for local Indigenous culture (e.g., Lee Long and O'Reilly 2009).

To my knowledge, dolphins have not been identified as critical components of any Ramsar listed wetlands in Australia and are therefore not required to have a set LAC associated with them (DEWHA 2008). Regardless, some sites have set a LAC relating to dolphins (e.g., 'a detectable decline in the population of Indo-Pacific humpback dolphins using the site': Lee Long and O'Reilly 2009) while others have not (e.g., EGCMA 2015). In general, a LAC may remain undefined due to insufficient information available for a species (e.g., Lee Long and O'Reilly 2009) or dedicated ECDs and/or management plans not having been developed for a site (e.g., Auditor General for Western Australia 2006).

1.4. Assessing whether dolphins are part of a wetland’s ecological character

There is no pre-described methodological framework to determine whether dolphins should be considered as part of the ecological character of a Ramsar listed wetland or as contributors to a site meeting criteria under which it can be listed as internationally important. Following the Ramsar Convention’s guidance (COP9, Resolution IX.1 Annex A, 2005) and the framework used in Australia (DEWHA 2008), factors that can be considered include species’ conservation status (e.g., IUCN Red List) and measurable attributes such as how many individuals use a listed site, their site fidelity, reliance on wetland resources (e.g., for food or reproduction) and their influence on a site’s defined ecological character. For a comprehensive assessment, dolphins’ contribution to ecosystem services (e.g., culture, aesthetics, tourism) should also be evaluated, however, this thesis focuses only on dolphins as biological components of the wetland and their involvement in ecosystem processes. As such, the methodology considered here only relates to gathering scientific information to evaluate biological and ecological parameters.

How many dolphins use a Ramsar wetland can be estimated using standard distance sampling (see Buckland et al. 2015) or capture-recapture methods based on photo-identification (e.g., Urian et al. 2015). Here, only the latter is considered as distance sampling methods do not allow individuals to be identified and therefore the resulting data cannot be used to investigate individuals’ site fidelity or population social or demographic structure. Photo-identification refers to a method where individuals can be identified and distinguished from each other from photographs of their unique natural markings (e.g., nicks and notches on dolphins’ dorsal fin, Würsig and Würsig 1977; Würsig and Jefferson 1990). This allows encounter histories, which capture where, when and with whom an individual was observed, to be created for individuals. Photo-identification data also enables individuals' site fidelity and association patterns (i.e., population social structure) to be investigated (Whitehead 2008a).

Bottlenose dolphin (*Tursiops* spp.) populations are often spatially and socially structured (Urian et al. 2009; Wiszniewski et al. 2009; Titcomb et al. 2015; Chabanne et al. 2017a). This makes photo-identification methods useful in both determining population partitioning based on biologically meaningful criteria (e.g., population spatial or social structure) and identifying whether a particular site (e.g., a Ramsar-listed wetland) is occupied by a distinct group (e.g., a social community) of dolphins. To understand whether social and spatial population partitioning is relevant in relation to an area of interest, it is important to include areas beyond the boundaries of the area of interest in the study design.

Whether a wetland is an important area to dolphins can be investigated by studying their behavioral activity (e.g., foraging, resting, socializing, travelling, mating, or calving) while they are present in the area. As such, behavioral observations may confirm how wetland areas are used by dolphins. However, as dolphins are often observed for a relatively short period of time during surveys with potentially long temporal gaps between observations and are mostly not observed at night, behavioral observations may not be sufficient in concluding whether individuals or populations are dependent on a wetland. Organisms that are part of the trophic structure of a wetland typically show higher carbon stable isotope ($\delta^{13}C$) values than organisms in more pelagic habitats (e.g., McCluskey et al. 2020). This provides a useful way of investigating whether dolphins that may move freely between habitats (e.g., from an estuary to coastal waters and into deeper pelagic waters) depend on wetland resources. A remote biopsy system developed for small cetaceans (Krützen et al. 2002) allows for skin samples to be collected from individuals for stable isotope analyses. Further, investigating stable isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of both consumer (e.g., dolphins) and prey (e.g., fish) will aid in understanding the diet of the predator and as such inform on their interaction with other species (e.g., Semmens et al. 2009).

If the above methods provide justification for dolphins to be considered part of the ecological character of a wetland (i.e., as a biological component involved in ecosystem processes), in context of the Ramsar Convention there is a requirement to maintain them as such. Additional information is then required to provide a baseline for measurable parameters that can inform the setting of a LAC and to develop an appropriate monitoring program. When a population's full range extends beyond the boundaries of a listed Ramsar site, the number of animals using or being supported by the site in a defined time period may form a baseline and be used to determine the LAC (e.g., waterbirds, Hale and Butcher 2007; humpback whales, Lee Long and O'Reilly 2009). However, if a Ramsar site encompasses a population's full range, demographic parameters such as population size, survival and reproductive rates may be used as measurable baseline parameters. The observed variation in these parameters over time can be used to inform a LAC and to establish an appropriate monitoring framework to detect changes in the population.

1.5. Indo-Pacific bottlenose dolphins in the Peel-Harvey Estuary

The Peel-Yalgorup Ramsar site (~265 km^2) in Western Australia includes the largest estuarine system in south-western Australia, the Peel-Harvey Estuary (PHE), coastal saline lakes and freshwater marshes (Fig. 1.1). The site is part of the East Asian-Australasian flyway, which represents collective water- and shorebird migration routes between their breeding grounds in the Arctic tundra and non-breeding areas in the southern hemisphere (Hansen et al. 2016). The Peel-Yalgorup System (PYS) is an important feeding and breeding ground for birds, supporting >100 species (Hale and Butcher 2007) and was designated a ‘Wetland of International Importance’ under the Ramsar Convention in 1990 (RIS 1998). The site currently meets seven of the nine criteria (COP6, Resolution VI.2, 1996; COP9 Doc.17, 2005; Ramsar Information Paper no. 5, 2007) for identifying Wetlands of International Importance (Table 1.1).

A comprehensive ecological character description (ECD) for the PYS was completed in 2007 (Hale and Butcher 2007). The ECD describes the critical components, processes and services of the wetland, quantifies a LAC for them, identifies water quality objectives and defines likely threats that may adversely impact the ecological character of the system (Hale and Butcher, 2007). The management of the site is shared by multiple Western Australia State Government agencies (e.g., Department of Water and Environmental Regulation, Department of Primary Industries, Department of Biodiversity, Conservation and Attractions) and other stakeholders (e.g., Peel-Harvey Catchment Council - PHCC) including the Traditional Custodians of the land, the local Noongar communities (Hale and Butcher 2007; PHCC 2009; 2017; DWER 2020). The aim of the management plan is to protect and/or restore the ecological character of the PYS and promote the wise use of the wetland by fostering roles and responsibilities of local stewards (PHCC 2009). Guided by the management plan, a CEPA strategy has been developed for the site (PHCC 2017). It aims to encourage government, community and industry to become more involved in the care and protection of the PYS in the face of the increased pressure from urban and industrial development. Since the PYS was listed under the Ramsar Convention, the population of Mandurah has increased by ~70% and is forecast to increase by a further ~44% by 2036 (Australian Bureau of Statistics 2021). This will add pressure on the

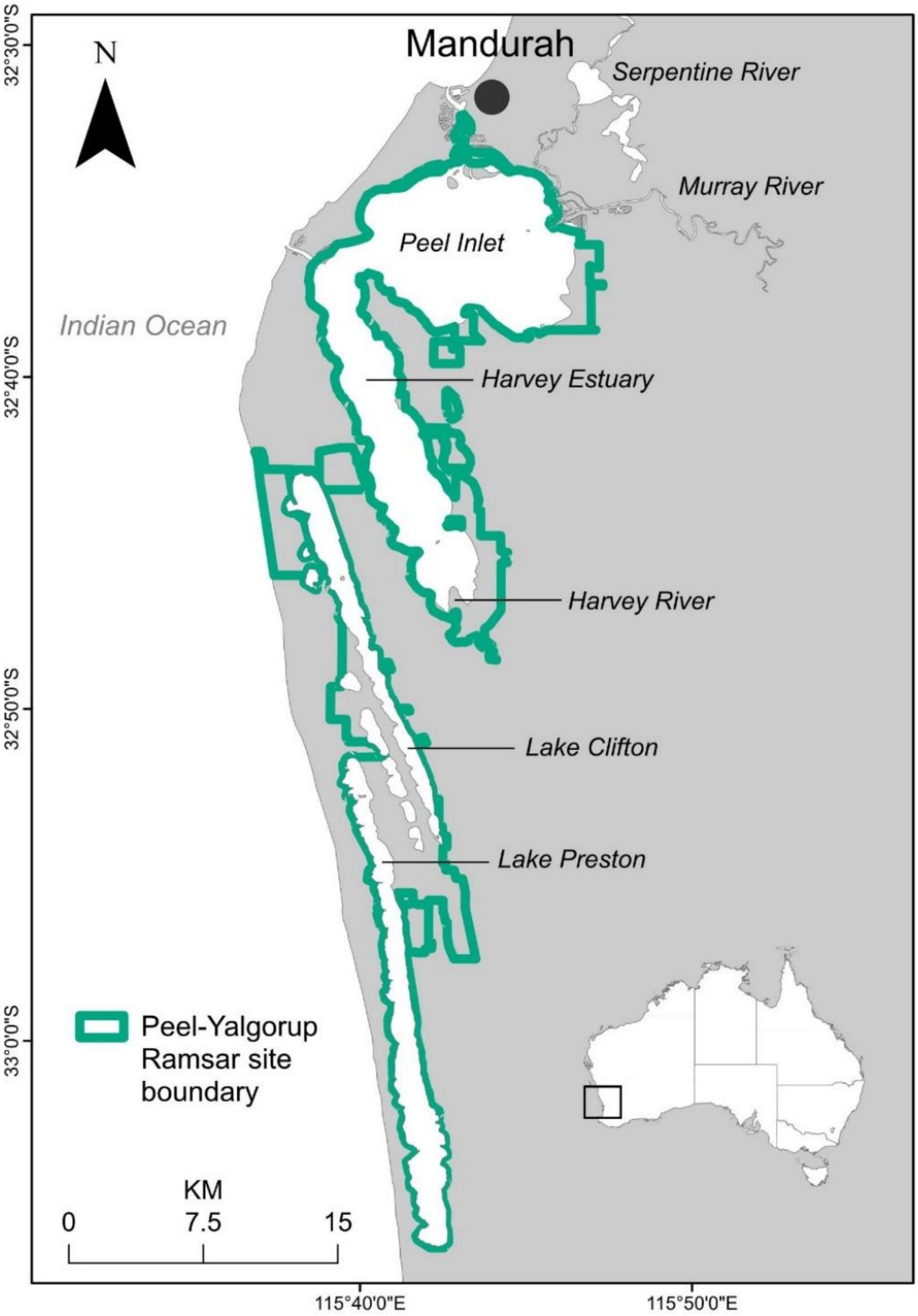

Figure 1.1. Boundary of the Ramsar-listed Peel-Yalgorup Wetland in Western Australia

wetlands through increased recreational use, nutrient and contaminant loads, groundwater extraction and development (Hale and Butcher, 2007). The PYS has been recognized as critical for the region's economy for its tourism and recreational value (e.g., fishing, crabbing, bird watching, water sports, boating, Hale and Butcher 2007; PHCC 2017). It is also of cultural and spiritual significance to the indigenous Noongar people (Hale and Butcher 2007; DWER 2020).

The PHE (~130 km^2), which forms a large part of the PYS, is a microtidal (tidal range ~0.5) estuary with two shallow basins (<2 m), the Peel Inlet and the Harvey Estuary (Fig. 1.1). Three rivers (the Serpentine, Murray and Harvey rivers) discharge into the Estuary, which is connected to the Indian Ocean via a natural opening (Mandurah Channel) and an artificial opening (Dawesville Channel). The Dawesville Channel was constructed in 1994 in response to adverse impacts of eutrophication in the system (Brearley 2005; Elliott et al. 2016). The opening of the Dawesville Channel has resulted in the estuary becoming more marine, which has led to changes in the ecological character of the estuary (Hale and Butcher 2007; Potter et al. 2016; Hallett et al. 2018; Valesini et al. 2019).

Currently, high phytoplankton productivity (Thomson 2019) together with macroalgae and seagrass, dominated by seagrass species *Ruppia megacarpa* (Krumholz, 2019), support a diversity of hyperbenthic and infaunal communities (Valesini et al. 2009; Wildsmith et al. 2009), >80 species of fish (Valesini et al. 2009; Potter et al. 2016) and >100 species of wetland dependent birds in the estuary (Hale and Butcher 2007).

Although not explicitly considered as components of the ecological character of the Peel-Yalgorup Ramsar site, the ECD for the site (Hale and Butcher 2007, page 61) mentions dolphins, noting that:

> *Although not well studied, there is anecdotal evidence that the Peel-Harvey Estuary supported a small population of bottlenose dolphins (Tursiops truncates {sic}). Animals were observed feeding in the estuary and travelling*

> *up the Serpentine River as far as Goegrup Lake. It is suspected that they were not residents in the estuary but using the estuary for feeding travelling between the estuary and the ocean via the Mandurah Channel.*

Historical stranding records also indicate that dolphins regularly use the PHE with a relatively high number of live strandings recorded between 1981 and 2010 (Groom and Coughran 2012). Dolphins are sighted year-round in the Mandurah Channel (Raeside 2012) and are recognized as a tourism attraction, with a tour operator, Mandurah Cruises (www.mandurahcruises.com), providing dolphin-watching cruises in the waterways. Considerable citizen science effort in the past few decades by the Mandurah Volunteer Dolphin Rescue Group further suggests that dolphins use the PHE year-round with individuals showing high site fidelity to the area. As such, although anecdotal information is available, it is not sufficient to evaluate whether dolphins are part of the ecological character of the site.

1.6. Thesis aim and structure

The overall aim of this thesis is to provide the scientific basis for managers to decide whether dolphins should be considered part of the ecological character of the Peel-Yalgorup Ramsar-listed wetland. The described methodological framework will be applied to evaluate whether Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) are a component of the ecological character of the site and involved in ecosystem processes. The suggested methodological framework (see section 1.4) allows for estimating how many dolphins use the PHE, their site fidelity and dependence on estuarine food sources. The measured parameters will form a baseline for dolphins using the site, which can be used to develop a LAC and a monitoring program for dolphins. This thesis does not consider dolphins' contribution to ecosystem services and benefits, which are likely to be significant for this site. Therefore, this thesis does not allow for full evaluation whether dolphins are critical components of the ecological character of the site, nor does it provide sufficient information for a comprehensive LAC to be set.

In addition to contributing to the primary aim of this thesis, the data chapters individually contribute to our knowledge on bottlenose dolphin population ecology, sociobiology and behavior, while specifically investigating intrapopulation partitioning according to multiple (i.e., social, spatial and isotopic) niche dimensions. This thesis will follow a structure where data chapters (Chapters 2, 3 and 4) are written as standalone manuscripts two of which have been submitted for publication. The specific aims of each chapter are detailed below.

Chapter 2 investigates Indo-Pacific bottlenose dolphin population structure and partitioning according to social, spatial and isotopic niche dimensions in Western Australia State waters inclusive and adjacent to the Peel-Harvey Estuary. Niche partitioning based on the above dimensions will inform whether the Peel-Harvey Estuary is occupied by a distinct population of dolphins based on ecologically meaningful criteria. This chapter will inform whether dolphins should be considered as a biological component of the ecological character of the Peel-Yalgorup Ramsar site.

Chapter 3 characterizes the social structure, demographics and viability of the Peel-Harvey dolphin population. The results of this chapter will provide a baseline against which changes in the population can be measured and will inform the development of a Limit of Acceptable Change (LAC) and a monitoring program for dolphins.

Chapter 4 investigates dolphin trophic interactions within the Peel-Harvey Estuary. The proportional contribution of fish feeding guilds to the diet of dolphins will be quantified and the annual fish biomass removed from the estuary by the resident dolphin population estimated. Intra-population isotopic niche partitioning corresponding to social structure will be examined. This chapter will inform on the consumptive effects of dolphins in the estuary (i.e., their involvement in ecosystem processes).

Chapter 5 draws together the results from the data chapters to evaluate whether dolphins are a biological component of the Peel-Yalgorup Ramsar site and whether they are involved in ecosystem processes to an extent that they can be considered part of the site's ecological character. The contribution of the established baseline information to determine the LAC for dolphins will be discussed and a monitoring program to detect changes in the population suggested.

Data

The data used in this thesis was collected on systematic boat-based photo-identification surveys conducted year-round between 2016 and 2017. Additional effort was conducted in 2018 and 2019. Dolphin tissue samples were collected between 2016 and 2018. To investigate trophic interactions, fish samples were collected as part of a separate study (2016 and 2017) documenting the fish community structure of the Peel-Harvey Estuary (Hallett et al. 2018). Data on dolphin births and deaths were supplemented by observations by the Mandurah Volunteer Dolphin Rescue Group and a local tour operator Mandurah Cruises.

Chapter 2

Social, spatial and isotopic niche partitioning identify an estuarine community of bottlenose dolphins as a discrete management unit

This chapter has been accepted as a co-authored paper: **Nicholson,** K., Loneragan, N., Finn H. and Bejder L. In review. Social, spatial and isotopic niche partitioning identify an estuarine community of bottlenose dolphins as a discrete management unit. *Aquatic Conservation: Marine and Freshwater Ecosystems.*

2.0. Abstract

Investigations of population structure across multiple niche dimensions can enable the identification of discrete management units within populations. This study examined social, spatial and isotopic niche partitioning in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) across ca. 600 km^2 of coastal and estuarine waters in south-western Australia, to evaluate whether estuarine dolphins should be treated as a discrete management unit. Photo-identification data and tissue samples were collected in 2016 and 2017 in a study area covering the Peel-Harvey Estuary (PHE) and adjacent coastal waters. A total of 1038 dolphin groups were encountered, and 481 individuals were identified. Tissue samples for stable isotope (δ^{13}C and δ^{15}N) analyses were collected from 96 individuals. Social structure and complexity analyses were conducted, home ranges for individuals and identified communities were estimated and differences in stable isotope composition among individuals and communities were examined. A socially, spatially and isotopically distinct dolphin community occurred in the PHE. The coastal waters contained four socially and spatially, but not isotopically, distinct communities, as well as a substantial number of dolphins (*n* = 185) who were sighted infrequently and therefore were not assigned to any community. The estuarine community had significantly higher mean δ^{13}C and significantly lower mean δ^{15}N values in their skin than any of the coastal communities. There is a strong scientific basis for treating the PHE community as a discrete management unit. The estuarine and coastal communities occupied different social environments, with coastal individuals sharing space with more transient individuals. This study shows the value of integrating information from multiple niche dimensions when identifying managements units and the need to consider all encountered individuals in management planning.

2.1. Introduction

Bottlenose dolphins (*Tursiops* spp.) occur in temperate and tropical coastal and estuarine waters, often with an apparently continuous distribution across adjoining coastal and estuarine systems within the species range (Wilson et al. 1997; Zolman 2002; Fury and Harrison, 2008; Hammond et al. 2012; Urian et al. 2014; Braulik et al. 2019). These continuous distribution patterns can make it difficult to identify discrete population segments that may require greater management attention because of anthropogenic pressures or other factors (Chabanne et al. 2017a; Chabanne et al. 2017b). Investigations of population structure using intraspecific partitioning in multiple niche dimensions (Hutchinson 1957) provides a potential basis for identifying management units.

Many bottlenose dolphin populations are socially and spatially structured (Urian et al. 2009; Wiszniewski et al. 2009; Titcomb et al. 2015; Chabanne et al. 2017a). This has implications for how a ‘population’ is defined (Thomas and Kunin 1999) and for the identification of pressures (e.g., resource competition and predation) and threats (e.g., disturbance, habitat loss and pollution) affecting it. Further, the complex nature of such structuring means that, depending on the management objective(s), the scientific basis for identifying management units within populations (e.g., Chabanne et al. 2017a; Giménez et al. 2018) should consider not only population genetic structure (Moritz, 1994; Palsbøll et al. 2007), but also niche partitioning based on population social structure (e.g., Urian et al. 2009; Wiszniewski et al. 2009) (social partitioning), temporal and spatial distribution of individuals (e.g., Titcomb et al. 2015; Genov et al. 2019) (spatial partitioning) and partitioning based on trophic ecology (e.g., Giménez et al. 2018) (isotopic partitioning). Such information can assist in evaluating whether population segments are sufficiently socially, spatially and isotopically distinct to warrant their treatment as discrete management units.

Analyses of social partitioning proceeds on a basis that social species occupy a social niche, which can be defined as a set of social environments, constructed by social interactions with conspecifics (Saltz et al. 2016). Individuals that belong to the same social group overlap at least to a degree in their space use and thus encounter the same resources and likely have similar diets (Darimont et al. 2004; Semmens et al. 2009). The interplay between the social and ecological environment, however, is difficult to separate. As such, combined, the two can be referred to as a socioecological environment where the ecological environment may affect the social environment and the social environment may determine individual space use patterns (Webber and Vander Wal 2018). Within the socioecological environment, individuals make decisions on both sociality and space use to maximize their fitness (McLoughlin et al. 2006; 2010; Silk 2007; Farine et al. 2015). This, in turn, results in heterogeneity in sociality and space use within populations. Therefore, the social niche concept provides a biologically meaningful criterion for discriminating between population segments.

Individuals' social niche can be investigated by studying interactions among conspecifics. Bottlenose dolphins live in complex social systems with fission-fusion dynamics where individual decision-making causes groups to frequently fission and fuse in response to conflicting or shared interests of group members (Connor et al. 2000; Sueur et al. 2011). Typically, such dynamics reflect heterogeneous environments, both social and ecological, where individual association patterns and habitat selection vary spatiotemporally (Aureli et al. 2008; Webber and Vander Wal 2018). An evolutionary trajectory by which this kind of grouping pattern may have arisen assumes extended associations to be advantageous for an individual. As a result, a society grows structured (Hinde 1976) with cohesive groups that fission and fuse due to ecological pressures, such as predation risk and access to mates (Connor et al. 1992; Connor et al. 2001; Heithaus and Dill 2002). Temporal demographic patterns (i.e., transience and temporary emigration, Silva et al. 2009) may further define population structure by allowing individuals that are spatially and temporally segregated, to associate with each other. Although individuals of *Tursiops* spp. occupy different social niches, they are typically part of socially distinct communities within a larger population (Urian et al. 2009; Wiszniewski et al. 2009; Chabanne et al. 2017; Genov et al. 2019).

Spatial partitioning also provides a useful criterion for identifying management units, particularly when applied in coordination with social partitioning information. For example, social communities can represent appropriate population segments (or 'local populations') for environmental impact assessments where the range of the community substantially overlaps with an area to be affected by a proposed development or activity (Chabanne et al. 2017a). However, a social community may not contain all the individuals that use the affected area. Methodologies to ensure the unbiased allocation of individuals into social communities often require sighting data to be truncated to exclude individuals sighted less than a specified minimum number of times. This truncation often leads to the exclusion of >50% of encountered individuals from social analyses and therefore from identified social communities (e.g., Wiszniewski et al. 2009; Titcomb et al. 2015; Chabanne et al. 2017a). This may lead to misidentification of critical habitat as well as underestimation of the number of animals affected by a proposed development or activity. As such, intra-population social community structure together with consideration of space use of individuals outside of identified communities should be considered for environmental impact assessments and other management decision-making.

Individuals’ ecological niche may be partly identified by stable isotope ratios in consumer tissues as they provide information on nutrient assimilation and consequently, individual resource and habitat use (Newsome et al. 2007b; Newsome et al. 2012). Carbon ($\delta^{13}C$) ratios identify sources of primary production and remain similar between producer and consumer reflecting individual’s recent foraging habitat (De Niro and Epstein 1978; Fry and Arnold, 1982) while nitrogen ($\delta^{15}N$) ratios increase with the length of the food chain and reflect the trophic level an individual occupies (Post 2002; Tollit et al. 2010). In aquatic ecosystems, organisms in estuaries and near coastal areas typically show higher $\delta^{13}C$ ratios than organisms in further offshore habitat (e.g., McCluskey et al. 2021). Therefore, stable isotope analyses provide a useful tool in identifying whether individuals are reliant on estuarine (i.e., more benthic) or coastal (i.e., more pelagic) food sources (e.g., Troina et al. 2020). In particular, stable isotope analyses can complement observational data (e.g., social interactions and individuals’ locational records) on wide-ranging species, such as dolphins, for which information may often be scarce across temporal scales.

This study examines social, spatial and ecological niche partitioning in Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) across ca. 600 km^2 of coastal and estuarine waters in south-western Australia, to evaluate whether estuarine dolphins should be treated as a discrete management unit. To support the evaluation, this study aims to determine whether the Peel-Harvey Estuary (PHE) is occupied by a social community or communities that can be considered spatially and isotopically distinct from any identified coastal communities and from any grouping of more transient individuals who are not part of any identified community. Findings on local dolphin population structure will assist decision-making about future development or activity that may affect dolphins in the PHE and adjacent coastal waters and will help contextualize dolphin abundance and other population demographic parameter estimates for the region.

2.2. Methods

2.2.1. Study area

The study area covered approximately 600 km^2 of Western Australian (WA) State waters including the PHE and adjacent coastal waters (Fig. 2.1). The PHE is connected to the Indian Ocean through two entrances: a natural opening (Mandurah Channel) and a man-made channel (Dawesville Channel). Three rivers, the Murray, Serpentine and Harvey, flow into the estuary from a catchment area of approximately 94,000 km^2 (Valesini et al. 2019). Although the rivers were not part of the dedicated study area, the Murray and Serpentine were visited opportunistically ~7.5 km upstream during the study. The study area included coastal waters extending ca. 25 kilometres north and south of the Mandurah Channel with the WA State water limit determining the offshore boundary (i.e., ~ 5.6 km from the coast).

2.2.2. Sampling design and photo-identification

Data collection was designed specifically for dolphin population demographic capture-recapture analyses based on individual animal photo-identification. The temporal and spatial sampling design was developed to optimize the probability that consecutive sampling occasions were independent and that individuals in the study area had an

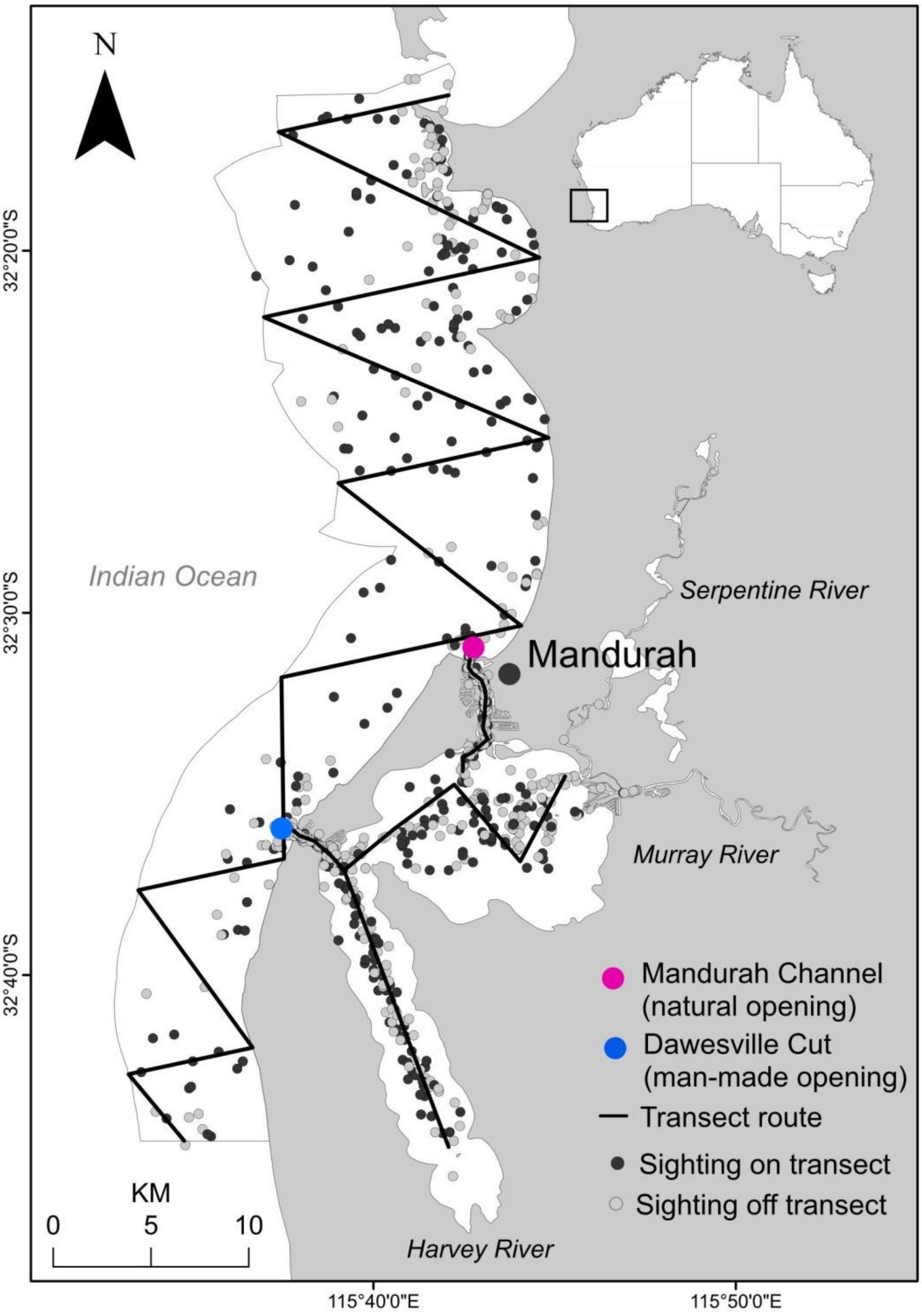

Figure 2.1. The polygon shows the coastal boundary of the dedicated study area, which includes State waters (3 nm from coast baseline) of Western Australia. The displayed transect is one of the 37 and 28 differently placed transects in the Peel-Harvey Estuary (PHE) and coastal waters, respectively. Transect routes were followed while searching for Indo-pacific bottlenose dolphins (*Tursiops aduncus*) for photo-identification surveys conducted in the PHE and adjacent coastal waters off Mandurah. Dolphin sighting locations within the dedicated study area between January 2016 and December 2017 are displayed.

equal probability of capture on each sampling occasion. Due to the complex shape of the estuary, a different transect design was applied in the PHE than in coastal waters. The PHE transects were ~40 km in length and followed a similar route each time, apart from in the Peel Inlet where a unique ‘zig-zag’ route was followed on each sampling occasion (see Fig. 2.1 for an example). The coastal transects also followed a ‘zig-zag’ pattern and were designed using Distance 6.2 software (Thomas et al. 2010). The position of the initial transect segment, which determined the position of the parallel segments, was selected at random from a coverage grid of points (points separated by a survey coverage width of 600 m) created over the study area. Each point in the coverage grid was available for selection for each transect (i.e., sampling with replacement). Balancing logistics and the ability to complete a coastal transect between one and three days (to optimise probability of closure within a sampling period), the transect line was designed to be ~120 km in length. Therefore, for each transect the parallel lines were set 9 km apart and in a 15° angle south to an East-West axis. The parallel lines were connected by additional segments to create a continuous ‘zig-zag’ design to ensure no ‘off effort’ transit between start and end points of transect segments. This process was repeated for each coastal transect.

To optimise the probability that all dolphin groups available for detection would be sighted, data collection only commenced in low wind and swell conditions with Beaufort Sea State (BSS) ≤ 2 and swell <1.5 m. If commenced, data collection continued in BSS = 3. A minimum of three transects covering the entire study area were conducted each austral season (summer: January-February; autumn: April-May; winter: July-August; and spring: October-November) in 2016 and 2017. Transects were conducted on a 5.6 m research vessel equipped with a 100 hp outboard engine at a speed of 8 to 10 knots. Four observers searched for dolphins out to 300 m on either side of the transect line, resulting in a 600 m ‘survey zone’. To increase sighting frequency for social analyses, in addition to dedicated transects, opportunistic dolphin group data were collected during sightings of groups encountered during transit to and from transect start and end points, as well as during fieldwork days when data were collected for other purposes (i.e., biopsy sampling and stereo-laser photogrammetry, van Aswegen et al. 2019). All data were collected and processed using the same protocols described below.

All dolphin groups encountered were surveyed. Group membership was defined by a ‘10-m chain rule’, where individuals within 10 m of each other were considered part of the same group (Smolker et al. 1992). A survey consisted of a minimum of five min ‘snapshot’ of the group during which GPS location, predominant behavior, group size and composition were recorded. Additionally, each dolphins’ dorsal fin was photographed for individual identification (Würsig and Würsig 1977; Würsig and Jefferson 1990) using a digital camera fitted with a 100-400 mm telephoto lens. Individuals were assigned as either independent individuals (i.e., adults and juveniles) or dependent calves according to visual inspection of their size and consistent association of a smaller individual (i.e., a calf) with an adult individual. Calves were estimated to be < 6 months old if foetal folds or lines were prominent on both sides of their body. Independent individuals therefore consist of juveniles, sub-adults and adults. A survey was considered completed once a good quality photograph (i.e., where individual’s dorsal fin was fully visible, in focus, perpendicular to the camera and filled a large proportion of the camera frame, e.g., Urian et al. 1999; Nicholson et al. 2012), was obtained of all group members. This was not always achieved due to the behavior of the animals, or when there was uncertainty over how many individuals were present in the group.

Photographs of each individual’s dorsal fin were compared with all others in the catalogue established for this study and to catalogues established by photo-identification studies conducted north and south of the study area, the Coastal and Estuarine Dolphin Project (CEDP, Chabanne et al. 2017a; Chabanne et al. 2017b) and the South-West Marine Research Program (SWMRP, Smith et al. 2012; Sprogis et al. 2018), respectively. All matches were confirmed by two independent observers. If there was no match, a minimum of four people searched all catalogues for a match before a unique identification code was given and the individual added to the catalogue.

2.2.3. Social analyses

To maximise sample size for social analyses, all individuals with confirmed identity (i.e., two independent observers agreed) from photographs, regardless of the photographic quality or fin distinctiveness, were included in the dataset. All social analyses were carried out using software program SOCPROG 2.9 (Whitehead 2009).

Association indices (AIs) estimate the proportion of time two individuals spend together and were calculated for each dyad in the dataset. Individuals were considered associated if they were observed in the same group during a sampling period defined as a day. This ‘gambit of the group’ approach is commonly used when studying cetaceans (e.g., Gowans and Whitehead 2001; Lusseau et al. 2003). It assumes that interactions take place within groups, all individuals in a group interact similarly with every other member and the proportion of time two individuals spend in the same group correlates with the rate of interaction between individuals. Individuals encountered <5 times were excluded from analyses as this was the threshold at which the coefficient of correlation between true and estimated AIs suggested an adequately representative pattern of true social structure (see below). Dependent calves were excluded from all analyses as high association rate between mother and calf would cause an upward bias in the resulting overall association indices for females.

In this study we used the half weight index (HWI) of association, which is considered least biased when a pair of individuals is more likely to be sighted apart than together and all associates of a given individual are not identified (Cairns and Schwager 1987). The HWI is typically chosen over other association indices when studying cetaceans as it accounts for observation bias inherent in photo-identification methods (e.g., Smolker et al. 1992; Cagnazzi et al. 2011; Chabanne et al. 2017a). The HWI was calculated for each dyad as $X/\left(X + Y_{AB} + \frac{1}{2}\ (Y_A + Y_B)\right)$ where X is the number of sampling periods in which two individuals, A and B, were recorded as associated; Y_{AB} the number of sampling periods in which A and B were observed in the same sampling period in different groups; Y_A the number of sampling periods in which just individual A was identified; and Y_B the number of sampling periods in which just individual B was identified.

A Pearson's correlation coefficient (PCC) with likelihood approximation was calculated between the true and estimated HWIs to measure how accurately social structure could be represented by the AIs (Whitehead 2008a). The PCC indicates the strength of the analyses to detect true social structure. A high correlation coefficient value (near 1.0) indicates that data are sufficient for excellent representation of true social structure. A value of ~0.8 indicates good and ~0.4 moderate representation of true social structure (Whitehead 2008b). The PCC was calculated first including all individuals in the data set and then excluding individuals who have been observed more than once, more than twice, more than three times and so forth until the PCC reached >0.4.

To investigate social differentiation, identified as the degree to which a pair of individuals within a population differ in their probability of association, the coefficient of variation of the true AIs was estimated (Whitehead 2008a). A coefficient of variation < 0.3 indicates a homogeneous society, while a value > 0.5 indicates well-differentiated society and a value > 2 is indicative of extremely differentiated society (Whitehead 2008a; Whitehead 2008b).

Permutation tests (Bejder et al. 1998; Whitehead 1999; Whitehead et al. 2005) were carried out to determine whether observed associations between individuals differed from that of a randomly associating population. Individuals within groups were randomly swapped (or ‘flipped’; Bejder et al. 1998), keeping group size and the number of times an animal was seen the same as in the original dataset. Flips were made within sampling periods (i.e., a day) within which there is likely to be little or no additions or deletions to the population due to the immigration/emigration and birth/death processes (Whitehead 1999). Using this approach, we ensure significant preference/avoidance is not detected due to some pairs of individuals being present in or absent from the study area (Whitehead et al. 2005). Subsequently, HWI were calculated for the new data matrix and the process repeated, always starting with the previously generated matrix. As a result, each data matrix was only slightly different from the previous one and none of the matrices (including the original one) were independent of each other. The difference in mean standard deviations between the observed and permuted HWI values was used as a test statistic (p-value) to determine whether the observed AI values were significantly different from the permuted values. The number of permutations required was determined by increasing the number of matrix permutations until the p-value stabilized (Bejder et al. 1998).

An eigenvector network algorithm (Newman 2004; 2006) was used to identify whether the study population could be divided into communities based on their association patterns (i.e., HWIs). Generally, AIs are considered high among individuals within the same community and low between individuals in different communities. A maximum modularity, which is the difference between the observed proportion and the expected proportion between the sum of the AIs within communities, was used to determine divisions of the population into communities. A Mantel test with 1,000 permutations was carried out to test whether AIs within and between communities were different.

Binomial mixture models (Weiss et al. 2019) and the Shannon's information index (Shannon and Weaver 1949) were used to quantify population social complexity. The social complexity can be defined as the diversity of relationships experienced by individuals (Weiss et al. 2019). It assumes that the AIs, quantifying the proportion of time a pair of individuals are associated with each other, belong to one of many relationships classes each of which comprise of similar relationships described by the HWI. Models were run with maximum of seven mixtures (i.e., relationship types) with Integrated Completed Likelihood used for model selection. Standard errors were calculated by jack-knifing on each sampling period.

2.2.4. Spatial and temporal distribution

Sighting locations of individuals assigned to a social community were pooled to represent the home range for each community. Following Royle et al. (2014), home range was defined as an area utilized by dolphins within the study area during the defined study period and is from here on referred to as an activity space. A non-parametric fixed kernel method (Silverman 1986; Worton 1989) was used to estimate utilization distribution (UD) for each community. To ensure inaccessible areas (i.e., land) were not considered as part of the animals' activity space, kernel density estimates (KDE) were derived using a kernel interpolation with barriers module in the spatial analyst toolbox in ArcMap 10.4 (e.g., MacLeod 2013, Sprogis et al. 2016). The UDs were estimated over a grid (cell size 200 m x 200 m) created over the study area. A smoothing parameter (i.e., bandwidth), *h*, changes the shape of the kernel depending on distance to data points that are allowed to contribute to a density estimation at a particular location. This parameter was set to 6,000 after visual inspection of kernels from varying values of *h*. To investigate whether some areas were utilized more frequently, both 50 and 95 percent volume contours (PVC) were calculated. The 50 PVC represents a core activity space for a community, containing 50% of all the locational records for community members. The 95 PVC represents a full activity space within the study area, containing 95% of all the locational records for community members. Overlap in communities' activity spaces was calculated as a percentage of area overlap, rather than a probability of encountering community members in another community's activity space. Sighting locations of individuals observed on <5 sampling occasions and therefore not assigned to any identified social community, were plotted separately to investigate space utilization by these individuals.

2.2.5. Stable isotope analyses

Tissue samples of blubber and skin were collected using a remote biopsy system (PAXARMS modified .22 calibre biopsy rifle) developed for small cetaceans (Krützen et al. 2002). Biopsy sampling was attempted on independent dolphins (i.e., not dependent calves) encountered when individual or group behavior was deemed suitable. To ensure an unbiased sample, when targeting an individual to biopsy, no preference was given to well-marked individuals over those who had relatively few marks, or better-known individuals over less frequently sighted ones. Samples were placed in an empty vile and stored in ice for transport into storage in -80°C freezer until processing for analyses.

The variability in tissue lipid content can alter bulk tissue $\delta^{13}C$ values (Logan et al. 2008; Newsome et al. 2018) as lipids have more negative $\delta^{13}C$ values relative to other biochemical compounds (DeNiro and Epstein, 1997). As recommended by deLecea and Charmoy (2015) and Gimenez et al. (2016), for accurate measurements of both $\delta^{13}C$ and $\delta^{15}N$, $\delta^{13}C$ was analysed in lipid free samples and $\delta^{15}N$ in bulk (i.e., untreated) samples. The bulk samples were oven-dried at 60°C for 24h and powdered with a mortar and pestle. The other aliquot underwent lipid extraction with three consecutive 24h soaks in 2:1 choloform:methanol solvent solution (Newsome et al. 2006; Newsome et al. 2018). These samples were then rinsed in deionised water, oven-dried and powdered as per the bulk samples. All samples were weighed to the nearest 10^{-2} µg, packed into tin capsules for $\delta^{13}C$ and $\delta^{15}N$ measurements and sent to the West Australian Biogeochemistry Centre at the University of Western Australia for analysis. Samples were analysed for $\delta^{13}C$ and $\delta^{15}N$, using a continues flow system consisting of a Delta V Plus mass spectrometer connected with a Thermo Flush 1112 via Conflo IV (Thermo-Finnigan/Germany). See analytical details in Skrzypek and Paul (2006).

All sampled individuals were assigned to groups based on the social community they belonged to. If a sampled individual did not belong to any of the identified social communities (i.e., individuals sighted <5 times), it was assigned to either a 'coastal' (i.e., individuals sampled in coastal State waters) or an 'offshore' (i.e., individuals sampled in Commonwealth waters) group. Tissue samples collected from members of social community E were combined with the 'coastal unknown' group for the analysis of variance due to low sample size (*n* = 3) in this group. The null hypothesis that there is no difference in mean $\delta^{13}C$ and $\delta^{15}N$ values between the groups was tested with the non-parametric Kruskal-Wallis test. The Shapiro-Wilk test was used to test for normality and the Brown-Forsythe for homogeneity of variance in the data. Where the null hypothesis was rejected, Dunn Test with Bonferroni adjusted p-values was used to determine which groups were significantly different from each other.

2.3. Results

2.3.1. Search effort and group encounters

Between January 2016 and December 2017, 222 days or part thereof, amounting to 1,281 h, were spent in the study area searching for and surveying dolphin groups. Thirty-seven transects were completed in the PHE and 28 in coastal waters. A total of 1,038 dolphin group surveys were conducted with 404 of the groups encountered on effort (i.e., along a transect line) and 634 off effort (i.e., not along a transect line; Fig. 2.1). A total of 980 dolphin group surveys were included in analyses after sightings with no identified individuals were removed. The average group size for groups encountered in the study area was 6.36 (SD 6.23, range 1-45, mode 2, median 4).

A total of 481 individuals were identified during the study: 374 independent individuals (i.e., adults and juveniles) and 107 calves, of which 39 were <6 months old during this study. Individuals had heterogeneous sighting frequencies (mean 11.23, SD 15.10, range 1-78, mode 1, median 5).

2.3.2. Social analyses

The strength of analyses to detect true social structure was considered adequate based on PCC of 0.46 (SE 0.02) between the true and estimated HWIs. The society was well-differentiated, with a coefficient of variation of the true HWI estimated at 1.19 (SE 0.02). This indicates that there is high variability in the degree to which pairs of individuals within the study area differ in their probability of association.

After restricting data to exclude dependent calves and individuals seen on <5 sampling occasions, 189 individuals were retained for analyses of community structure. When testing for preferred/avoided associations, the standard deviation of the mean observed HWI was significantly higher (P <0.001) than for the randomly permuted mean for all individuals. This indicates that individuals associated preferentially and/or avoided each other overall.

The eigenvector network algorithm identified five communities (modularity 0.61) in the study area. A modularity of >0.3 is a useful division of the data (Newman 2004). Out of the 189 individuals retained for analyses, 61 individuals were assigned to community A (Peel-Harvey), 51 to community B (Shoalwater), 21 to community C (Comet Bay), 39 to community D (Dawesville Channel) and 17 to community E (Coastal South; Fig. 2.2b). HWIs between and within identified communities were dissimilar, with within community HWI 16 times higher than those between communities (Mantel test permutation P <0.001, Mantel test analytical approximation P = <0.001, T = 66.52, r = 0.57; Table 2.1). Each community comprised of a mixture of adults, juveniles and calves of both sexes.

The mixture model that best fitted the data suggested three relationship classes for dolphins utilizing the study area, with association complexity of S = 0.98 (SE 0.03). Majority of relationship (78%) were classed as extremely low (mean HWI 0.006) association relationships, a small proportion (16%) as low association (mean HWI 0.12) relationships and some (4%) as relatively strong (mean HWI 0.43) association relationships.

Table 2.1. Observed Half Weight Indices (HWI) of association for five Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) social communities identified in estuarine and coastal waters off Mandurah, Western Australia. Individuals dependent on their mother and observed on <5 sampling occasions were excluded from these calculations.

Community	**Observed mean HWI (SD)**	**Observed mean of maximum HWI (SD)**	**Observed mean number of associates HWI (SD)**
Overall	0.04 (0.02)	0.60 (0.23)	8.49 (3.51)
Within	0.16 (0.10)	0.60 (0.23)	7.45 (3.20)
Between	0.01 (0.01)	0.12 (0.09)	1.03 (1.02)
A (Estuarine)	0.12 (0.05)	0.55 (0.21)	8.33 (2.80)
B (Coastal)	0.09 (0.04)	0.54 (0.21)	5.71 (2.03)
C (Coastal)	0.27 (0.09)	0.68 (0.23)	6.36 (1.73)
D (Coastal)	0.25 (0.09)	0.66 (0.22)	10.36 (3.36)
E (Coastal)	0.20 (0.10)	0.69 (0.28)	4.45 (1.77)

2.3.3. Spatial and temporal distribution

The size and distribution of the full and core activity spaces (95% and 50% utilization distributions, respectively) varied among communities (Table 2.2, Figs. 2.2a and 2.3). One of the communities, community A (Peel-Harvey), showed year-round site fidelity to the PHE with its range extending only slightly into coastal waters (Fig. 2.2a). The other four communities (B, C, D and E) resided in coastal waters, with their core activity spaces including one, or both, of the estuary mouths in at least one season (Fig. 2.3). All communities, apart from B and E, which occupied the northern and southern ends of the study area respectively, overlapped in space use. Only community A's core activity space overlapped with the core activity space of all other communities. This is due to community A's core activity space including both estuary mouths, while the

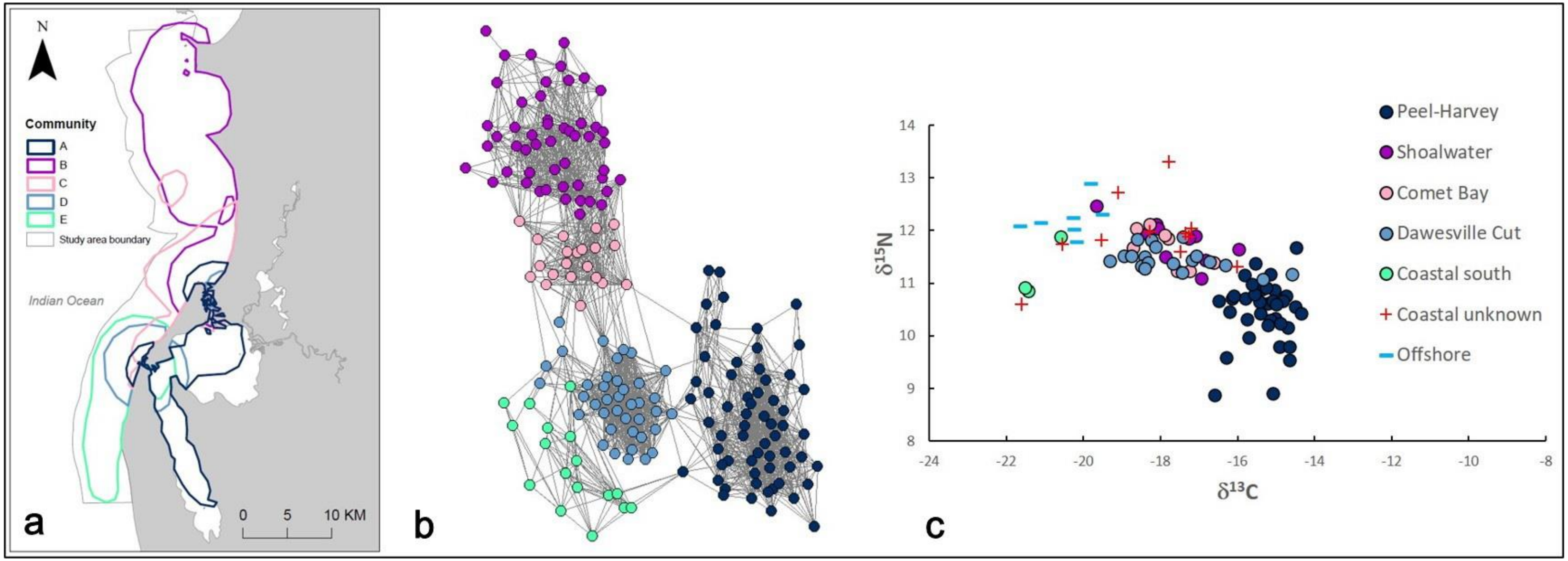

Figure 2.2. Full activity space (a) of five Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) social communities identified in coastal and estuarine waters off Mandurah, Western Australia. The social network diagram (b) depicts social structure of dolphins using the study area with each node representing an individual (n=189) and colour representing the social community each individual belongs to. Lines between nodes depict individuals' social links to others. Only associations with a half weight index (HWI) of association > 0.12 are presented as this was identified the mean HWI for low level association relationships. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope (SI) ratios in skin tissue of sampled dolphins (c). Colours represent the social community each individual belongs to with additional shapes showing SI ratios for individuals not identified as part of any social cluster.

core activity space of all other communities included only one or the other entrances to the estuary. The core areas of community B and C were discrete from core areas of communities D and E (Table 2.2, Fig. 2.3).

Table 2.2. Total area (km^2) and percentage overlap in full and core activity spaces (95% and 50% utilization distributions, respectively) of five Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) social communities off Mandurah, Western Australia. Rows indicate the percentage overlap in relation to communities' estimated activity space size.

Community (total/core area in km^2)	**A Estuarine**	**B Coastal**	**C Coastal**	**D Coastal**	**E Coastal**
A (102.0 / 28.7)	-	12.5 (18.9)	17.0 (2.4)	25.9 (16.4)	14.6 (2.4)
B (222.6 / 32.5)	5.7 (16.8)	-	23.8 (8.7)	1.3 (n/a)	n/a (n/a)
C (92.9 / 2.9)	18.7 (84.6)	57.1 (96.6)	-	14.1 (n/a)	12.5 (n/a)
D (54.2 / 8.8)	48.7 (53.3)	5.5 (n/a)	24.1 (n/a)	-	77.4 (50.2)
E (104.0 /9.2)	14.3 (6.1)	n/a (n/a)	10.8 (n/a)	40.1 (48.0)	-

Temporal variation in communities' activity space with seasons was observed. Autumn was the only season where all communities' core activity spaces included one of the mouths of the estuary (Fig. 2.3). In winter, community E, which utilizes the southern part of the coastal area, was absent altogether. In fact, no dolphins were observed south of the Dawesville Channel during winter. All other communities' core activity spaces still included the mouths of the estuary during winter. In spring and summer, the core activity space of community B shifted to exclude Mandurah Channel and the estuarine community A shifted to exclude Dawesville Channel. Each season the core activity spaces of communities A and C included Mandurah Channel, while the core activity space of community D included of Dawesville Channel.

A total of 185 independent individuals were observed on <5 sampling occasions and were therefore not assigned to any of the five identified social communities. Of these, 87 individuals were seen once, 39 individuals twice, 32

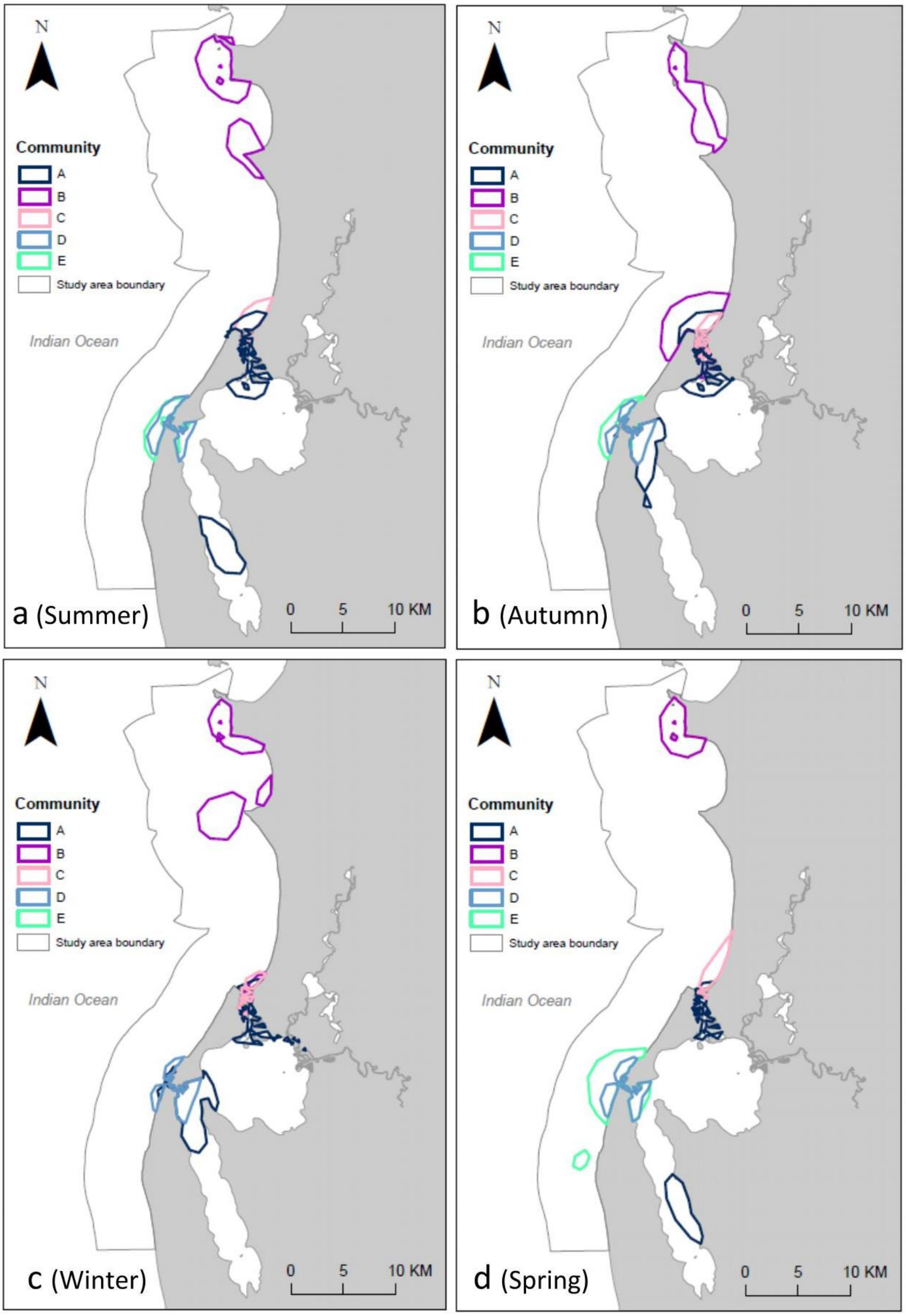

Figure 2.3. Temporal (a = summer, b =autumn, c = winter, d = spring) and spatial distribution of core activity space of five Indo-Pacific bottlenose dolphin (*Tursiops aduncus)* social communities. Core activity spaces are based on 50 percent contour volumes calculated from kernel density estimates and represents areas of higher use within a community's total activity space.

individuals three times and 27 individuals four times during the study period. Of the total sightings of these individuals (*n* = 447), 28% were observed in summer, 32% in autumn and 20% in both winter and spring. All these individuals were observed in coastal waters or in Dawesville Channel.

Some of the individuals (*n* = 38) observed in the study area were also photographed outside of its boundaries. Eleven individuals were encountered north of the study area (Chabanne et al. 2017a; Chabanne et al. 2017b). For example, one of these individuals, A4 (Fig. 2.4), was observed in the study area only once but was identified by Chabanne et al. (2017a) as being part of a community occupying a coastal bay, Owen Anchorage, to the north of the study area (Chabanne, 2018, unpublished data). Additionally, four individuals were sighted off Bunbury ~100 km south of the study area (Smith et al. 2012; Sprogis et al. 2017). One of these individuals, A5, was observed once in the study area in May 2016 and prior to this, it had been sighted off Bunbury on six occasions between 2009 and 2015 (Symons, 2018, unpublished data). As part of the Mandurah Dolphin Research Project effort, additional to that detailed in this study, one individual, A2, encountered in the dedicated study area was also sighted on the northern side of Rottnest Island. Additionally, at least 22 individuals sighted in the study area were also sighted to the west, outside the study area boundary in Commonwealth waters (see examples of locational records for select individuals in Fig. 2.4).

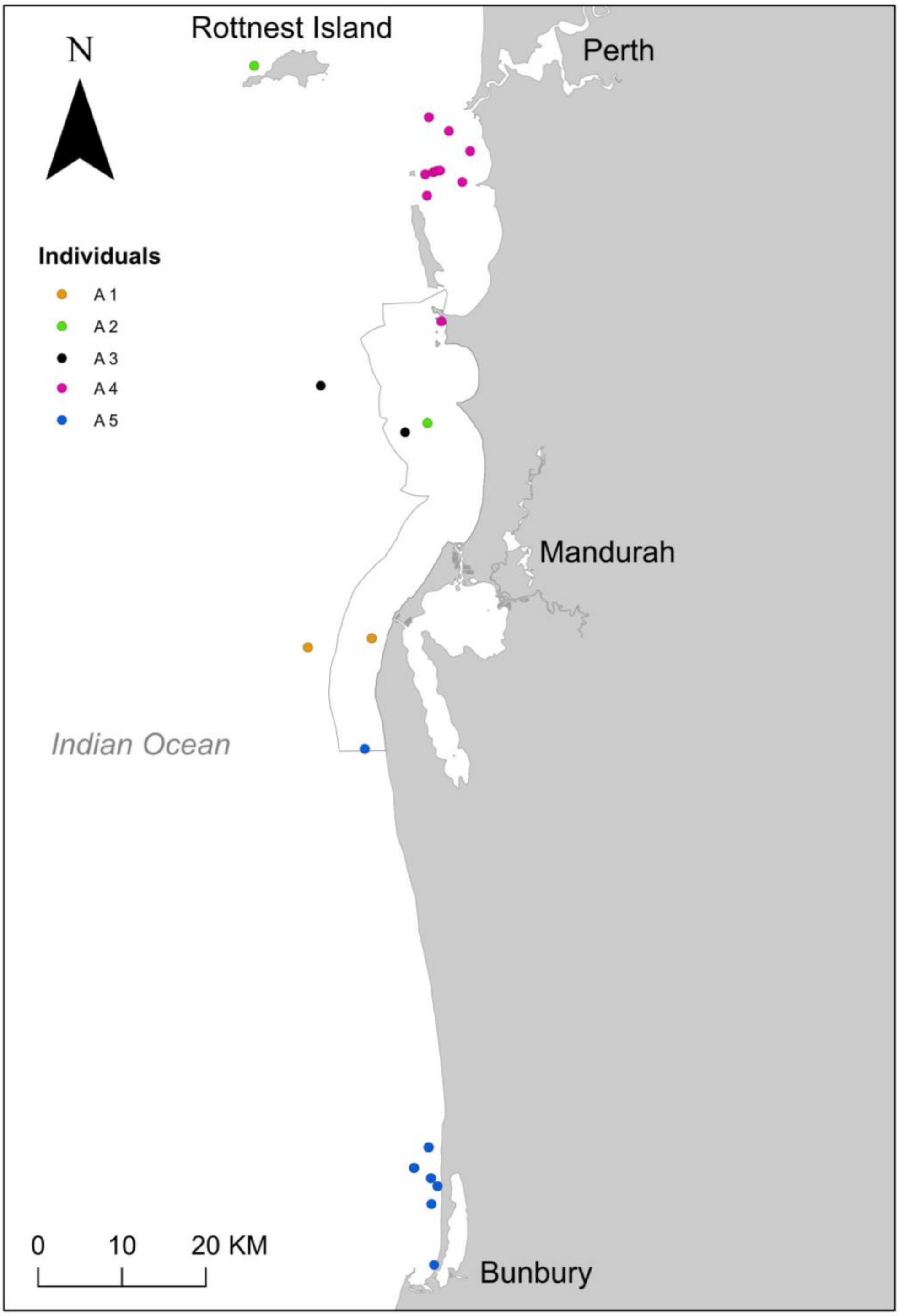

Figure 2.4. Sighting locations for five Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) individuals observed only once in the defined study area (dedicated study area boundary indicated by the polygon) off Mandurah, Western Australia. These individuals were sighted outside the study area during research effort (not detailed in this study) for collecting tissue samples of dolphins for stable isotope and genetic analyses and during research effort by the South-West Marine Research Program and the Coastal and Estuarine Dolphin Project.

2.3.4. Stable isotope analyses

A total of 96 tissue samples were collected and analysed for $\delta^{13}C$ and $\delta^{15}N$ concentrations (Table 2.3, Fig. 2.2c). Samples from members of social community E were combined with the 'coastal unknown' group for the analysis of variance with the mean $\delta^{13}C$ for this group -29.07 (SD 1.93) and mean $\delta^{15}N$ 11.13 (0.58). The Kruskal-Wallis test detected a significant difference in $\delta^{13}C$ ($X_5^2 = 65.076$, $P < 0.001$) and $\delta^{15}N$ ($X_5^2 = 69.678$, $P < 0.001$) values between the groups. The post-hoc Dunn test revealed that community A (i.e., the estuarine social community) had significantly higher $\delta^{13}C$ ($P < 0.01$) and significantly lower $\delta^{15}N$ ($P < 0.001$) values than all other communities and the 'coastal unknown' and 'offshore' groups (Table 2.3, Fig. 2.3c, Appendix A Table A1). The mean $\delta^{13}C$ value for community A was -15.41 (SD 0.74), while the mean for all coastal communities combined was -17.63 (SD 2.15; Table 2.3). The mean $\delta^{15}N$ value for community A was 9.86 (SD 0.65), while the mean for all coastal communities combined was 10.86 (SD 0.83).

Table 2.3. Mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values for five social communities and two groups based on sampling location of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) identified in coastal and estuarine waters off Mandurah, Western Australia.

Community/Group	**n**	**Mean $\delta^{13}C$ (SD)**	**Mean $\delta^{15}N$ (SD)**
A (Estuarine)	39	-15.41 (0.74)	9.86 (0.65)
B (Coastal)	10	-17.62 (1.02)	11.03 (0.39)
C (Coastal)	8	-17.84 (0.71)	11.18 (0.35)
D (Coastal)	19	-17.65 (1.24)	10.96 (0.22)
E (Coastal)	3	-21.17 (0.51)	10.72 (0.58)
Coastal unknown †	10	-18.70 (1.60)	11.31 (0.55)
Offshore ‡	7	-20.40 (0.74)	11.71 (0.34)
Coastal (combined)	57	-17.63 (2.15)	10.86 (0.83)

† = individuals sampled in WA State waters but not assigned to any social community
‡ = individuals sampled in Commonwealth waters and not assigned to any social community

2.4. Discussion

This study identified a socially, spatially and isotopically distinct community of Indo-Pacific bottlenose dolphins residing in the Peel-Harvey Estuary (PHE). Four socially and spatially distinct coastal communities were also identified; however, no significant isotopic differences were detected among these. Coastal communities were distributed in a north-south axis along the coast with one community showing high year-round site-fidelity to one of the entrance channels to the estuary (i.e., Dawesville Channel). All communities used one or both entrance channels during autumn. The identified niche partitioning in multiple dimensions provides a strong scientific basis for treating the estuarine community (A) as a discrete management unit to coastal communities (B, C, D and E).

2.4.1. Social partitioning

Five socially distinct communities were identified during this study. Social complexity was characterized by individuals maintaining three classes of relationships, corresponding to extremely low association relationships connecting the social communities and generally low but also a small proportion of high association relationships observed within the communities. Similar social partitioning has been identified in other bottlenose dolphin (*Tursiops* spp.) populations (e.g., Gubbins 2002; Wiszniewski et al. 2009; Titcomb et al. 2015; Chabanne et al. 2017a; Genov et al. 2019; Pleslić et al. 2019) with fine scale social structure arising from males and females, as well as adults and juveniles, having generally contrasting association patterns (Smolker 1992; Connor et al. 1992; Connor et al. 2000; Gero et al. 2005; Wells 2014; but see Lusseau et al. 2003). Males form temporally stable alliances (Connor et al. 1992; Connor et al. 2011; Owen et al. 2002; Wells 2014; Connor and

Krützen 2015; but see Genov et al. 2019), females vary from being solitary to having a large network of affiliates (Smolker 1992; Wells 2014) and juveniles, free from mating system constraints, may form relatively short-term and behaviorally specific associations that may mirror adult associations (Gero et al. 2005; Galezo et al. 2020; Gerber et al. 2020). The small proportion of high association relationships observed in this study represents or occurs within social clusters identified as individuals that associate at a higher rate with members of their own rather than other social clusters within their social community.

As in this study, Chabanne et al. (2017a) identified socially and spatially distinct dolphin communities in a location directly north of the study area and detected stronger associations between individuals of the same community than between individuals of different communities. Therefore, we believe that increasing the spatial extent of this study would identify additional social communities while the described social complexity (i.e., three levels of relationships) would remain the same. Although association strengths across different levels of social structure may vary among populations (e.g., Wiszniewski et al. 2009; Chabanne et al. 2017a), we hypothesize that the three classes of differentiated relationships (i.e., associations between communities, within communities and within social clusters) identified here represent the general patterns of associations and social complexity for *T. aduncus*.

Although individuals in all communities showed similar patterns of association, the results of this study suggest that the PHE community and collectively the coastal communities occupy different social environments. Only five coastal individuals that were part of the identified communities were observed in the PHE (excluding the entrance channels), while all individuals (n = 185) not assigned to any identified community (due to their low sighting frequency) were observed in coastal waters. As such, members of coastal communities need to navigate a social environment with higher number of less familiar conspecifics, while members of the estuarine community consistently encounter individuals that they are more familiar with. This needs further investigation, however, as here it is assumed that individuals that are transient or nomadic in the study area are also unfamiliar to the individuals showing high site fidelity to the study area. Given bottlenose dolphins show life-long (at least 20 years) social recognition of conspecifics (Bruck 2013), individuals perceived as transient and nomadic due to the short temporal scale of this study, may in fact be regular visitors to the area and therefore not unfamiliar to members of the coastal communities.

2.4.2. Spatial partitioning

The spatial distribution of the identified social communities clearly corresponded to estuarine and marine habitats. Although many studies have reported dolphins regularly using estuaries, individuals that enter them are often also found in coastal waters (e.g., Urian et al. 2014; Smith et al. 2016; Sprogis et al. 2016) with movement in and out of some estuaries related to tidal phases (Harzen 1998) or seasons (Wilson et al. 1997). Like this study, Chabanne et al. (2017a), identified a distinct social community of dolphins that occupied the Swan-Canning Estuary in Western Australia. That community’s activity space, however, extended further into coastal waters than the activity space of the PHE dolphin community. Other studies have focused on estuarine dolphins but have not included coastal waters in their study design (e.g., Fury and Harrison 2008; Wiszniewski et al. 2009) or related social structure to individuals’ space use (e.g., Young and Phillips 2002; Brooks et al. 2017; Passadore et al. 2017; Arso Civil et al. 2019). This makes it difficult to assess whether niche partitioning according to social structure in bottlenose dolphin populations generally corresponds to marine and estuarine habitats.

In this study, coastal communities were latitudinally distributed, with all but two communities that used the opposite ends of the study area overlapping in their full activity space. This sympatric, isolation by distance community distribution is typical for coastal and estuarine dolphins (e.g., Titcomb et al. 2015; Chabanne et al. 2017a) and is likely shaped by intraspecific competition between individuals or social communities (Wilson et al. 1997).

The communities' overlapping core activity spaces identified the two estuary mouths as favoured regions by dolphins within the study area. Relatively narrow channels with strong currents are known to be preferentially used by bottlenose dolphins (Wilson et al. 1997). They may concentrate prey moving from estuary to marine waters, or vice versa and attract prey due to the hydrodynamics and tidal currents (Loneragan et al. 1986; Loneragan et al. 1989; Valesini et al. 2009; Potter et al. 2016). Additionally, there may be an increase in feeding efficiency that outweighs energy expenditure as dolphins can utilize currents (Shane 1990; Bailey and Thompson 2010) and use structures such as channel and canal walls and dead ends to herd fish against, as has been observed in the study area (Chapter 4).

All communities' core areas were inclusive of either Mandurah Channel or Dawesville Channel, or both in the case of community A, in autumn. The channels are likely to have larger quantity of high calorific value fish, such as *Pelates octolineatus* and *Arripis truttaceus* (McCluskey et al. 2016), available during this time. *P. octolineatus* is relatively abundant in the PHE (Loneragan et al. 1986, Potter et al. 2016) and mature individuals emigrate through the channels to spawn in the marine environment in autumn (Veale et al. 2016). In contrast, adult *A. truttaceus* migrate north along the West Australian coast in autumn and early winter to spawn with schools entering bays and estuaries along the coast (Gomon et al. 2008). During this study, dolphins were observed in and around the channels feeding on both these species mainly in April and May (austral autumn; Nicholson, 2021, unpublished data). Although, in general, individuals' spatial patterns are likely related to foraging behavior and opportunities (Hastie et al. 2004), the observed temporal overlap in communities' distribution also coincides with peak mating and calving season (Chapter 3). The overlapping core areas for communities in autumn likely reflects an increase in foraging opportunities in the channels, which in turn may facilitate mating opportunities across communities.

Although spatial overlap was observed between the estuarine and coastal communities seasonally, this study did not investigate fine scale temporal patterns, which may occur, in space use. Bottlenose dolphin communities may partition spatiotemporally within a day, with members of different communities using the same area at different times of the day (Genov et al. 2019). There is a risk of conflict should members from different communities encounter each other in the same area. This may lead to avoidance of areas mainly occupied by a particular community (Genoves et al. 2018) or to stratified movement of all individuals in response to increase in number of dolphins in an area (Wilson et al. 1997). Stratified movement was not detected in this study, but coastal individuals did not frequent the estuarine habitat and the estuarine individuals did not frequent the coastal habitat beyond the entrance channels or coastal areas directly adjacent to them.

Coastal individuals that were not part of community D were commonly observed in Dawesville Channel while community D was present. Community D had a smaller overall range compared to other communities and an apparent strong year-round site fidelity to the Dawesville Channel. This community shares approximately 50% of its overall and core area with community A and E and is a sole occupant of only a small part of its range in winter, when community E is absent from the study area. Community D occupies Dawesville Channel in all behavioral states (i.e., resting, foraging and socializing) whereas members of other communities are typically observed in Dawesville Channel either while foraging, socializing, or travelling through (Nicholson, unpublished data). While foraging behavior and opportunities and competition between individuals or social groups may shape the spatial distribution in the population (Wilson et al. 1997; Hastie et al. 2004), when prey is abundant, individuals may engage in scramble competition with less antagonistic behavior expected between conspecifics (Whitehead and Rendell 2014). This may explain the co-existence of individuals from different communities in the channel areas.

The core areas of community A and B were bimodal suggesting two distinct areas are important for these communities and individuals potentially having heterogeneous space use patterns within their range. In bottlenose dolphins, such heterogeneity has been linked to sexual segregation in ranging patterns (Owen et al. 2002; Krützen et al. 2004; Tsai and Mann 2013; Sprogis et al. 2016) and individual variation in foraging tactics (Mann and Sargeant 2003; Sargeant et al. 2007). The core area of community B was in the very northern part of the study area year-round but also extended to just outside the Mandurah Channel in autumn and winter. It appears that only particular individuals venture south during these seasons while others do not (Nicholson, unpublished data). Similarly, in community A, some individuals more frequently use Mandurah Channel while others prefer the Peel Inlet or Harvey Estuary (Chapter 4). This could also explain the absence of coastal community E in winter. Individuals belonging to community E may be part of a larger community with a core area south of the study area. A cohort of this community may venture further north (i.e., into the study area) seasonally for foraging or mating opportunities. Therefore, it is likely that individuals who socially link the communities, are ones who show preference to habitat in the peripheral range of their community.

2.4.3. Isotopic partitioning

The estuarine community was isotopically distinct from the coastal communities with significantly higher mean $\delta^{13}C$ and significantly lower mean $\delta^{15}N$ values. The higher $\delta^{13}C$ values indicate a greater contribution of benthic carbon in the estuarine environment in contrast to the contribution of plankton carbon in coastal environments (e.g., McCluskey et al. 2021). This is consistent with findings from other studies as, generally, individuals showing high site fidelity to estuaries or near coastal areas have higher $\delta^{13}C$ values than the gradually lower values observed the further from coast the individual's activity space is located (Holyoake et al. 2011; Barros et al. 2010; Gibbs et al. 2011; McCluskey et al. 2021). Although the relative $\delta^{13}C$ values suggest members of the estuarine community rely on estuarine primary production and are part of the estuarine food web, the high variability in $\delta^{15}N$ values suggests considerable intra-community partitioning in their diet.

Similar to some studies (Barros et al. 2010; Gibbs et al. 2011) and in contrast to others (Holyoake et al. 2010; McCluskey et al. 2021), this study found dolphins with high site fidelity to estuaries to feed at a lower trophic position than their coastal counterparts. Differences in $\delta^{15}N$ values may reflect variability in trophic level occupied by dolphins in different ecosystems but may also reflect variation in nitrogen isotope values of basal resources (Fry 2006; Phillips 2012; Lorrain et al. 2015). Like Kiszka et al. (2012), this study did not find significant differences in carbon and nitrogen stable isotope ratios among spatially adjoining coastal communities. Although the complexity in trophic ecology makes generalizations difficult (Schmitz 2010), it is likely that contrasting habitat within dolphins' range leads to higher intraspecific partitioning in resource use (e.g., Sargeant et al. 2007; Patterson and Mann 2011).

2.4.4. Management implications and recommendations

Evidence of community niche partitioning in social, spatial and isotopic dimensions provides a strong scientific basis for treating the estuarine community (A) as a discrete management unit within a coastal and estuarine area covering 600 km^2 that includes four coastal communities (B, C, D and E) and dolphins that occur more transiently within coastal waters. The use of social, spatial and isotopic partitioning to identify the estuarine community (A) as a management unit is consistent with the definition of a management unit as a *geographical area* with restricted interchange of the individuals of interest with adjacent areas (Taylor and Dizon 1999) and with previous studies that identified management units based on social communities and their space use (Chabanne et al. 2017a) or ecological tracers (Barros et al. 2010; Giménez et al. 2018).

The study area contained the full extent of the estuarine community's distribution to the west (i.e., coastal boundary) but not to the east (i.e., riverine habitat). Stranding records indicate that dolphins travel further upstream than the extent of the search effort in this study (Groom and Coughran 2012; Nicholson et al. 2019). As coastal individuals did not frequent the estuary, individuals with habitat preferences for the eastern shores of the estuarine system are not expected to interact with members of coastal communities. As such, community A represents the true size (in terms of juveniles and adults) and distribution of a biologically meaningful community of individuals.

Although coastal communities (B, C, D and E) were identified as socially and spatially distinct, considering them separate management units from each other may be inappropriate. The study area covered the coastal communities' range in terms of individuals' use of the estuary but did not encompass the full home range of all coastal individuals as many were sighted outside the study area's offshore boundary. The number of individuals in the identified coastal communities does not necessarily reflect the true number of individuals in these communities or the number of individuals using the study area given that approximately half of all encountered individuals in coastal habitat were not assigned to communities. For the purposes of environmental impact assessments, the total number of individuals who might be affected by new developments or activities in coastal waters may therefore be underestimated if only relying on information on number of individuals in identified communities. The information provided on the coastal community structure and distribution should be considered where appropriate, however, caution is recommended as further study is required to fully understand the social, spatial and ecological dynamics of dolphins occupying coastal areas adjacent to the PHE.

The estuarine community and the coastal communities collectively are exposed to different pressures and threats. The estuarine dolphins overlap to a greater extent with anthropogenic activities as the PHE is heavily used for recreational activities and supports both recreational and commercial fisheries for fin fish and blue swimmer crab (*Portunus armatus*; Hale and Butcher 2007; Gaughan et al. 2019; Obregón et al. 2020). The estuary has also been identified as a bottlenose dolphin live stranding hotspot (Groom and Coughran 2012). Given that all (*n* = 6) but one dolphin who were recorded live stranded during this study were identified as members of the estuarine community (Nicholson, unpublished data), dolphins residing in the estuary are hypothesised to have a higher probability of stranding than coastal individuals. In contrast, coastal dolphins are likely influenced by a higher degree of predation pressure, which is evident from shark bite injuries and scarring observed in coastal individuals but not on the estuarine ones (Nicholson, unpublished data).

This study was relatively short in duration compared with the multi-decadal lifespan of delphinid species. The social, spatial and isotopic structure of the identified communities is likely to be dynamic in response to extrinsic (e.g., prey availability and habitat modification) and intrinsic (e.g., changes in demographic structure) factors. For appropriate short-term management of the estuarine community, further work is required to evaluate the status (e.g., declining, increasing, or stable abundance) of the community. For long term management, a natural progression of this research is to analyse population genetic structure. Continued monitoring in the estuarine environment, inclusive of the entrance channels, to encompass all communities' core areas is recommended. This approach would capture how individual, estuarine and coastal, continue to use and depend on the PHE over time and allow dolphins to be used as estuarine and marine ecosystem sentinels (e.g., Wells et al. 2004)

2.4.5. Conclusions

The investigation of population structure in multiple niche dimensions allowed a socially, spatially and isotopically distinct dolphin community to be identified in the Peel-Harvey Estuary. The examination of sighting patterns of all encountered individuals confirmed that the members of the estuarine dolphin community occupied a different social environment than members of the identified coastal communities who shared space with more transient individuals. The defined size and spatial range of the estuarine dolphin community reflects its true size and range allowing the estuarine community to be defined as a management unit that should be considered separate to coastal communities.

Chapter 3

Demographics, age structure and viability of an estuarine population of Indo-Pacific bottlenose dolphins

3.0. Abstract

Effective management relies on demographic parameter estimates, which are required to assess population status, predict trends and evaluate risk of extinction. This study investigated age, sex and social structure of a community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary in Western Australia and whether demographic parameters (i.e., apparent survival, mortality, immigration and reproductive rates) are heterogeneous according to these attributes. A Population Viability Analysis (PVA) was used to assess current community status. Additional 15 PVA models were run to explore the impacts of carrying capacity, reduced adult female and yearling mortality and increased reproductive rate on the community growth rate. Systematic boat-based photo-identification surveys (n = 483) were conducted in the estuary between 2016 and 2019. The community comprised 88 (SD 4.43) individuals organised in social clusters whose age and sex structure corresponded to typical bottlenose dolphin association patterns. Demographic parameters were heterogeneous according to age, sex and social cluster. The community is closed, with no immigration and population demographic changes driven by births, deaths and the likely permanent emigration of juvenile males. The PVA forecasted a slowly declining community (r = -0.004, SD 0.062) with a low probability (<1%) of extinction in the next 100 years. Management action should prioritize reducing adult female and yearling mortality while maintaining the relatively high reproductive rate in this community. This may be achieved by ensuring zero human caused mortality and ensuring adverse impacts to the population are considered in future development planning.

3.1. Introduction

Wildlife managers require reliable population demographic parameter estimates so that they can assess population status, predict trends and evaluate vulnerability to threats and risk of extinction (Taylor 1995; Thomas and Kunin 1999; Coulson et al. 2001). However, managers often face several practical and methodological challenges in acquiring such information. First, demographic parameter estimates, as well as their accuracy and precision, vary depending on the temporal and spatial scale at which a population is observed (Thomas and Kunin 1999). This variability makes these parameters challenging to obtain for taxa, like delphinids, that are wide-ranging, long-lived, slowly reproducing and often distributed across space without clear population boundaries. Second, although abundance, apparent survival (i.e., no distinction between death and permanent emigration) and temporary emigration estimates are available for several delphinid species (e.g., Slooten and Davies 2011; Nicholson et al. 2012; Tyne et al. 2014; Zanardo et al. 2016), it is not always clear how the population in focus for management is (or should be) defined and therefore how the resulting estimates should be interpreted. Third, managers commonly rely on population declines as a criterion to trigger management action for delphinids (e.g., Lee Long and O'Reilly 2009), even though there is often a low statistical power to detect population declines in a timeframe that allows for management interventions to halt or reverse a decline (Taylor and Gerrodette 1993; Taylor et al. 2007; Tyne et al. 2016; Symons et al. 2018).

Given these challenges, it may often be more appropriate for managers to base decision-making on Population Viability Analysis (PVA) that allows for the estimation of population growth rate and extinction probability based on population demographic parameters (Lacy 1993; 2000; Thompson et al. 2000; Lacy et al. 2005).

A PVA allows managers to apply a precautionary approach depending on the projected trend for a population (Thompson et al. 2000; Manlik et al. 2016). The demographic parameters used as model inputs must be reliable if the population trajectory is to be modeled properly and they must be interpretated based on a suitable definition of the population in question.

Population demographic parameters (e.g., reproductive, mortality, emigration and immigration rates), which are required to estimate population growth rate, commonly vary by age (Arso Civil et al. 2019) and sex (Stolen and Barlow 2003; Sprogis et al. 2016). Both these parameters are difficult to determine for all individuals in delphinid populations. This leads to difficulty in determining population age structure, which influences population growth rate, and in accounting for age- and sex-specific patterns in mortality and dispersal when forecasting population trends (e.g., Araújo et al. 2014; Manlik et al. 2016; Blaźquez et al. 2020). Although approximate birth dates (Galezo et al. 2020; Gerber et al. 2020), sighting histories (Wells 2014) and growth layers in teeth (Hohn et al. 1989) can be used to infer an individuals' age, visual inspection of body length is commonly used to assign individuals into broad age classes (Smolker et al. 1992; Parra et al. 2006). This approach, however, may not just result in incorrect assignment of age classes for individuals but also lead to demographic parameters being estimated for adults only (Zanardo et al. 2016) or for all independent (i.e., non-calf) individuals combined (Nicholson et al. 2012; Smith et al. 2012; Passadore et al. 2017). Fortunately, recent methodological advances using non-invasive stereo-laser photogrammetry to infer the length of individuals allows more detailed population age structure to be estimated and individuals to be assigned to age classes more reliably (Cheney et al. 2018; van Aswegen et al. 2019). This enables demographic parameters to be estimated separately for different ages or age classes. Designating individuals as either male or female also often relies on either visual observation of their genitalia, the presence of a dependent calf (Smolker et al. 1992; Mann et al. 2000) or confirmation from molecular analysis (Krützen et al. 2004; Möller and Beheregaray 2004). For some species/populations, dorsal fin markings have also been used to infer individuals' sex (Rowe et al. 2009; Brown et al. 2016). Regardless of the method(s) used, the ability to investigate age- and sex-specific patterns in demographic parameters allows more refined input parameters to be used in forecasting population trends over time.

Demographic parameters also vary based on population social structure and individuals' habitat use (Frère et al. 2010; Chabanne et al. 2017). Individuals who are closely associated are more likely to use the same area, encounter the same resources and have similar diet (Darimont et al. 2004; Semmens et al. 2009). This leads to highly associating individuals, or those using the same habitat, being exposed to the same threats, such as exposure to toxins or other human stressors (Wells et al. 2005; Yordy et al. 2010; Twiner et al. 2011; Chabanne et al. 2017a; Kemper et al. 2019; Senigaglia et al. 2019). These, in turn, may cause intrapopulation heterogeneity in demographic parameters like survival and reproductive rates (Donaldson et al. 2010; Atkins et al. 2016; Senigaglia et al. 2019). Investigating variation in demographic parameters according to social structure and habitat use, will aid in identifying threats to individuals across population structure and identifying priorities for management action.

Bottlenose dolphins (*Tursiops* spp.) live in complex social systems with fission-fusion dynamics where group size and composition changes frequently (Connor et al. 2000; Aureli et al. 2008). Many populations are comprised of socially and spatially distinct communities with some associations occurring among members of different communities (e.g., Urian et al. 2009; Wiszniewski et al. 2009; Titcomb et al. 2015; Chabanne et al. 2017a). Within communities, members form higher-level associations (i.e., social clusters) that often reflect sex- and age-specific association patterns for *Tursiops* spp. (Connor et al. 2000). Adult association patterns are influenced by mating system constrain, while juvenile association patterns reflect adult reproductive strategies with individuals also forming behaviorally specific associations (Gero et al. 2005; Krzyszczyk et al. 2017; Galezo et al. 2020; Gerber et al. 2020). Adult female associations are influenced by foraging strategies (Smolker et al. 1997; Mann and Sargeant 2003; Krützen et al. 2005) and reproductive state (Wells 1987; Möller and Harcourt 2008; Smith et al. 2016; Diaz-Aguirre et al. 2020). As such, high variability is observed in female association patterns within and among populations, ranging from solitary individuals to individuals with a large network of affiliates (Wells 1991; Smolker et al. 1992). In contrast, male association patterns are driven by competition and access to estrous females which has led to male alliances forming in many populations (Wells 1991; Connor et al. 1992; Owen et al. 2002; Connor et al. 2011; Wiszniewski et al. 2012; Ermak et al. 2017). The most complex multi-level alliances have been recorded in Shark Bay, Western Australia (Connor et al. 1992; Connor et al. 2011; Connor and Krützen 2015). In contrast, long-term alliances are absent from some bottlenose dolphin populations (Lusseau et al. 2007; Baker et al. 2020). Given age- and sex-specific association patterns lead to social structure within communities (or populations), which may correspond to individuals' space and resource use (Chapter 4), investigating how demographic parameters vary by age and sex allows more realistic population trajectories to be modeled.

The Peel-Harvey Estuary (PHE) in Western Australia is occupied by a year-round resident Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) community, which is socially, spatially and isotopically distinct from identified communities in adjacent coastal waters (Chapter 2). This study investigates community age, sex and social structure, in particular whether identified social clusters correspond to typical age- and sex-specific patterns described for bottlenose dolphins elsewhere. Demographic parameters (i.e., apparent survival, mortality, immigration, emigration and reproductive rates) will be calculated and heterogeneity according to age, sex and social cluster in these parameters explored. The population trajectory (i.e., stable, declining or decreasing) based on the current demographic parameter values will be assessed using a PVA incorporating population age structure and age- and sex-specific mortality rates. It is hypothesized this community is a closed population where population changes are largely determined by birth and death processes (Thomas and Kunin 1999).

3.2. Methods

3.2.1. Study area

The Peel-Harvey (~130 km^2) is the largest estuary in south-western Australia and is part of the Ramsar-listed Peel-Yalgorup wetland system. It is a shallow (mainly < 2 m deep) microtidal (tidal range ~0.5 m) estuary connected to the Indian Ocean via two openings: Mandurah Channel and Dawesville Channel (Fig.3.1). Three rivers, the Murray, Serpentine and Harvey, flow into two basins, the Peel Inlet and the Harvey Estuary. The estuary supports migratory and other waterbirds (Hale and Butcher 2007) and functions as an important nursery, breeding and feeding ground for numerous fish species (Loneragan et al. 1986; 1987; Potter et al. 2016; Hallett et al. 2019). The City of Mandurah, with a population of ~85,000 people (Australian Bureau of Statistics

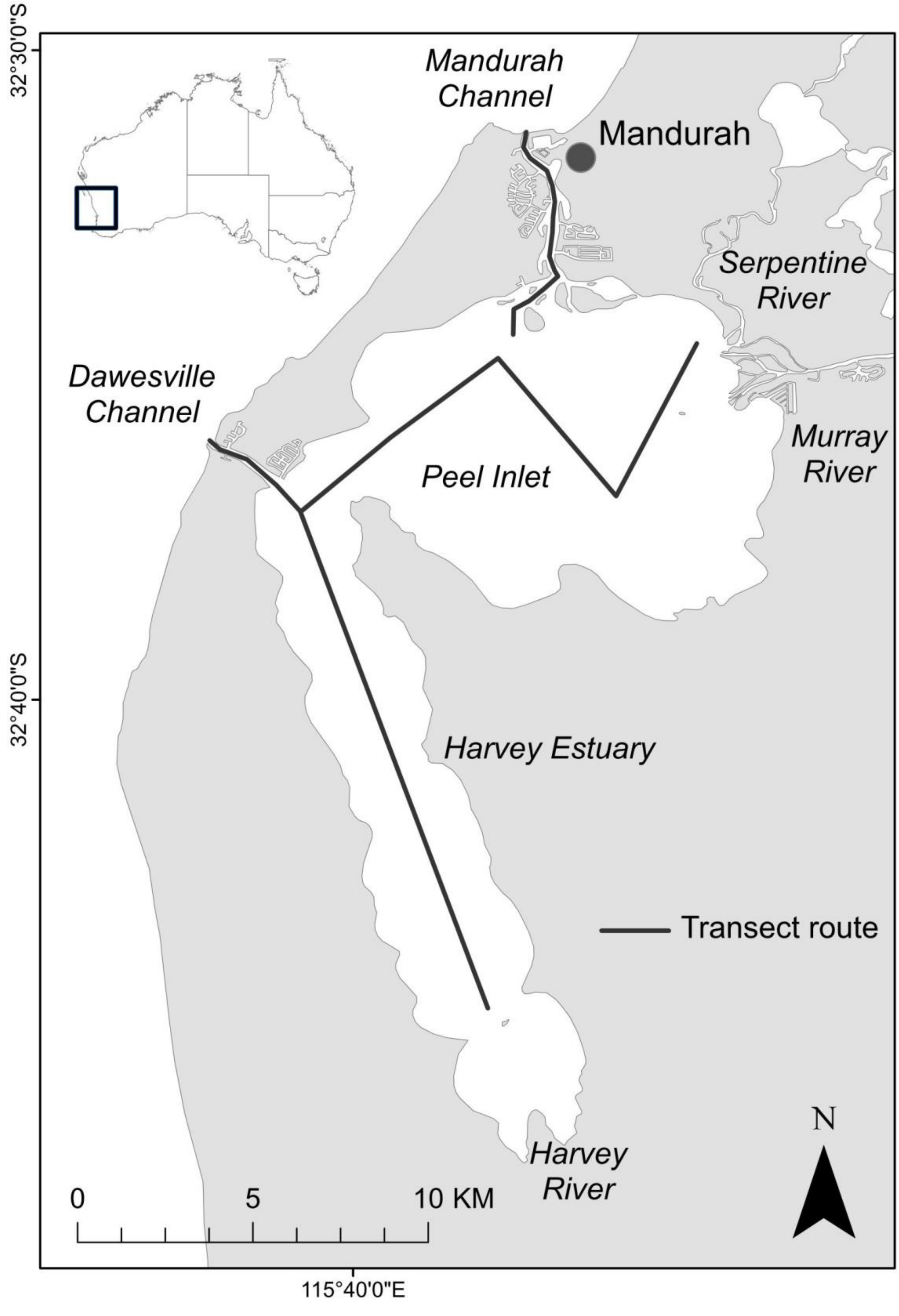

Figure 3.1. The Peel-Harvey Estuary, Western Australia, study area with an example of a transect route for boat-based photo-identification surveys targeting Indo-Pacific bottlenose dolphin (*Tursiops aduncus*).

2020), is located on the estuary with the foreshore along Mandurah Channel and Dawesville Channel, in particular, extensively modified by development (e.g., canals, breakwalls, jetties). The waterways are used extensively for recreational activities and are important for both recreational and commercial finfish and blue swimmer crab (*Portunus armatus*) fisheries (Gaughan 2019; Obregón et al. 2020).

3.2.2. Data collection and photo-identification

Boat-based photo-identification surveys for dolphins were conducted between 2016 and 2019 throughout the estuary. A minimum of three predetermined transects (Fig. 3.1) during each Austral season (summer: Dec – Feb, autumn: Mar – May, winter: Jun – Aug, spring: Sept – Nov) were run between January 2016 and November 2018 on board a 5.5 m vessel. Transects were completed within a day and followed the same route apart from in the Peel-Inlet where a unique 'zig-zag' pattern was followed on each sampling occasion (see example in Fig. 3.1). The Serpentine and Murray Rivers were not part of the study design but were visited at least once every season to ~7.5 km upstream. The Harvey River was inaccessible due to shallowness of the southern parts of the estuary.

When dolphins were encountered, a minimum five-minute survey was conducted to record the location, behavior and group composition of sighted individuals. Group membership was defined by a '10-meter chain rule' where individuals are part of the same group if they are within 10 m of any other group member (Smolker et al. 1992). The dorsal fin of each individual was photographed for unique markings (e.g., nicks and notches) allowing for individual identification (Würsig and Würsig, 1977). Dorsal fin shape and additional markings, such as scarring and lesions, were used to aid in identification of individuals that had not acquired sufficient dorsal fin nicks and notches visible from both sides of the dorsal fin. Photographs were checked prior to leaving a group to ensure a good quality photograph (i.e., dorsal fin fully visible, in focus and perpendicular to the camera: Urian et al. 1999; Rosel et al. 2011; Nicholson et al. 2012) was obtained of each individual. Occasionally, a survey was terminated prior to obtaining good quality photographs due to the behavior of dolphins or when it was uncertain how many individuals were present in a group. The same survey protocol was applied during additional research effort conducted within the estuary between 2016 and 2019 to collect tissue samples for genetic analyses and stereo-laser photogrammetry data for aging individuals (van Aswegen et al. 2019).

The best quality photograph of each individual's dorsal fin obtained during each encounter was graded for quality as per Nicholson et al. (2012). Dorsal fin photographs were compared to others in the catalogue established for individuals encountered in the estuary and adjacent coastal waters. A match was confirmed by two independent observers. If there was no match, four independent observers searched the catalogue for a match prior to the individual being assigned a unique identification code and added to the catalogue. Only individuals identified from excellent quality photographs (as per Nicholson et al. 2012) were added to the catalogue. To maximise sample size for analyses, individuals whose identity was confirmed by two independent observers, regardless of photographic quality or fin distinctiveness, were included in subsequent analyses.

Data collected in 2016 and 2017 were used for social structure analyses while data collected between 2016 and 2019 were used to calculate demographic parameters. Supplemental information on births and deaths in the estuarine dolphin community, as well as photographic confirmation of resident individuals being alive and present in the estuary, came from monitoring effort by the Mandurah Dolphin Volunteer Rescue Group and a tour operator Mandurah Cruises.

3.2.3. Age and sex determination

For some individuals, minimum age was inferred based on a consistent association with a reproductive female and/or dependent calf or, when known, the approximate birth dates. Dolphin live stranding records since 1990 (Groom and Coughran 2012) were also used to estimate the minimum age of some individuals. Individuals >10 years of age were considered sexually mature (i.e., adults) based on information on wild (Wallen et al. 2017) and captive (Wells et al. 1987; Brook et al. 2000) animals elsewhere. Juveniles were identified as sexually immature based on visual inspection of their length, them not being recorded with a calf and/or being estimated to be <10 years of age by laser-photogrammetry methods. Calves were defined as presumed offspring (>1 year old) of an adult female they consistently associated with. Calves who were <1 year old are referred to as yearlings. Visual confirmation from photographs of genitalia and the consistent presence of a calf were used to identify individuals as male or female.

Approximate age of individuals was estimated from an available growth curve for the population developed as part of a separate study using data collected in the PHE and Bunbury (~90 km south of the study area) where the age of many individuals is known (van Aswegen et al. 2019). The growth curve was developed using remote stereo-laser photogrammetry (i.e., two lasers fixed to a camera reflecting two points at a known distance (10 cm) apart on the dolphin’s body when taking a photograph). The distance between a dolphin’s blowhole and dorsal fin insertion has proven to be a valuable proxy measurement for total body length and can be used to infer approximate age of individuals when validated against the length of known aged individuals (Cheney et al. 2018; van Aswegen et al. 2019). The age of immature individuals at any given length derived from the growth curve is approximate due to the variability in size of similarly aged individuals (van Aswegen et al. 2019). Age estimates may be biased for sexually mature individuals as at physical maturity (12 – 15 years) growth ceases due to the fusion of vertebral epiphyses (Cockcroft and Ross 1990).

3.2.4. Social structure analyses

Social analyses were conducted on SOCPROG 2.9 (Whitehead 2009). To investigate association patterns within the estuarine community, an association index estimating the proportion of time two individuals spent together, was calculated for each dyad. A half weight index of association (HWI) was used as it is considered least biased when all associates of a given individual are not identified (Cairns and Schwager 1987). The HWI accounts for inherent bias introduced through photo-identification methods when all individuals of a group may have not been identified during a photo-identification survey. Individuals were considered associated if they were observed in the same group during a sampling period defined as a day (Gowans and Whitehead 2001; Lusseau et al. 2003). Dependent calves were excluded from all social analyses.

A Pearson's correlation coefficient (PCC) with likelihood approximation was calculated between true and estimated HWIs to test whether the HWIs were representative of true social structure (Whitehead 2008a). The PCC was first calculated including all individuals encountered and then progressively for sub-sets of individuals observed more than once, more than twice, more than three times and so forth until the threshold for adequate representation (PCC > 0.4) was reached (Whitehead 2008b). A coefficient of variation of true HWIs was estimated to investigate the degree of social differentiation within the community (Whitehead 2008a). Permutation tests were then conducted to determine whether the observed HWIs differed from that of randomly associating individuals (Bejder et al. 1998; Whitehead 1999; Whitehead et al. 2005). The difference in mean standard deviation between observed and permuted HWIs was used as a test statistic to determine whether the observed HWIs were significantly different from the permuted HWIs. A Mantel test with 1,000 permutations was used to test whether strength of association differed between sex and age classes.

To test whether dyadic association patterns correlated with dyadic overlap in space use, an asymmetric matrix of proportional overlap in activity space for each pair of individuals was calculated. First, a 95% utilization distribution (UD) was estimated for each individual using the Epanechnikov kernel function (Epanechnikov 1969) with an *ad hoc* (h_{ref}) smoothing parameter (Worton 1989; Silverman 1986) over a grid (cell size 100 m x 100 m) created over the study area. The R (R Core Team 2020) package adehabitatHR version 0.4.18 (Calenge 2020) was used for spatial analyses. As this package does not support highly irregular shapes, like the PHE, as boundaries that animals cannot cross (e.g., Sprogis et al. 2016; Barry and McIntyre 2011) when estimating the UD, land was removed from UDs *post hoc* using a boolean land mask. Utilization distribution overlaps between dyads were calculated as the proportion of activity space of one individual covered by the activity space of another individual. A Mantel Z-test with 1000 permutations was used to test for correlation between HWIs and activity space overlaps.

Null and Lagged Association Rates (NLARs and LARs, respectively) were calculated to investigate temporal patterning of associations within the population. The NLAR is the expected LAR if individuals are associating randomly and the LAR is the probability that two individuals associating at a given time are also associating later, with various time lags (Whitehead 1995). All individuals regardless of how many times they were encountered were included in this analysis as restricting data to frequently observed individuals is likely to positively bias the LARs (Baird and Whitehead 2000; Lusseau et al. 2003). A jackknife procedure with a grouping factor of one (jackknifing on each sampling period) was used to assess the precision of the estimated LARs (Efron and Stein 1981). Eight predetermined models describing temporal patterns of association were fitted to the LARs. The set of models are explained by one, or a combination, of the following (1) ‘constant companions’, which form temporally stable associations; (2) ‘casual acquaintances’, which associate for some time, disassociate and may reassociate and (3) ‘rapid disassociations’ which describes individuals disassociating within one time period. Estimated model parameters include the proportion of ‘constant companions’ (α), proportion of first and second level ‘casual acquaintances’ (γ and φ, respectively) and rate of disassociation between first and second level ‘casual acquaintances’ (β and ε, respectively). The estimated duration of association among first and second level ‘casual acquaintances’ was calculated as $1/\beta$ and $1/\varepsilon$, respectively. The Quasi Akaike Information Criterion (QAIC), which compensates for over-dispersed count data when using Poisson or binomial models, such as LAR models, was used as a measure of relative model fit. The model with the lowest QAIC was selected as best describing the temporal patterning of associations.

An average linkage hierarchical cluster analysis, which calculates a cophenetic correlation coefficient (CCC), was carried out to investigate whether the dolphin community comprised social clusters (i.e., individuals that associate at a higher rate with individuals within their cluster than with individuals in other clusters) reflecting fine scale social structure within the community. A Mantel test with 1,000 permutations was used to test whether HWIs within and among clusters differed significantly.

3.2.5. Population viability analysis and demographic parameters

Population Viability Analyses (PVAs) were conducted using VORTEX software version 10.2.9 (Lacy and Pollak 2017). VORTEX models wildlife population dynamics via age-based Monte Carlo simulations of deterministic and stochastic effects and estimates the population growth rate (*r*) and extinction probabilities under different scenarios (Lacy 1993). It treats population processes (e.g., breeding and death) as discrete, sequential events, with probabilistic outcomes and calculates a mean population growth rate based on a cohort life-table with mean birth and age specific death rates that are determined by the user. Population demographic parameters (e.g., population size, age and sex structure, annual mean reproductive and mortality rates), required as input parameters for the model, were calculated for the dolphin community using data collected between 2016 and 2019 (see Table 3.1). The VORTEX models were run with 1000 iterations for 100 timesteps (i.e., years) with extinction defined as only one sex remaining in the population.

The initial population size for the models was determined by the number of individuals alive in the estuarine social community in 2016. Known (i.e., from birth records), estimated (i.e., from stereo-laser photogrammetry measurements) and best guess (i.e., from calving or live stranding records) ages were used to create a population age distribution for both sexes in 2016. This was used as the initial age distribution for the model (Appendix B, Fig. B.1). Immature individuals, based on visual inspection of their length, whose age was not known or estimated, were assigned to be six years old (i.e., the age at midpoint in the

Table 3.1. Demographic parameters used for a Population Viability Analysis for a resident community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) occupying the Peel-Harvey Estuary in Western Australia. Parameter estimates reflect population structure in 2016. Notations: F = Female, M = Male, SDEV = Standard deviation due to environmental variance.

Model parameter	**Input value**
Initial population size	86
Carrying capacity	150
Age class distribution (%)	
Yearlings	F = 8.14 M = 3.49
Calves	F = 5.81 M = 11.63
Juveniles	F = 11.63 M = 15.12
Adults	F = 29.07 M = 15.12
Reproductive system	
Age of female maturity	10 years
Age of male maturity	10 years
Maximum age	40 years
Sex ratio at birth	50:50
Reproductive rate	38.54 (SDEV 14.37)
Males in breeding pool (%)	56.5[1]
Weaning age	3 years
Mean annual mortality rates	
Yearlings (males and females combined)	24.76 (SDev 1.51)
Calves (males and females combined)	0 .00 (SDev 1.51)
Juvenile males	12.70 (SDEV 1.51)
Juvenile females	8.87 (SDEV 1.51)
Adult males	6.28 (SDEV 1.51)
Adult females	5.05 (SDEV 1.51)

[1] Estimate of males in breeding pool was taken from Krützen et al. 2004a

juvenile age class). Unknown age adults were assigned to be 23 years old (i.e., the age at midpoint in the adult age class). The maximum age of reproduction was set to 35 years for both sexes based on the oldest individual, a female, observed in the system living to at least 33 years old (assuming she was at least 10 years old when she had her first calf) while producing a calf at 32 years old and the oldest male estimated to have died at 35 years old, based on being at least 6 years old at first live stranding (Nicholson, unpublished data).

The carrying capacity (*K*) for dolphins in the PHE is unknown and may vary among years and seasons in response to primary production or prey availability (Young and Phillips 2002). To allow for population expansion, the carrying capacity for the base model was set to 150 individuals.

An annual reproductive rate was calculated by dividing the number of sexually mature females by the number of calves born in the community within a given calendar year. The mean annual reproductive rate was used as an input parameter for the base model. As death and permanent emigration could not be fully separated, annual mortality rates were calculated as the proportion of individuals that were confirmed deceased or disappeared (i.e., not observed over two sampling seasons) from the community during a calendar year. Mean annual mortality rates were calculated separately for each age and sex class and were used as input parameters for the PVA: yearling mortality rate was applied to ages from zero to one, calf mortality rate from one to three, juvenile mortality rate from three to ten, and adult mortality rate from age ten onwards. Standard deviations due to environmental variance (SD_{EV}), which refers to variation in demographic parameters due to random fluctuations in the environment (e.g., weather, prey availability, predation pressure), were calculated for reproductive and mortality rates. Environmental variation was modelled by drawing random numbers from binomial distributions with user-specified mean and SD_{EV} to determine the percentage of females reproducing and individuals dying each year (Lacy 1993; Lacy et al. 2017). Given the short duration of this study and low interannual variability in non-yearling mortality rates, it was not possible to separate SD_{EV} for adult, juvenile and calf mortality rates. As such, the SD_{EV} for yearling mortality rate was applied to all mortality rates. Alternative SD_{EV} values were trialled by decreasing and increasing SD_{EV} by 0.5 increments up to the value of total observed variation while keeping all other input parameters the same. Given the similarity in estimated population growth rates and extinction probabilities (Appendix B Table B.1), the alternate SD_{EV} values are not considered or discussed further. Environmental variation in reproduction and mortality were modelled independent from each other.

There is no population specific information on genetic structure, including inbreeding, and the proportion of males that contribute to the gene pool; both parameters can be incorporated in the PVA. Given members of the estuarine community interact with members of coastal communities (Chapter 2), which likely facilitates gene flow between communities, inbreeding depression was not considered in the model. Following Manlik et al. (2016) the proportion of males contributing to the gene pool was set to 56.6%, which is a midpoint of possible values between 13 and 100% reported by Krützen et al. (2004) for bottlenose dolphins in Shark Bay, Western Australia.

To explore the effect of carrying capacity (K) on the estimated population growth rate, two additional models were run: one with $K = 86$ individuals (i.e., system is at carrying capacity) and one with $K = 100$ (i.e., to allow for slight population expansion). Additionally, a model with stable population age structure (estimated from a life table in VORTEX), as opposed to the estimated age structure specified in this study, was run to investigate whether this had an impact on the resulting population growth rate. To inform management, 12 further models were run to evaluate the effect of increase in reproductive rate, adult female and/or yearling survival on population growth rate. Keeping all other parameters as described above (i.e., base model), mean annual reproductive rate and adult female and yearling survival were increased by 1, 5, and 10 percent (Appendix B Table B.2).

Although not required as input parameters for the model, apparent survival and immigration rates were also calculated. Individuals were confirmed deceased only if they were observed post-mortem. Individuals that were not observed in two consecutive sampling seasons (i.e., six months) were considered as having either died or emigrated. Yearlings were assumed deceased if their mother was observed without them on more than three occasions. The apparent annual survival rate was calculated for each age class (i.e., adults, juveniles, calves and yearlings) as the proportion of individuals alive in the community during a calendar year surviving to the subsequent calendar year. Immigration rate was calculated as the proportion of individuals that were observed to consistently associate with members of the defined estuarine community for at least two consecutive seasons (i.e., six months).

3.3. Results

3.3.1. Effort and group encounters

Thirty-seven transects, were run between January 2016 and November 2017 in the PHE equating to approximately 350 hours of effort. Additionally, during this time, opportunistic search effort throughout the estuary was conducted on 48 days (~253 hours). A total of 628 dolphin groups were encountered, of which 483 comprised estuarine resident dolphins based on social community structure (Chapter 2). The remaining groups were encountered in Dawesville Channel and comprised solely of individuals identified as part of social communities residing in coastal waters (Chapter 2). Thirteen transects were conducted in the estuary in 2018 (~109 hours) with additional effort conducted on six days (~40 hours). This effort resulted in 177 dolphin group surveys. In 2019, six days (~43 hours) were spent in the estuary with a further 50 dolphin groups encountered.

3.3.2. Population age and sex structure

The dolphin community comprised on average 11% yearlings, 15% dependent calves (> 1 year old), 32% juveniles and 42% adults (see estimated ages of individuals in Appendix B, Tables B.3, B.4 and B.5). Sex ratios were approximately equal in all age classes, except adults, where 33% were males and 67% females (Table 3.2).

Table 3.2. Population demographic parameters for a community of Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) resident to the Peel-Harvey Estuary. Parameters were calculated from photo-identification data collected year-round between 2016 and 2019. All values apart from number of individuals deceased or emigrated are presented as a mean (SD) over the study period. Age class and sex of all individuals identified as part of the community were known. Individuals were confirmed deceased only if observed post-mortem while those considered deceased or having emigrated from the community were not observed during a period of at least 6 months.

Age class	**Community composition (%) *N* = 88 (4.43)**	**Sex ratio (m:f)**	**Apparent survival (SD)**	**Deceased individuals (*n*)**	**Deceased or emigrated individuals (*n*)**
Adults	41.80 (3.01)	33:67	0.95 (0.02)	5	3
Juveniles	32.40 (6.00)	58:42	0.88 (0.03)	4	8
Calves	15.41 (6.98)	47:53	1.00 (0.00)	-	-
Yearlings	10.39 (5.06)	50:50	0.75 (0.19)	9	-

3.3.3. Social structure

A Pearson's correlation coefficient of 0.79 (SE 0.03) confirmed that the data were sufficient for analyses to provide a good representation of true social structure (Whitehead 2008b). The coefficient of variation in HWIs was 0.87 (SE 0.04) indicating the community was socially well-differentiated, with individuals varying in their association patterns and strength (Whitehead 2008a; 2008b). The coefficient of variation of mean observed HWIs was also significantly higher ($P < 0.001$) than that for the permuted HWIs indicating individuals associated preferentially within the community. All independent individuals (n = 62) were sighted on >6 sampling occasions during the study and were included in social analyses as the PCC reached an acceptable threshold (i.e., >0.04) when including individuals encountered >6 times. Association rates within sex (Mantel test: t = 7.35, P < 0.001) and age (Mantel test: t = 5.92, P <0.001) classes were significantly higher than between classes (Table 3.3) with association strength positively correlating with proportion of activity space overlap between dyads (P <0.001).

The Lagged Association Rates for both adult males and females were above the NLAR for all time lags, indicating that individuals within this community form long lasting, preferred associations (Fig. 3.2). Of the eight models initially fitted to the LARs, three were excluded from the model set for adult males due to the resulting negative parameter estimates indicating that these models did not fit the data. The same model, $g(\tau) = \alpha + \gamma \exp(-\beta\tau)$, best described the patterns of association for both adult (n = 39) males and females (Tables 3.4 and 3.5). This model represents a system of ‘rapid disassociations, casual acquaintances and constant companions’.

The parameter estimates describing male association patterns were $\hat{\alpha}$ = 0.57 (SE 0.06), $\hat{\gamma}$ = 0.13 (SE 1.00) and $\hat{\beta}$ = 0.03 (SE 5.22). Here, out of all associations (including repeats) of a male, 57% were with temporally stable associates and 13% with associates with whom associations lasted for 33 (SE 0.19) days. Rapid disassociations, typically considered to last for less than a day, accounted for the remaining 30% of associations. The parameter estimates for the model describing temporal association patterns of females were $\hat{\alpha}$ = 0.18 (SE 0.05), $\hat{\gamma}$ = 0.11 (SE 132.85) and $\hat{\beta}$ = 0.02 (SE 7.02). Of all associations of a female, 18% were with temporally stable associates and 11% with associates with whom associations lasted for 50 (SE 0.14) days. Rapid disassociations accounted for 71% of associations.

Table 3.3. Mean sighting frequency (SD) and Half-Weight Index of association (HWI) among demographic groups and social clusters of the resident community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the Peel-Harvey Estuary.

Group	**n**	**Mean sighting frequency (SD)**	**Mean HWI (SD)**	**Max HWI (SD)**
Overall	62	28.00 (11.90)	0.12 (0.05)	0.55 (0.21)
Males – Males	25	32.54 (11.81)	0.21 (0.05)	0.72 (0.18)
Females – Females	34	24.26 (10.66)	0.12 (0.04)	0.40 (0.11)
Males – Females	-	-	0.10 (0.05)	0.32 (0.16)
Females – Males	-	-	0.10 (0.06)	0.27 (0.15)
Adults – Adults	39	29.51 (12.85)	0.12 (0.04)	0.52 (0.24)
Juveniles –Juveniles	23	25.39 (9.67)	0.22 (0.09)	0.57 (0.18)
Adult – Juveniles	-	-	0.10 (0.05)	0.25 (0.11)
Juveniles – Adults	-	-	0.10 (0.04)	0.31 (0.12)
Within clusters	-	-	0.37 (0.16)	0.56 (0.21)
Between clusters	-	-	0.08 (0.03)	0.28 (0.07)
Within Cluster AM1	6	45.83 (5.57)	0.62 (0.62)	0.84 (0.10)
Within Cluster AM2	7	34.50 (6.57)	0.54 (0.07)	0.85 (0.10)
Within Cluster AF1	7	37.14 (10.92)	0.25 (0.03)	0.38 (0.11)
Within Cluster AF2	2	7.50 (0.71)*	0.40 (0.00)	0.40 (0.00)
Within Cluster JM	5	37.40 (5.08)	0.45 (0.06)	0.55 (0.06)
Within Cluster M1	21	23.71 (5.96)	0.32 (0.07)	0.55 (0.14)
Within Cluster M2	10	20.56 (7.04)	0.21 (0.04)	0.37 (0.07)
Within Cluster A	2	19.50 (2.12)	0.21 (0.00)	0.21 (0.00)
Within Cluster B	2	8.50 (0.71)*	0.82 (0.00)	0.82 (0.00)
Loner 1	1	41	0.08 (0.00)	0.23 (0.00)
Loner 2	1	11*	0.02 (0.00)	0.18 (0.00)

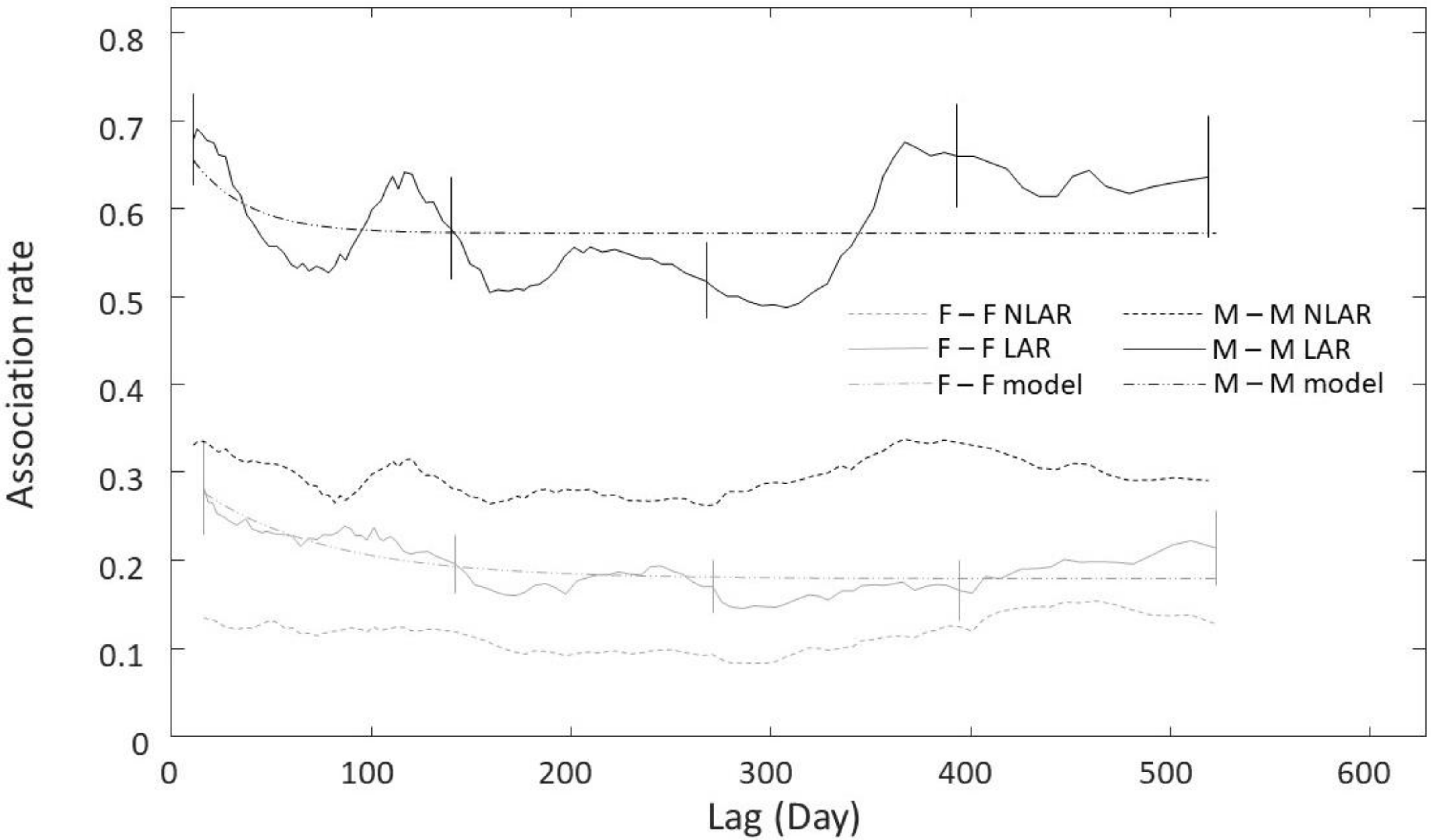

Figure 3.2. Null (NLAR) and Lagged Association Rates (LAR) and the best fitting model to describe the temporal patterns of association of adult Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary in Western Australia. Notations: F-F = association between adult females, M-M = association between adult males.

Table 3.4. Models describing temporal patterning in associations between males fitted to Lagged Association Rates of all bottlenose dolphin (*Tursiops aduncus*) individuals observed in estuarine waters off Mandurah, Western Australia. Notations: $g(\tau)$= lagged association rate (time in days), α= proportion of preferred companions, β= rate of disassociation between first level casual acquaintances, γ= proportion of first level casual acquaintances.

Model	Description	QAIC	ΔQAIC
$g(\tau) = \alpha + \gamma \exp(-\beta\tau)$	Rapid disassociations Preferred companions Casual acquaintances	16937	
$g(\tau) = \alpha$	Rapid disassociation Preferred companions	16972	35
$g(\tau) = \alpha + \gamma \exp(-\beta\tau)$ $\gamma = 1 - \alpha$	Preferred companions Casual acquaintances	16974	37
$g(\tau) = \exp(-\beta\tau)$	Casual acquaintances	21161	4224
$g(\tau) = 1$	Preferred companions	193216	21748

Table 3.5. Models describing temporal patterning in associations between females fitted to Lagged Association Rates of all bottlenose dolphin (*Tursiops aduncus*) individuals observed in estuarine and coastal waters off Mandurah, Western Australia. Notations: $g(\tau)$= lagged association rate (time in days), α= proportion of preferred companions, β= rate of disassociation between first level casual acquaintances, γ= proportion of first level casual acquaintances, φ= proportion of second level casual acquaintances.

Model	Description	QAIC	ΔQAIC
$g(\tau) = \alpha + \gamma \exp(-\beta\tau)$	Rapid disassociations Preferred companions Casual acquaintances	7428	
$g(\tau) = \gamma \exp(-\beta\tau) + \varphi\exp(-\varepsilon\tau)$	Rapid disassociation Two levels of casual acquaintances	7446	18
$g(\tau) = \gamma\exp(-\beta\tau)$	Rapid disassociations Casual acquaintances	7451	23
$g(\tau) = \gamma \exp(-\beta\tau) + \varphi\exp(-\varepsilon\tau)$ $\varphi = 1 - \gamma$	Two levels of casual acquaintances	7452	24
$g(\tau) = \alpha + \gamma \exp(-\beta\tau)$ $\gamma = 1 - \alpha$	Preferred companions Casual acquaintances	7454	26
$g(\tau) = \alpha$	Rapid disassociation Preferred companions	7464	36
$g(\tau) = \exp(-\beta\tau)$	Casual acquaintances	11526	4098
$g(\tau) = 1$	Preferred companions	218241	210813

Hierarchical cluster analysis provided a representative dendrogram (CCC = 0.87, Bridge 1993) dividing the community into nine social clusters and two individuals that were the sole members of their cluster (Fig. 3.3). Within cluster associations were significantly higher than associations among clusters (Mantel test: t = 19.22, *P* <0.001) Social clusters varied in size and demographics (Table 3.6). Adults were organised in single-sex clusters apart from two clusters (M1 and M2) which comprised adult females and juveniles of both sexes (Fig. 3.3). One cluster was comprised solely of juveniles, all of them males estimated between 4 and 5 years old in 2016 (Appendix B Table B.4). Mortality (Table 3.6) and reproductive rates were heterogeneous among clusters. The proportion of individuals that were dependent calves during this study and either died as yearlings, or shortly after weaning, varied by social clusters; 28.6% for AF1, 66.7% for AF2, 21% for M1 and 60% for M2.

Table 3.6. Age and sex composition and mortality within social clusters of a resident estuarine community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the Peel-Harvey Estuary, Western Australia. All parameters are based on data collected between 2016 and 2019. Mortality is inclusive of potential permanent emigration. Notations: A = Adult, J = Juvenile, M = Male, F = Female, U = Unknown, - = Not Applicable

Social cluster	Cluster composition Age (A/J) Sex (M/F/U)	Non-calf mortality (% of total mortality)	Calf mortality (% of total mortality)
AM1	6 AM	1 (8)	-
AM2	6 AM	1 (8)	-
AF1	7 AF	1 (8)	4/14 (24)
AF2	2 AF	1 (8)	2/3 (12)
JM	5 JM	2 (17)	-
M1	10 AF, 4 JF, 7 JM	-	4/19 (24)
M2	5 AF, 3 JF, 1JU	1AF, 1JF (17)	5/10 (29)
Cluster A	1 AF, 1 JF	1AF (8)	2/2 (12)
Cluster B	2 JM	2JM (17)	-
Loner 1	1 AF	-	-
Loner 2	1 AM	1AM (8)	-
Total	62	12	17/48

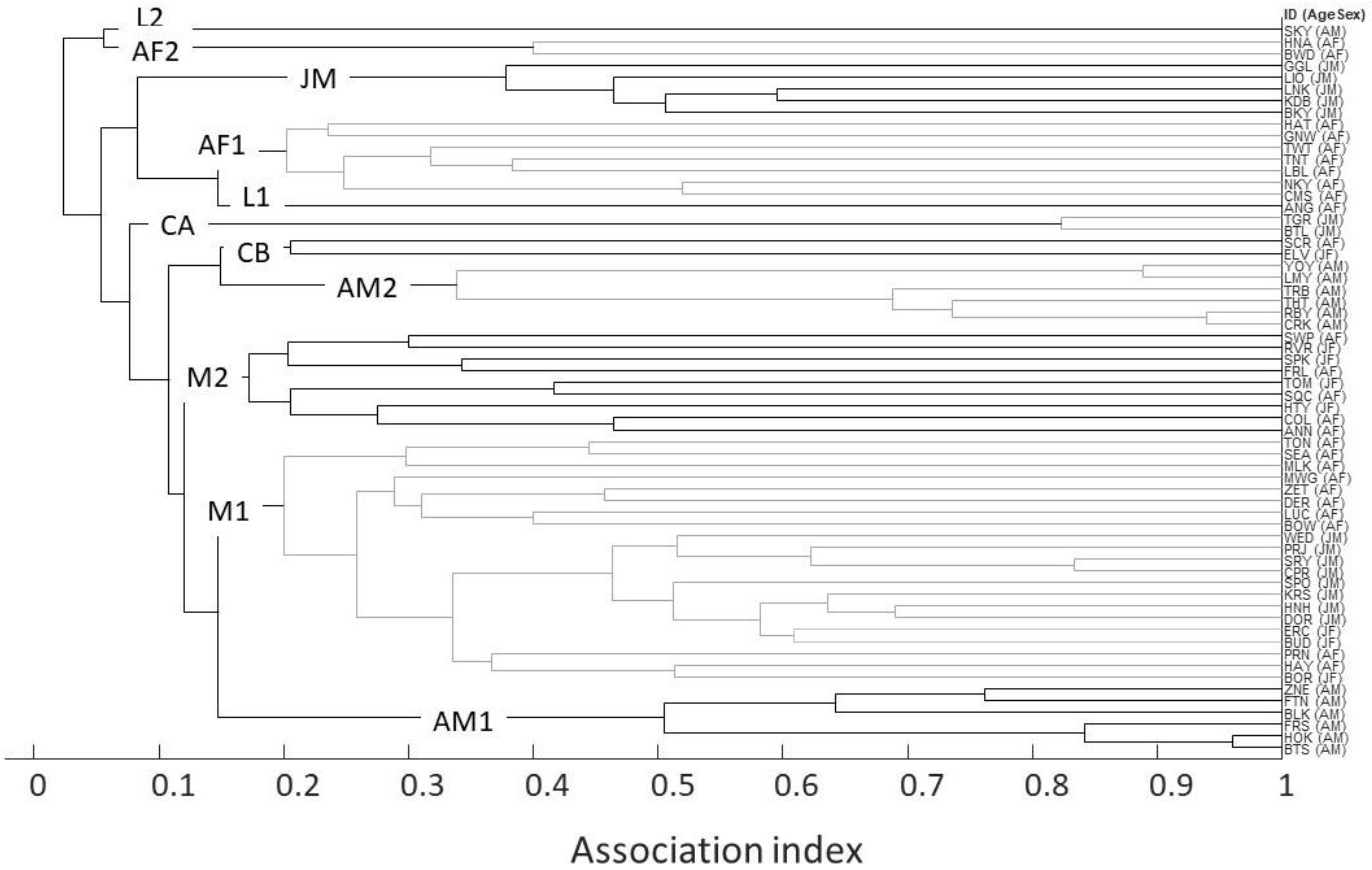

Figure 3.3. Average linkage cluster analysis dendrogram showing social structure of a community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary in Western Australia. The dendrogram shows the community is divided into nine social clusters and two lone individuals (L1 and L2). Two clusters comprise solely of adult males (AM1 and AM2), two solely of adult females (AF1 and AF2) and two a mix of adult females and juveniles of both sexes (M1 and M2). Two clusters comprise juvenile males (JM and CA), while one cluster comprise an adult and a juvenile female (CB). Notations: A = Adult, J = Juvenile, M = Male, F = Female.

3.3.4. Demographic parameters and Population Viability Analysis (PVA)

Between January 2016 and December 2019, a total of 113 individuals were identified as part of the estuarine dolphin community with a mean of 88 (SD 4.43, range 84 - 94) individuals alive at the end of each calendar year. The initial population size in 2016 was 86 individuals.

A total of 37 calves were born to 25 estuarine resident females during this study (Appendix B Table B.3). An annual variability from 5 to 16 (mean 9.25, SD 4.99) was observed in the number of calves being born. This directly related to the number of females available to produce a new calf (i.e., females whose calf was two years old, females who had lost a calf or females who had become mature). Births were observed between November and June with the majority (73 %) of calves born between March and May (Appendix B Fig. B.2). Three individuals, estimated between 8 and 15 years of age (at the time of giving birth), had their first calf during this study. An additional female was confirmed mature from a post-mortem exam but had not produced a calf (Stephens, unpublished data). The mean annual reproductive rate for the community was 0.39 (SD 0.20). The observed interbirth interval was between 2 and 4 years (mean 3.30, SD 0.86) when considering females that successfully weaned their previous calf.

Eighteen individuals were confirmed deceased and a further 11 either died or emigrated from the estuary between 2016 and 2019 (Table 3.2). Juvenile males contributed 54.5% (*n* = 6) to individuals that either died or emigrated while other age/sex classes contributed < 18.2% each. Juvenile males and females both contributed 11.1% to confirmed mortalities, while adult females contributed 22.2%, adult males 5.6% and yearlings 50.0%. Overall, apparent survival rates varied among age classes with the lowest survival observed for yearlings and the highest for dependent calves > 1 year old (Table 6). There was no immigration to the estuarine dolphin community during this study nor was any individual not part of the defined community observed consistently in the estuary.

The base PVA model using input parameters summarised in Table 3.1., forecast a declining population with a slightly negative population growth rate (-0.004, SD 0.062; Fig. 3.4). The estimated extinction probability was 0.010 (SE 0.003) with estimated 67 (SD 35) individuals alive in 100 years.

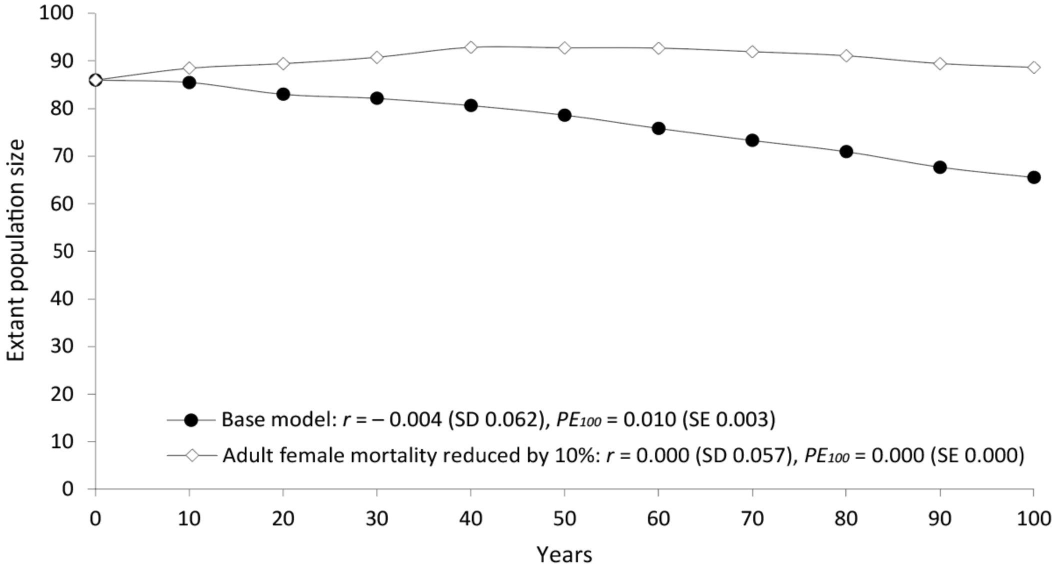

Figure 3.4. Population trajectory modelled by Monte Carlo simulations of deterministic and stochastic effects for a community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary, Western Australia. Notations: r = population growth rate, PE_{100} = probability of extinction in 100 years.

The model with stable age distribution estimated near identical population growth rate and extinction probability as the base model (Table 3.7). Assuming the population is currently at carrying capacity or allowing for only a slight expansion of the population, however, resulted in reduced population size and increased, although still very low, extinction probabilities over 100 years (Table 3.7, Appendix B Table B.2). The PVA models with adult female mortality decreased by 10% resulted in a

Table 3.7. Effects of parameter variation on mean population growth rate (*r*), probability of extinction (*PE*) and population size in 100 years forecast for an Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) population resident to the Peel-Harvey Estuary in Western Australia. Notations: *K* = carrying capacity, AFm = adult female mortality rate, Ym = yearling (i.e., individuals < 1 years old) mortality rate, RR = reproductive rate, SD = standard deviation.

Model	***K***	**AFm**	**Ym**	**RR**	***r* (SD)**	***PE* (SE)**	***N* (SD)**
PVA_base	150	5.05	24.76	38.53	- 0.004 (0.062)	0.007 (0.003)	67 (35)
PVA_stable_age_distribution	150	5.05	24.76	38.53	- 0.004 (0.062)	0.009 (0.003)	66 (35)
PVA_K_86	86	5.05	24.76	38.53	- 0.004 (0.066)	0.010 (0.003)	49 (21)
PVA_K_100	100	5.05	24.76	38.53	- 0.004 (0.063)	0.011 (0.003)	55 (24)
PVA_RR_+10%	150	5.05	24.76	41.52	0.000 (0.057)	0.002 (0.001)	90 (37)
PVA_AFm_-10%	150	4.55	24.76	38.53	0.000 (0.057)	0.000 (0.000)	89 (36)
PVA_AFm_-5%_Ym_-10%	150	4.80	22.13	38.53	0.000 (0.041)	0.001 (0.001)	90 (37)

positive mean population growth rate (*r*) with ~90 individuals alive and zero probability of extinction in the next 100 years (Table 3.7). A model with a 10% increase in reproductive rate and one with a combination of 5% and 10% decrease in adult female and yearling mortality, respectively, also produced a positive *r* but forecast a very low probability of extinction in the next 100 years.

3.4. Discussion

This study found that the resident Peel-Harvey Estuary (PHE) dolphin community comprised nine social clusters and two lone individuals. All clusters comprised solely males or females, apart from two that comprised adult females and juveniles of both sexes. Although the calf and juvenile sex ratios were close to parity, there was nearly twice as many adult female dolphins than males in the community. The population trajectory was modelled while taking into account community age and sex structure and age class and sex-specific apparent survival rates. The population growth rate was slightly negative but the probability of extinction in the next 100 years was low. Decreasing adult female and yearling mortality rates and increasing the reproductive rate resulted in higher population growth rates. No immigration into the community was recorded during the study suggesting additions to the community are solely through the birth process. Apparent survival, confirmed mortality and reproductive rates were heterogeneous among social clusters.

3.4.1. Social structure

Individuals in the PHE community formed preferential associations with individuals of the same sex and age class with strength of associations correlating with individuals' space use patterns. Similar association patterns are described for other populations of

Tursiops spp. For example, in Shark Bay, adults and juveniles form stronger associations with individuals of the same sex with juvenile association patterns reflecting adult reproductive strategies while allowing for exploration of the social environment without the risk of reproductive competition or inbreeding (Connor et al. 1992; Smolker et al. 1992; Gero et al. 2005; Krzyszczyk et al. 2017; Galezo et al. 2020).

The estuarine population comprised nine social clusters representing the relatively small number of high association relationships formed by individuals in this population (Chapter 2). Social clusters solely comprising adults also comprised only either females or males. Males formed stronger associations with other males than females did with other females and a larger proportion of their associations occurred with temporally stable associates. Association index values between 0.2 and 0.6 among adult males are expected for second-order male alliances (Connor et al. 1992). As such, the strength of association among adult males within social clusters in the PHE indicates that these clusters represent second-order alliances. Within both adult male clusters, AM1 and AM2, there were further division where individuals formed likely first-order alliances based on association indices >0.7 expected for these (Connor et al. 1992; Connor et al. 2011).

Association indices between males and females were lower than those within sex classes. This pattern is similar to other bottlenose dolphin populations with associations between mature males and females linked to female reproductive state (Wells et al. 1987; Smolker et al. 1992). Although the PHE dolphin community comprises more than twice as many adult females than males, the operational sex ratio (i.e., the ratio between potentially receptive males to receptive females at any given time, Emlen 1976) may still be unfavourable for males in years when the number of females in estrous is low. The number of estrous females (based on births and the number of females with dependent calves each year, Appendix B Table B.3) varied between five and 18 during this study. As such, regardless of the skewed adult sex-ratio, males face higher competition for females during the years when there is low availability of estrous females. Increased male bias in operational sex ratio may lead to increased male aggression and mate defence (Weir et al. 2011) and is expected to lead to male alliance formation (Whitehead and Connor 2005; Diaz-Aguirre et al. 2018). As such the operational sex ratio may explain alliance formation in the PHE population. It is likely that males that are part of the estuarine community respond to increased competition in some years by herding females outside their community. During 2016 and 2017 when there were five and six estrous females (based on calving records the following year and all other mature females being with a dependent calf) in the PHE community, respectively, males were observed with coastal females within the estuary (Nicholson, unpublished data). These females were not observed in estuarine waters on any other occasions. Similar observations of a female being directed outside her home range by males have been observed in other bottlenose dolphin populations (Watson 2005; Kopps et al. 2014). Future studies on consortships would provide better understanding on male-female associations as well as male reproductive strategies in this population.

Juveniles in the Peel-Harvey community preferentially associated with other juveniles and formed closer associations with select juveniles of the same sex. This is consistent with findings of other studies, which describe bottlenose dolphin juveniles living in highly dynamic groups with other juveniles (Connor et al. 2000; Gero et al. 2005; Wells 2014) while showing preference for same sex associates (Owen et al. 2002; Owen 2003; Krzyszczyk et al. 2017; Galezo et al. 2020; Gerber et al. 2020).

Juveniles in the mixed age cluster, M2, were an exception. They formed stronger associations with adult females than other juveniles. At least two of the three juvenile females in this cluster reached sexual maturity in 2019 indicating they were older juveniles during most of the study. Additionally, cluster M2 only had one confirmed male juvenile, while 64% of cluster M1 juveniles (n = 11 individuals) were males estimated to be between three to six years old. These factors may explain the differing association patterns of juveniles among social clusters. Longer-term investigation is required to investigate the juvenile social strategies and stability of male associations into maturity in this population.

3.4.2. Reproduction and calving success

The mean annual female reproductive rate in the PHE dolphin community was higher than those that have been reported for other Indo-Pacific bottlenose dolphin populations. For example, Manlik et al. (2016) estimated an annual reproductive rate of 13.58 (SD 8.64) for a population of dolphins in Bunbury, approximately 100 km south of the study area. Three-year reproductive rates of 40.74 (SD_{EV} 13.54) and 58.35 (SD_{EV} 9.38) were also estimated for dolphin populations in Bunbury and Shark Bay, Western Australia, respectively (Manlik et al. 2016). During this study, all mature females gave birth within a three-year interval, with a few females giving birth on multiple occasions (i.e., a three-year reproductive rate >100%). It is possible that the higher reproductive rates observed in the PHE, in part, reflect the high level of year-round monitoring of this community whereby most, if not all, births are detected.

Reproductive success, defined as the number of calves surviving to independence, was heterogeneous among social clusters. Females in clusters AF2 and M2 lost proportionately more calves than females in other social clusters. Intrapopulation heterogeneity in reproductive success has been reported for bottlenose dolphin populations elsewhere (e.g., Wells 2000; Mann et al. 2000; Senigaglia et al. 2019). The mother's age and level of experience may be related to her reproductive success (Wells 2000; 2003; Wells et al. 2005; Yordy et al. 2010). Mature females in clusters AF2 and M2 were estimated to be between 14 and 35 years old in 2016 with all of them having given birth at least once before the commencement of this study. Given that mature females in social clusters AF1 were estimated to be between 8 and 32 years old and in cluster M1, 11 and 21 years old and these clusters have higher reproductive success than AF2 and M2, it is unlikely the heterogeneity in reproductive success among social clusters can be fully explained by mothers' age. Calves in larger groups have higher survival rates in some populations (Wells 2000) as they may benefit more from socialization, allomaternal care and learning through observation and additionally have higher protection from predators, aggressive conspecifics and boat collisions (Wells 2014). Social cluster AF2 consists only of two members, making this a possible contributing factor to its lower reproductive success. However, social cluster M2 had ten members while cluster AF1, which had higher reproductive success, only seven members. It is therefore unlikely that group or social cluster size alone influences reproductive success in this population.

The lower reproductive success of social clusters AF2 and M2 may relate to their space use patterns, which may lead to higher chronic exposure to biotoxins (Chapter 4) and higher degree of inbreeding as mature females in these clusters are unlikely to come across coastal unfamiliar males (Chapter 2). The core activity space of AF2 and M2 covers the eastern Peel Inlet and extends to the rivers (Chapter 4), both of which show signs of significant eutrophication with potentially harmful algae dominating the phytoplankton communities (Thomson 2019). Sea mullet (*Mugil* *cephalus*), which is abundant in the rivers and contributes substantially to the diet of these clusters (Chapter 4), is a known vector for conveying algal toxins up the food chain (Fire et al. 2008). Dolphins frequenting the riverine habitat (i.e., clusters AF2 and M2), as opposed to basin or channel habitats (i.e., other social clusters), may thus be more exposed to algal toxins (e.g., cyanotoxins, karlotoxins, domoic acid and other neurotoxins based on algae listed in Thomson 2019), some of which are associated with immunosuppression and modulation in dolphins (Twiner et al. 2011). To my knowledge, algal toxins have not directly been linked to lower reproductive success in dolphins, however, other toxins such as polychlorinated biphenyls and heavy metals are associated with reproductive abnormalities and failure in several populations (Schwacke et al. 2002; Wells et al. 2005; Kemper et al. 2019). Similarly, inbred females as well as females with inbred calves may have reduced fitness represented by lower calving success (Hedrick and Kalinowski 2000; Keller and Waller 2002; Frère et al. 2010). Further investigation is required to understand whether exposure to toxins and inbreeding affect the health, in particular reproductive health, of dolphins in the PHE.

3.4.3. Apparent survival, mortality and emigration

The relatively high apparent survival rate for adults in the estuary was comparable to that estimated for a *T. aduncus* population in Bunbury and slightly higher than estimated for a population in Shark Bay, Western Australia (Manlik et al. 2016). There were, however, approximately twice as many mature females than males in the Peel-Harvey community despite sex ratios being close to parity in both dependent calves and juveniles. Similarly, Kogi et al. (2004) found that while subadult sex ratio in a population of *T. aduncus* around Mikura Island in Japan was significantly skewed towards males, the adult sex ratio was significantly skewed towards females. In contrast, Manlik et al. (2016) reported a sex ratio slightly skewed towards females (i.e., 45:55) for a population in Bunbury and an equal sex ratio for the population in Shark Bay. Higher adult male mortality could lead to the observed skewed sex ratio (e.g., Scott et al. 1990) in the PHE community, however, it is unlikely given adult male mortality was markedly lower than adult female mortality. Another possibility resulting in the skewed adult sex ratio could be permanent emigration by juvenile males, who were the most observed age/sex class to disappear from the estuary while their confirmed mortalities were low. Similar observations were made for a bottlenose dolphin (*Tursiops truncatus*) population in Sarasota, Florida, where 83.3% of deceased or permanently emigrated individuals were juvenile males (Wells and Scott 1990). It is typical for mammals with promiscuous mating systems, like dolphins (Connor et al. 1996), to have a high proportion of juvenile males to permanently emigrate in response to competition for mates and to achieve outcrossing (Dobson 1982). This type of dispersal would produce vagrant males who would either establish a new home range excluding their natal range (Lidicker 1975) or remain nomadic. Many studies on bottlenose dolphins report a proportion of individuals sighted to having been observed only once and labelled as transient in relation to the study area (e.g., Möller et al. 2002; Fury and Harrison 2008; Chabanne et al. 2017a). Here I suggest that some of these individuals could be emigrant males looking for mating opportunities or to permanently occupy a socially vacant niche (Saltz et al. 2016). In this study, individuals who may have permanently emigrated from the study area have not been sighted since their disappearance. This was despite them being sufficiently ‘marked’ and substantial survey effort in the waters adjacent to the PHE. This suggests that it is possible not all bottlenose dolphin males continue to use part of their natal range as reported by other studies (e.g., Scott et al. 1990; Krützen et al. 2004; Tsai and Mann 2013). It could be that subordinate juvenile males adopt a strategy of permanently emigrating to ensure non-zero fitness (e.g., Saltz et al. 2016). This hypothesis requires further investigation for the PHE dolphin community.

3.4.4. Population viability and management priorities

Although the population growth rate (based on demographic parameters over four years) was estimated to be slightly negative, the community can be considered relatively stable over time should the demographic parameters remain as described. Regardless, given that immigration to the community was not recorded, the status of the community makes it vulnerable to external stressors that may affect individuals' survival or reproductive success.

The demographic parameters calculated and used as PVA inputs for the base model in this study, were considered largely unbiased. All individuals identified as part of the community were regularly sighted to confirm they were alive and resided in the estuary. Carcasses were retrieved/identified for a relatively high number (45%) of individuals (adults and juveniles) that went missing from the community. Additionally, all sexually mature females were observed either with a dependent calf or with a newborn calf throughout the study, leading to the assumption that all births, apart from possibly one, were detected. Due to known and estimated ages for most individuals, it was possible to define a population age structure and reliably assign individuals into age classes. The sex of all individuals in the community, including calves, was also known. This allowed for stage (i.e., juvenile/adult)- and sex-specific apparent survival rates to be incorporated in modelling the population trajectory and extinction risk. Given the short duration of this study, it is recommended that the population demographic parameters are revised in the future with a longer-term data set.

To change the forecast population trajectory and to maintain a resident population of ~90 dolphins, results of the alternate PVA models suggest management action should aim to increase reproductive rates and/or decrease adult female and yearling mortality. The primary focus should be given to reducing adult female and yearling mortality as the population appears to currently be at its reproductive capacity. This is based on all mature females having given birth as expected every two to four years while being with a dependent calf during the years when they did not reproduce. Reducing adult female and/or yearling mortality by 10, or even just five percent annually, however, is also not possible given the low number of individuals lost each year. As such, it is recommended that no more than an average of one adult female is lost from the community each year, while considering action to reduce yearling mortalities over time. To ensure effective management action is taken, further research is required to investigate the main causes of mortality in this community and to separate natural mortality from non-natural (e.g., human caused) mortality.

Discarded recreational fishing gear poses a risk to the health of individuals in the PHE dolphin community. The estuary is an important fishing area for recreational fishers, with commercial fishers also operating in the area (Hale and Butcher 2007; Gaughan 2019). No adverse impacts from commercial fishing have been recognised for this dolphin community, however, four individuals and an additional three coastal dolphins who regularly use the Dawesville Channel, have been observed entangled in recreational fishing gear between 2016 and 2020 (Nicholson, unpublished data). Discarded fishing gear has also been recognised as a major threat to marine megafauna globally (Moore et al. 2009; Stelfox et al. 2016) with recreational fishing gear, mainly fishing line, recorded affecting estuarine and coastal bottlenose dolphins (Mann et al. 1995; Wells et al. 2008; 2013; Miketa et al. 2017; Marks et al. 2020; McHugh et al. 2021). Educating the public on impacts of discarded fishing gear on wildlife is imperative to deal with the source of the problem while building capacity in local dolphin incident response is highly recommended to ensure quick disentanglement of individuals to ensure their survival (Wells et al. 2008; 2013).

A relatively high number of dolphin live strandings have been recorded in the PHE (Groom and Coughran, 2012). Live strandings were related to 21% of mortalities recorded during this study (Nicholson et al. 2019). Most live stranded dolphins have been individuals deemed in good health that were caught by low tides behind or on sandbars with mortalities mostly related to individuals suffering severe sunburn (Nicholson, unpublished data). Monitoring for live strandings during summer months (i.e., when individuals are at high risk of getting severely sunburnt) and ensuring a quick response to relocate stranded individuals to deeper water should remain a management priority that may aid in reducing adult female mortality in this population.

For many marine mammal populations, depending on their population growth rate, some human caused mortality may be acceptable (Gerrodette et al. 1996; Read and Wade 2000; Parra and Cagnazzi 2016). In such cases, a Potential Biological Removal (PBR) may be calculated. The PBR estimates the maximum number of individuals that may be removed, excluding natural mortality, while allowing a stock (i.e., a group of marine mammals of the same species in a common spatial arrangement that interbreed when mature) to reach or maintain an optimum sustainable population (*Marine Mammal Protection Act 1972* (U.S.); Wade 1998). Given the slightly negative population growth rate estimated by the base model for the PHE dolphin community, management should aim for zero human caused mortality (e.g., mortality due to fishing line entanglements), decrease in mortality due to live strandings and maintenance of reproductive success for this community.

Exposure to other human activities (e.g., boating, dredging, noise, pollution) can also lead to direct and indirect impacts on dolphins including animals moving temporarily or permanently away from an area (Watson-Capps et al. 2005; Bejder et al. 2006; Pirotta et al. 2013). Additionally, there may be population level consequences through lowered reproductive success (Kemper et al. 2019; Senigaglia et al. 2019), increased mortality (Wells and Scott 1997; Wells et al. 2008; 2013) and decreased health of individuals (Wells et al. 2005; Twiner et al. 2011). The PHE has been highly modified over time with the second entrance, Dawesville Channel, engineered in 1994 to relieve symptoms of eutrophication (Brearly 2005; Elliot et al. 2016). Additionally, multiple canal systems, break walls and other structures have been constructed, in particular along both entrance channel foreshores. These structural modifications have resulted in changes in the ecosystem (Hale and Butcher 2007; Potter et al. 2016) that have likely influenced the carrying capacity of the PHE for dolphins. The PVA models with reduced carrying capacity for the system resulted in decreased community size over time. As such, an entire ecosystem approach to management is required to ensure the system can support >100 dolphins. The human population of City of Mandurah, which fringes the estuary, is forecast to increase (forecast.id.com.au/mandurah), which will likely lead to further human use of the estuary and development around it. It is recommended that future development planning considers impacts on the resident dolphin community to ensure its persistence over time.

3.4.5. Conclusions and recommendations

Based on the findings of this study, the resident Peel-Harvey Estuary dolphin community can be considered a closed population with no immigration and demographic changes driven by birth and death processes, as well as the likely emigration of immature males. The community has typical age- and sex-specific bottlenose dolphin association patterns with heterogeneous reproductive success and apparent survival among social clusters. Although the adult sex ratio was highly skewed toward females, the operational sex ratio, which in some years was highly skewed toward males, may be the driver for male alliance formation identified in this community. With the current population structure and calculated demographic parameters, the estimated population growth rate was slightly negative. This makes the community particularly vulnerable to external stressors that may affect individuals' survival and reproductive success.

It is recommended that demographic parameter values presented in this study are revised in the future with a longer-term data set. Determining the causes of mortality and live stranding should also be prioritized. As a precautionary approach, management should aim for zero human caused mortality while building capacity to detect and quickly respond to dolphin live strandings that are prevalent in the estuary. Future development planning should consider impacts on dolphins, in particular to ensure the reproductive output of this community is maintained. Long-term, systematic monitoring (i.e.,Hawkins et al. 2017) of this community is recommended to detect changes in community structure and demographic parameters which may lead to a changed status of the community in the future.

Chapter 4

Ecological niche partitioning among social clusters of a resident estuarine apex predator

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4.0. Abstract

Conspecifics may vary in their space use and diet leading to niche partitioning within populations. In social species, such partitioning may correspond to social structure as closely associated individuals likely encounter the same resources. This study investigated whether space use and diet varied among social clusters of a resident estuarine population of Indo-Pacific bottlenose dolphins. Dolphin photo-identification and behavioral data, as well as tissue samples for stable isotope analysis, were collected during boat-based surveys in the Peel-Harvey Estuary, Western Australia. Potential dolphin prey species were also collected for stable isotope analyses. Dolphin social clusters were heterogeneous in assimilated $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios in their skin, indicating differences in their diet. A mixing model estimated detritivorous fish as the main dietary source for the clusters showing high site fidelity to the eastern shores of the estuary and the rivers. These social clusters occupied the lowest trophic position in the dolphin population. Benthic omnivores and carnivores contributed most to the diet of clusters whose members showed high site fidelity to the two estuary entrances. These clusters occupied the highest trophic position. Clusters with high site fidelity to estuary basins were between the two opposing trophic positions. The dolphins' foraging behavior and trophic interactions deemed them an apex predator in the Peel-Harvey Estuary, with their collective minimum annual food intake (~200,000 kg) exceeding annual fish biomass removed by commercial fishers. As top predators in the system, dolphins may supress prey populations through consumption and as agents of intimidation by changing prey distribution and behavior. This study provides scientific basis for recognizing dolphins as an important component of the Peel-Harvey Estuary ecosystem.

4.1. Introduction

Trophic interactions and spatial distribution are prominent dimensions of a species' ecological niche (Grinell 1917; Elton 1927; Hutchinson 1957). Conspecifics may vary in their diet and space use patterns, leading to niche partitioning within populations (Bolnick et al. 2003). In social species, such partitioning may correspond to population social structure as highly associated individuals occupy the same habitat and encounter the same prey (Darimont et al. 2004; Semmens *et al*. 2009).

Bottlenose dolphins (*Tursiops* spp.) are often organized in social communities (hereafter 'populations') comprising males and females of all ages (e.g., Urian et al. 2009; Wiszniewski et al. 2009; Chabanne et al. 2017a; Genov et al. 2019). Adults preferentially associate with members of the same sex (Connor et al. 1992; Smolker et al. 1992; although see Lusseau et al. 2003) while juveniles live in more dynamic groups (Gero et al. 2005; Galezo et al. 2020). As a result, social clusters, in which individuals associate more frequently with one another than with members of other clusters, may be identified within populations. Resource partitioning corresponding to such social structure has been recorded for dolphins (Chilvers and Corkeron 2001) yet has received less attention than partitioning by habitat (Sargeant et al. 2007; Barros et al. 2010; Gibbs et al. 2011) or foraging tactic (Mann and Sargeant 2003; Sargeant et al. 2005; Allen et al. 2011; Krützen et al. 2014).

Bottlenose dolphins exhibit diverse foraging behaviors (Shane 1990; Mann and Sargeant 2003), with the tactic employed determined by habitat features (e.g., Sargeant et al. 2007; Torres and Read 2009) or prey characteristics (Patterson and Mann 2011; Smith and Sprogis 2016; Sprogis et al. 2017). Prey selection is driven by maximizing net energy gain and depends on prey availability, abundance and distribution, inter- and intraspecific competition and the consumer's ability to harvest resources

(MacArthur and Pianka 1966; Bolnick 2001; Svanbäck and Bolnick 2007). Typically, bottlenose dolphin diet comprises large proportions of a few fish species and numerous less frequently or occasionally consumed prey (Cockcroft and Ross 1990; Mead and Potter 1990; Amir et al. 2005). When dominant dietary items do not correspond to the most abundant or available prey in the environment, they are preferentially chosen by consumers (McCabe et al. 2010). potentially leading to intrapopulation variability in diet.

As higher-order predators, dolphins may control prey populations and community structure and therefore contribute to consumer (i.e., top-down) control in the system (Leopold 1943; Estes and Duggins 1995; Bowen 1997). They may also influence ecosystem structure by disturbing the benthos, which may impact invertebrate communities (Nerini 1984; Oliver and Slattery 1985; Oliver *et al*. 1985) and via recycling of nitrogen through defecation (Roman and McCarthy 2010). The presence of predators may also produce a ‘landscape of fear’ (Laundré et al. 2010) by which predation risk influences prey distribution and behavior and thereby their foraging ecology and life-history (Lima and Dill 1990; Brown et al. 1999; Heithaus and Dill 2002; Wirsing et al. 2007; Ale and Whelan 2008; Heithaus et al. 2009). The complexity of trophic and behavioral interactions makes it difficult to infer dolphins’ role in dynamic systems where both bottom-up and top-down control are likely to act in concert (Schmitz 2010). Nevertheless, characterizing foraging and trophic ecology of predators and quantifying their diet will elucidate the effects they may have on prey populations, community structure and ecosystem function.

Estuaries are productive ecosystems, where high nutrient availability and primary production support complex trophic interactions (Bianchi et al. 2006). Consequently, estuaries host high densities of prey for piscivorous top predators such as birds, sharks and dolphins (e.g., Matich and Heithaus 2014; Rossman et al. 2015; Tweedley et al. 2016). Bottlenose dolphins (*Tursiops* spp.) are commonly found in and show varying levels of site fidelity to different estuaries (e.g., Wilson et al. 1997; Zolman 2002; Fury and Harrison 2008; Urian et al. 2014). The Peel-Harvey Estuary (PHE) in Western Australia is occupied by a resident population of ~90 Indo-Pacific bottlenose dolphins (*Tursiops aduncus*; Chapter 3). This population comprises nine social clusters and two lone individuals and has been identified socially, spatially and isotopically distinct from dolphin populations found in adjacent coastal waters (Chapter 2). In this study, intrapopulation partitioning in space use and diet of the Peel-Harvey Estuary dolphin population was investigated. Dolphin behavioral observations were used to identify targeted and consumed prey species while stable isotope ratios of carbon and nitrogen in both the consumer and prey were used to quantify the proportional contribution of sources (i.e., fish) to social clusters' diet. The annual food intake of the dolphin population was also estimated.

4.2. Methods

4.2.1. Study area

The PHE (~130 km^2) is a microtidal (tidal range ~0.5m) temperate estuary consisting of two shallow (<2 m deep) basins (Fig. 4.1). Three rivers flow into the estuary from a catchment area of approximately 94, 000 km^2 (Valesini *et al*. 2019). The estuary is permanently open, connected to the sea by two relatively narrow channels: the Mandurah Channel, a natural opening; and the Dawesville Channel, an artificial opening. The fringing vegetation consists of salt marsh and paperbark communities (Hale and Kobryn 2009), although a proportion of the shoreline has been significantly altered by development (e.g., canal systems, housing and other infrastructure).

The region experiences a Mediterranean climate with cool, wet winters and hot, dry summers. Approximately 90% of the mean annual rainfall (~800mm) and 95% of the river flow occur between May and October (Valesini et al. 2019). Mean salinities in the basins remain close to marine salinity (34 - 37 ppt) while the rivers are brackish with high variability between 5 ppt (winter) and up to 71 ppt (summer) in the Serpentine River (Thomson 2019). Mean water temperature varies from 10-12°C in the winter to high 20s in the summer (annual averages 18.5-20.4°C, Thomson 2019). Phytoplankton is co-dominated by diatoms and cryptophytes in the basins, by diatoms and dinophytes in the Murray River and by cyanobacteria in the Serpentine River (Thomson 2019). Macrophyte communities are dominated by seagrass species *Ruppia megacarpa* (Krumholz 2019). The high estuarine productivity supports a diversity of hyperbenthic and infaunal communities (Valesini et al. 2009; Wildsmith et al. 2009), > 80 species of fish (Valesini et al. 2009; Potter et al. 2016) and >100 species of wetland dependant birds (Hale and Butcher 2007). The PHE is part of the Ramsar-listed Peel-Yalgorup wetland system.

4.2.2. Data collection

Dolphin photo-identification surveys were conducted throughout the PHE and in adjacent coastal waters on board a 5.6 m research vessel between January 2016 and November 2017. Predetermined transects were run every season (≥ three in each season) in the estuary (*n* = 37) and coastal waters (*n* = 28). Data collected in coastal waters were not included in this study apart from locational records of identified estuarine resident dolphins encountered outside the estuary.

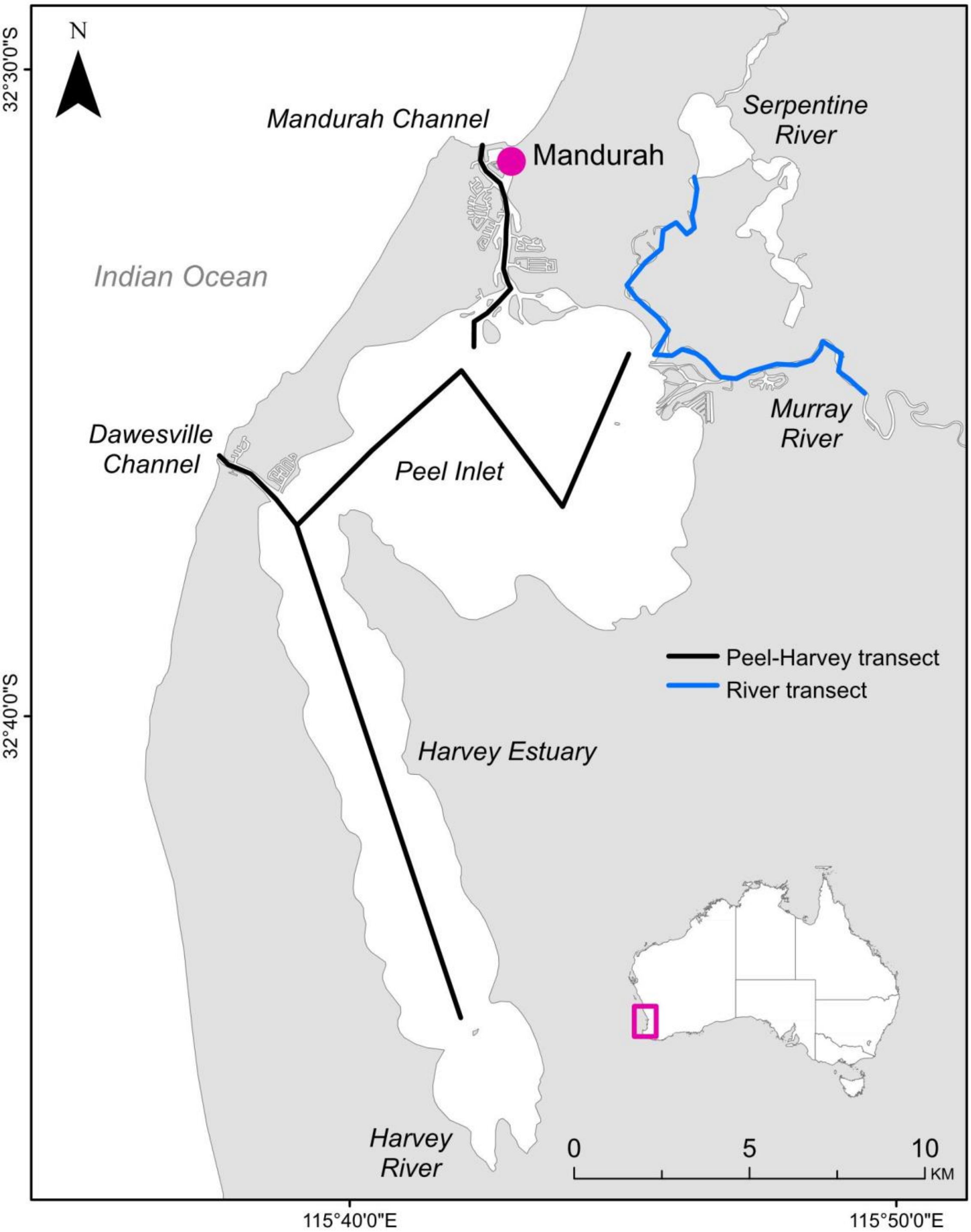


Figure 4.1. The Peel-Harvey Estuary (~130 km2) in Western Australia was surveyed for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). Boat-based transects were run a minimum of three times each season following the same route apart from in the Peel-Inlet where a unique ‘zig-zag’ pattern was followed on each sampling occasion between January 2016 and November 2017. The river transect was run opportunistically.

In the PHE, transects followed a similar route apart from in the Peel Inlet where a unique ‘zig-zag’ pattern was followed on each sampling occasion (Fig. 4.1). The Serpentine and Murray rivers were not part of the dedicated study area but were surveyed every season to ~ 7.5 km upstream (Fig. 4.1). Additional search effort was conducted to collect dolphin tissue samples and laser photogrammetry data for aging individuals (van Aswegen et al. 2019).

A group of dolphins was defined using a ‘10-meter chain rule’ where individuals are part of the same group if they are within 10 m of any other group member (Smolker et al. 1992). Individual/group location was recorded, and dorsal fin photographs were taken for individual identification (Würsig and Würsig, 1977). Predominant behavior (i.e., > 50% of group members engaged, Mann 1999) of foraging, travelling, socializing, resting or unknown was recorded for the first five minutes and thereafter opportunistically. Previously described foraging tactics of peduncle dive foraging, bottom grubbing, snacking (Mann and Sargeant 2003; Sargeant et al. 2007), tossing (Sprogis et al. 2017), tail-whacking (Scott et al. 1990; Shane 1990), foraging along/against structures (described in this study) and begging (Finn et al. 2008; Senigaglia et al. 2019) were recorded (Table 4.1). Behavioral events (e.g., fish chases, handling or capture of prey) were recorded opportunistically. Prey items were identified from photographs by two independent, experienced fish ecologists.

Table 4.1. Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) foraging tactics, and associated prey species, observed consistently in the Peel-Harvey Estuary, Western Australia. Surveys refer to a minimum of five-minute behavioral observation of a group or an individual. Foraging/feeding was observed in a total of 236 surveys.

Foraging tactic	**Description**	**Prey species identified**	**Number of surveys observed in**
Bottom grubbing	Dolphin is oriented vertically in the water column, probing into the substrate, or weed patch with its rostrum. A turbid sediment plume is often observed at the water's surface and dolphin may surface with mud on rostrum and head	*Cnidoglanis macrocephalus* (n=5) *Pelates octolineatus* (n=3) *Sillago schomburgkii* (n=2) *Nematalosa vlaminghi* (n=1) *Pseudorhombus jenynsii* (n=1) *Gerres subfasciatus* (n=1)	49
Peduncle dive foraging (> 1 individual)	Dolphins are often widespread (>10m) changing directions in respect to each other at each surfacing with peduncle dive (peduncle raised out of the water as dolphin descends) the main surfacing type. Birds are often associated with this feedingtactic	*Pelates octolineatus* (n=3) *Sillago* sp. (n=3) *Gerres subfasciatus* (n=1) *Rhabdosargus sarba* (n=1)	47
Tossing	Dolphin tosses prey out of the water. Often preceded by bottom grub or chase in open water	*Cnidoglanis macrocephalus* (n=12) *Rhabdosargus sarba* (n=2) *Arripis truttacea* (n = 1) *Octopus cf. O. tetricus* (n=1) *Platycephalus laevigatus* (n=1) *Pseudorhombus jenynsii* (n=1) *Sillago schomburgkii* (n=1) *Mugil cephalus* (n=1)	30
Foraging along/against structures	Dolphin swims along a structure changing direction or stopping in response to fish movement. If fish is hiding between rocks or structures beyond reach, dolphin may engage in stalking (i.e., stay stationary in front of where the prey is hiding)	*Mugil cephalus* (n=2) *Aldrichetta forsteri* (n=1) *Aldrichetta forsteri/ Mugil cephalus* (n=2) *Arripis truttacea* (n=1)	26
Tail-whacking	Dolphin stops abruptly turning and swinging its flukes sharply, often producing a big fanlike splash. Fish are often flown up in the air. Tail-whacks are frequently preceded by a rooster-tail (i.e., a fast swim with a sheet of water trailing off the dorsal fin)	*Mugil cephalus* (n=4) *Aldrichetta forsteri* (n=1) *Rhabdosargus sarba* (n=1)	25
Snacking	Dolphin swims inverted close to the water surface chasing and capturing fish	*Hyporhamphus* sp. (n=4) *Rhabdosargus sarba* (n=2) *Aldrichetta forsteri* (n=2) *Pelates octolineatus* (n=1)	17
Begging	Dolphin approaches a stationary or slow-moving vessel, most often to the side or stern and remains close to it. Dolphin may also lift head out of the water and open its mouth.	n/a	0

4.2.3. Space use by social clusters

Seven social clusters and a lone adult female (LF) in the resident PHE dolphin population, identified using an average linkage hierarchical cluster analysis, were included in this study (Chapter 3). Two clusters (AM1 and AM2) comprised adult males, two clusters (AF1 and AF2) adult females, one cluster (JM) juvenile males and two clusters (M1 and M2) had a mixture of adult females and juveniles of both sexes. One lone male and two additional social clusters, collectively comprising five individuals, were not sampled for stable isotope analyses and were therefore excluded from analyses.

A non-parametric fixed kernel method (Silverman 1986; Worton 1989) was used to estimate the utilization distribution (UD) for each dolphin social cluster. Locational records of individuals within clusters were combined to represent clusters' spatial distribution. The UD for each cluster was estimated using the Epanechnikov kernel function (Epanechnikov 1969) over a grid (cell size 100 m x 100 m) created over the study area. The ad hoc (h_{ref}) smoothing parameter (Silverman 1986; Worton 1989) was used to determine the shape of the kernels as visual inspections may be subjective and least-squares cross validation method were not considered appropriate for the data structure in this study (Silverman 1986). Both 50% and 95% kernels were estimated to reflect the core and full UDs, respectively, for each cluster.

Ideally, UDs would be estimated considering boundaries that animals cannot cross (Barry and McIntyre 2011; Sprogis et al. 2016). The R package adehabitatHR version 0.4.18 (Calenge 2020) used for UD analyses, however, does not support highly irregular shapes, like the PHE, as boundaries. Therefore, land was removed from UDs *post hoc* using a boolean land mask followed by renormalizing the kernel density estimates. The UD overlaps between social clusters were calculated as the probability of a member of one cluster being found in the UD of another cluster and vice versa (Ostfeld 1986).

4.2.4. Stable isotope analyses

Dolphin skin samples (*n* = 38) were collected for stable isotope analyses using a remote biopsy system (PAXARMS modified .22 calibre biopsy rifle) developed for small cetaceans (Krützen et al. 2002). Samples were collected from adult and juvenile dolphins, placed in an empty vial and stored on ice for transport to storage in −80°C freezer.

Fish samples were collected from the shallow nearshore and deeper offshore waters of both estuary basins (i.e., northern and southern Harvey Estuary, eastern and western Peel Inlet) and two of the rivers (Murray and Serpentine) between February and September 2017. Fish were collected using seine and gill nets as part of a separate study documenting the fish community structure of the estuary (Hallett et al. 2019). Fish retained for stable isotope analysis (*n* =141) ranged in length from 19 mm to 357 mm and belonged to 24 potential dolphin prey species (including ten species not observed being consumed by dolphins) and to a variety of feeding guilds (i.e., Benthic detritivore, Herbivore, Omnivore, Benthic carnivore, Benthic omnivore or Water column feeder, as assigned via reference to FishBase: Froese and Pauly 2019; Table 4.2). Whole fish were transferred on ice and stored in −20°C freezer until processing for stable isotope analyses.

Dolphin skin samples were divided into two aliquots, one for $\delta^{15}N$ measurements from bulk (i.e., untreated) samples and the other for $\delta^{13}C$ measurements from lipid-extracted samples (deLecea and Charmoy 2015: Gimenez et al. 2016). The bulk samples were oven-dried at 60°C for 24 h and powdered with a mortar and pestle.

Table 4.2. Mean carbon (δ^{13}C) and nitrogen (δ^{15}N) values in the muscle tissue of fish species included as sources in a mixing model to estimate feeding guild contributions to Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) diet in the Peel-Harvey Estuary. Notations**:** SD = Standard Deviation, - = no sample, * = identified as dolphin prey from behavioral observations.

Feeding guild	**Common name**	**Peel Inlet, Harvey Estuary, Serpentine River**			**Murray River**		
Species		**δ^{13}C ‰ (SD)**	**δ^{15}N ‰ (SD)**	**n**	**δ^{13}C ‰ (SD)**	**δ^{15}N ‰ (SD)**	**n**
Benthic Detritivore		**-14.20 (1.41)**	**6.98 (1.15)**	**8**	**-16.21 (1.97)**	**6.60 (0.61)**	**7**
*Mugil cephalus**	Sea mullet	-12.69 (0.47)	5.49 (0.21)	2	-16.19 (2.47)	6.34 (0.38)	4
*Nematalosa vlaminghi**	Perth herring	-14.70 (1.23)	7.47 (0.81)	6	-16.23 (1.60)	6.96 (0.76)	3
Herbivore		**-15.36 (0.93)**	**7.90 (0.23)**	**6**	**-20.28 (2.63)**	**9.35 (0.69)**	**3**
*Pelates octolineatus**	Western striped grunter	-15.36 (0.93)	7.90 (0.23)	6	-20.28 (2.63)	9.35 (0.69)	3
Omnivore		**-16.38 (1.87)**	**8.68 (0.71)**	**4**	**-19.32 (2.07)**	**9.00 (0.26)**	**3**
*Rhabdosargus sarba**	Tarwhine	-16.38 (1.87)	8.68 (0.71)	4	-19.32 (2.07)	9.00 (0.26)	3
Benthic Carnivore/Water Column		**-15.84 (1.33)**	**8.89 (0.91)**	**21**	-	-	-
Atherinosoma elongata	Elongate hardyhead	-15.50 (1.40)	8.60 (0.73)	9	-	-	-
Favonigobius lateralis	Southern longfin goby	-15.05 (1.09)	8.49 (0.55)	3	-	-	-
Gymnapistes marmoratus	Soldier	-15.75 (1.24)	8.41 (1.60)	3	-	-	-
Leptatherina presbyteroides	Silverfish	-16.72 (1.78)	9.78 (0.09)	6	-	-	-
Benthic Carnivore		**-16.38 (1.29)**	**9.01 (0.85)**	**25**	**-21.52 (1.13)**	**9.93 (0.72)**	**3**
*Cnidoglanis macrocephalus**	Estuary catfish	-16.96 (0.64)	8.80 (0.42)	2	-	-	-
Ostorhinchus rueppellii	Western gobbleguts	-16.24 (1.34)	9.18 (0.30)	6	-	-	-
*Pseudorhombus jenynsii**	Small toothed flounder	-17.69 (0.00)	9.20 (0.00)	1	-20.32 (0.00)	9.10 (0.00)	1
*Sillaginodes punctatus**	King George whiting	-15.76 (1.20)	8.29 (0.88)	8	-	-	-
*Sillago burrus**	Trumpeter whiting	-18.12 (2.64)	9.56 (1.45)	2	-22.12 (0.61)	10.34 (0.01)	2
*Sillago schomburgkii**	Yellowfin whiting	-15.93 (0.68)	9.18 (0.43)	3	-	-	-
*Sillago vittata**	Western school whiting	-16.75 (0.09)	10.11 (0.30)	3	-	-	-
Benthic Omnivore		**-16.55 (1.11)**	**9.27 (0.79)**	**17**	**-24.16 (5.02)**	**10.07 (0.77)**	**10**
Acanthopagrus butcheri	Black bream	-	-	-	-28.68 (2.45)	10.92 (0.37)	4
*Aldrichetta forsteri**	Yelloweye mullet	-16.59 (1.17)	9.12 (0.90)	9	-22.96 (3.49)	9.54 (0.16)	3
*Gerres subfasciatus**	Common Siverbiddy	-16.33 (1.07)	9.64 (0.35)	**7**	-19.33 (3.70)	9.47 (0.16)	3
Haletta semifasciata	Blue weed whiting	-17.79 (0.00)	8.04 (0.00)	1	-	-	-
Water Column		**-17.73 (1.71)**	**10.95 (1.41)**	**29**	**-21.64 (2.78)**	**10.70 (0.81)**	**5**
*Arripis georgianus**	Australian herring	-18.78 (0.98)	11.04 (1.18)	12	-	-	-
*Arripis truttacea**	Western Australian salmon	-16.09 (0.46)	11.11 (0.15)	6	-	-	-
Atherinomorus vaigiensis	Common hardyhead	-17.72 (0.11)	9.88 (0.11)	3	-20.99 (2.86)	10.51 (0.25)	3
Engraulis australis	Australian anchovy	-	-	-	-20.21 (0.00)	9.95 (0.00)	1
Pomatomus saltatrix	Tailor	-17.40 (2.40)	11.10 (2.28)	8	-25.00 (0.00)	12.04 (0.00)	1

The other aliquot underwent lipid extraction with three consecutive 24 h soaks in 2:1 choloform:methanol solvent solution (Newsome et al. 2006). Samples were then rinsed in deionised water, oven dried and powdered as per bulk samples.

Fish dorsal muscle samples were oven-dried to constant weight at 60°C for 24 h and powdered using a tissue-lyser. Two aliquots were prepared from the homogenized tissue. One aliquot underwent lipid extraction following methods described in Logan et al. (2008). Samples were immersed in 2:1 choloroform:methanol solvent solution, mixed for 30 seconds and left for at least 30 minutes. Samples were then centrifuged for 10 min at 2500 rpm. The supernatant, containing solvent and lipids, was discarded. The process was repeated until the supernatant was clear following centrifugation. Samples were then rinsed in 2:1 choloroform:methanol solvent solution and dried at 50°C. All samples were weighed to the nearest 0.01 mg, packed into tin capsules and sent to the West Australian Biogeochemistry Centre at the University of Western Australia for δ^{15}N and δ^{13}C measurements using a continuous flow system (Delta V Plus mass spectrometer, with a Thermo Flush 1112 via Conflo IV [Thermo-Finnigan/Germany]). Details of the analytical technique can be found in Skrzypek and Paul (2006). The δ^{13}C and δ^{15}N values are given in per mil (‰) difference between the sample and the international standards of Vienna Pee Dee belemnite carbonate and atmospheric nitrogen, respectively.

4.2.5. Isotopic partitioning among social clusters

Six social clusters were included in testing the null hypothesis of no difference in isotopic composition among social clusters: LF and cluster AF2 (*n* = 2) were excluded due to low sample sizes. More than 50% of individuals in each of the other social clusters were sampled (Table 4.3) Data exploration was performed by visual inspection of box-plots and QQ-plots. The Shapiro-Wilk test was used to test the null hypothesis that $\delta^{13}C$ and $\delta^{15}N$ values within clusters were normally distributed. If they were, the Bartlett test was used to test for homogeneous variance among groups, if not, the Levene's test was used. One-way ANOVA was used to test whether mean stable isotope values differed significantly among clusters for normally distributed and homogeneous data, whereas Welch's ANOVA, followed by Games-Howell *post-hoc* test, was used when data were normally distributed but heterogeneous. The t-test and the Mann-Whitney U test were used to test whether $\delta^{13}C$ and $\delta^{15}N$ values differed significantly between juveniles and adults, males and females and seasons (spring and autumn). Based on δ13C and δ15N turnover rates in bottlenose dolphin (*Tursiops truncatus*) skin (Gimenez et al. 2016), sampling seasons of spring and autumn likely reflect isotopic composition of individuals in winter and summer, respectively.

4.2.6. Dietary sources

Seven social clusters and LF were included in the analysis to investigate the contribution of prey taxa, based on carbon and nitrogen assimilation, to their diet. A set of six Bayesian mixing models with different covariate structures were applied using the MixSIAR package (Stock and Semmens 2016; Stock et al. 2018) in R (R Core Team 2019). The null model considered all individuals in the population to share the same diet while other fitted models allowed variation in diet according to sex, age (i.e., adult/juvenile) and social cluster membership (Table 4). The covariates of sex and age were modelled as fixed effects and social cluster membership as a random effect. Models with hierarchical structure, where variability according to sex, age and/or individual within social clusters was allowed, were also considered. These models, however, had convergence issues and are therefore not discussed further.

Table 4.3. Mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) values in the skin of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) of seven social clusters identified as resident in the Peel-Harvey Estuary, Western Australia. Notations: SD = Standard Deviation, Su = summer, At = autumn, W = winter, Sp = spring, n/a = not applicable

Social cluster	***n* Sampled/ Members**	**Mean sighting frequency (SD)**	**Sampled (Su/At/W/Sp)**	**Mean $\delta^{13}C$ (SD) ‰**	**Mean $\delta^{15}N$ (SD) ‰**
Adult Male 1 (AM1)	3/6	48.00 (5.57)	0/3/0/0	-15.41 (0.23)	10.61 (0.30)
Adult Male 2 (AM2)	5/6	33.20 (6.42)	0/4/0/1	-15.63 (0.45)	10.00 (0.16)
Adult Female 1 (AF1)	5/7	41.8 (5.36)	1/3/1/1	-15.28 (0.58)	10.30 (0.34)
Adult Female 2 (AF2)	2/2	9.5 (0.70)	0/1/0/1	-14.62 (0.66)	8.65 (0.34)
Juvenile Male (JM)	4/5	36.25 (5.06)	0/2/1/1	-15.08 (0.23)	10.24 (0.14)
Mixed sex/age 1 (M1)	11/21	22.27 (4.61)	1/3/0/7	-15.28 (0.52)	9.90 (0.35)
Mixed sex/age 2 (M2)	7/10	19.14 (7.13)	0/7/0/0	-15.61 (1.00)	9.10 (0.70)
Lone Female (LF)	1/1	41	0/0/1/0	-15.82 (n/a)	10.52 (n/a)
Adults	25/39	29.51 (12.85)	6/16/1/6	-15.24 (0.55)	9.95 (0.57)
Juveniles	13/25	25.90 (8.46)	0/7/1/5	-15.54 (0.72)	9.68 (0.78)
Males	16/29	36.17 (8.14)	0/12/1/3	-15.46 (0.48)	10.02 (0.59)
Females	22/35	25.29 (10.48)	2/11/1/8	-15.26 (0.71)	9.73 (0.68)
Overall	**38/6**	**30.04 (10.90)**	**2/23/2/11**	**-15.34 (0.62)**	**9.85 (0.65)**

Dolphin prey species caught in the two basins and rivers within the estuary were pooled by region (i.e., Peel Inlet, Harvey Estuary, Serpentine and Murray Rivers) to test whether $\delta^{13}C$ values varied among them. Fish muscle $\delta^{13}C$ values of fish from the Murray River were significantly lower than those from the other regions (Welch's ANOVA: $F_{3,25} = 9.44$, $P < 0.01$; Games-Howell post-hoc: Murray River – Harvey Estuary $T_{32} = 5.08$, $P < 0.001$; Murray River – Peel Inlet $T_{32} = 4.45$, $P < 0.001$; Murray River – Serpentine River $T_{27} = 3.80$, $P < 0.05$). Therefore, for the mixing model, fish caught in the Murray River were considered separate to fish caught in other regions (Table 4.2).

To further simplify the mixing space, blue swimmer crab (*Portunus armatus*) and banded toadfish (*Torquigener pleurogramma*) were removed from source data as they were assumed not to be regularly consumed by dolphins (Barros and Odell 1990; Corkeron et al. 1990; Huisman and Twomey 2008). Sources were aggregated by feeding guild with δ13C and δ15N values of each sample included in the mixing model. Trophic discrimination factor (i.e., difference in the isotopic ratio between consumer and its diet) was set to 1.01 (SD = 0.37) for $\delta^{13}C$ and 1.57 (SD = 0.52) for $\delta^{15}N$ (Gimenez et al. 2016). All mixing models were fitted with generalist (i.e., uninformative) priors with a Dirichlet distribution (i.e., all combinations of the proportions are equally likely) and a multiplicative error term (i.e., process*residual). Markov Chain Monte Carlo simulations were used to estimate the probability, 'posterior', distribution of dietary contribution for each source (i.e., the proportional contribution of each fish feeding guild to a social cluster's diet). Three chains were run with their length set to 1,000,000 with a burn-in of 500,000 and thinning of 500. The Gelman-Rubin and Geweke diagnostics together with visual inspection of the Markov chains were used to confirm convergence of the model (Gelman et al. 2013). The

Deviance Information Criterion (Spiegelhalter et al. 2002) was used to evaluate relative model fit.

4.2.7. Total food intake by the dolphin population

An approximation of annual food intake of the dolphin population was made based on 64 independent individuals being present in the population in 2016 and 2017 (Chapter 3 reports 62 individuals to which two orphaned calves were added for this study). Adults (*n* = 39) were assigned a weight of 200 kg, based on a length-weight curve for coastal *Tursiops truncatus* in North America (Mead and Potter 1990) and the respective asymptotic total lengths of 246 cm and 244 cm estimated for males and females in the Peel-Harvey population (van Aswegen et al. 2019). Sexually immature individuals separated from their mother were considered juveniles (*n* = 25). Based on the estimated length of 187.1 cm (95% CI = 186.5 – 187.7 cm) for individuals reaching the end of their third year of life (van Aswegen et al. 2019), juveniles in this study would weigh between ~90 and 200 kg and were each assigned an average weight of 145 kg. The annual food intake estimation for the population is based on dolphins consuming 5.2 - 6.3% of their body mass per day (Cheal and Gales 1992).

4.3. Results

4.3.1. Behavioral observations

Behavioral surveys were conducted on 483 dolphin groups encountered in the PHE between January 2016 and November 2017. Foraging was identified as the predominant activity in 206 surveys with feeding events observed in a further 30 surveys. These surveys resulted in seventeen species being identified as dolphin prey (Table 4.1, Appendix C Fig. C.1). The most observed species caught by dolphins was the estuary catfish (*Cnidoglanis macrocephalus* - 23%), followed by sea mullet (*Mugil cephalus* - 13%), tarwhine (*Rhabdosargus sarba* - 11%) and western striped grunter (*Pelates octolineatus* - 9%). Garfish (*Hyporhampus* spp.) was observed as prey on four occasions and rock flathead (*Platycephalus laevigatus*) and octopus (*Octopus tetricus*) on one occasion each. These three species were not caught during fish sampling and therefore were not included as sources in the stable isotope mixing model. Of all the prey species identified, 14% were benthic detritivores, 20% herbivores and omnivores, 53% benthic omnivores and carnivores and 13% water column feeders (Table 4.2).

The most often observed dolphin foraging tactics were bottom grubbing and peduncle dive foraging, both of which targeted mainly benthic species (Table 4.1, Appendix C Fig. C.2). Dolphins tossing prey primarily involved adults of estuary catfish (60%), foraging along or against structures either sea or yelloweye mullet (*Aldrichetta forsteri*) while tail-whacking was mostly associated with sea mullet. Although dolphins were observed to ‘snack’ (i.e., swimming inverted close to the water’s surface chasing/capturing fish) on multiple species, garfish was the only species observed to be targeted solely by this tactic (Table 4.1). Leap and porpoise foraging, where dolphins within a group are moving multidirectionally and continuously leaping or porpoising within an area (Mann and Sargeant 2003), was observed during two surveys. Based on behavioral observations, a combination of benthic omnivores and carnivores and the herbivorous western striped grunter were targeted in 61% of surveys, sea mullet (a detritivore) in 16%, either of the mullet species in 17% and water column species in 11%. These exceed 100% as during some surveys multiple tactics were used to target different prey species. Birds (*Hydroprogne caspia*, *Thalasseus bergii*, *Croicocephalus novaehollandiae* and *Pelecanus conspicillatus*) were associated with foraging dolphins in 19% of the surveys.

4.3.2. Space use by social clusters

Overall, the 95% utilization distributions (UDs) of social clusters extended over the basins, entrance channels to the estuary and into the Serpentine and Murray rivers (Fig. 4.2). The 50% UDs, reflecting the core activity space for each cluster, differed among clusters. The core activity space of cluster AF1 comprised Mandurah Channel while for clusters AM1, JM and LF the core activity space was bimodal over both Mandurah and Dawesville Channels (Fig. 4.2). The core activity space for AM2 was primarily in the Peel-Inlet and Harvey Estuary, while that for M1 covered nearly the entire Harvey Estuary. The core activity space of AF2 and M2 extended into the rivers (Fig. 4.2). The probability of individuals of one social cluster being in another social cluster's activity space varied among clusters and was asymmetric (Table 4.4). For the 95% UDs, probability ranged from 0.27 to 0.92 for different cluster combinations. For the 50% UDs, the probabilities were lower, between 0 and 0.49.

4.3.3. Isotopic partitioning among social clusters

The $\delta^{13}C$ values for dolphin skin tissue ranged from −16.98‰ to −14.15‰ and the $\delta^{15}N$ values from 8.09‰ to 10.88‰ (Fig. 4.3, Table 4.3). Mean $\delta^{13}C$ values did not differ significantly among social clusters ($F_{5,30} = 0.64$, $P > 0.05$), males and females ($T_{36} = 0.95$, $P > 0.05$), juveniles and adults ($T_{36} = -1.41$, $P > 0.05$) or seasons ($T_{32} = -0.04$, $P > 0.05$). The mean $\delta^{15}N$ values were normally distributed within groups ($P > 0.05$) but heteroscedastic (*Bartlett's K-squared*$_5$ = 13.34, $P < 0.05$) with statistically significant difference detected in $\delta^{15}N$ values among social clusters ($F_{5,11} = 5.66$, $P < 0.01$). Cluster M2 had significantly lower $\delta^{15}N$ values than clusters AM1, AF1 and JM (*post-hoc* Games-Howell test $P < 0.05$). Individuals in cluster AF2 had the lowest $\delta^{15}N$

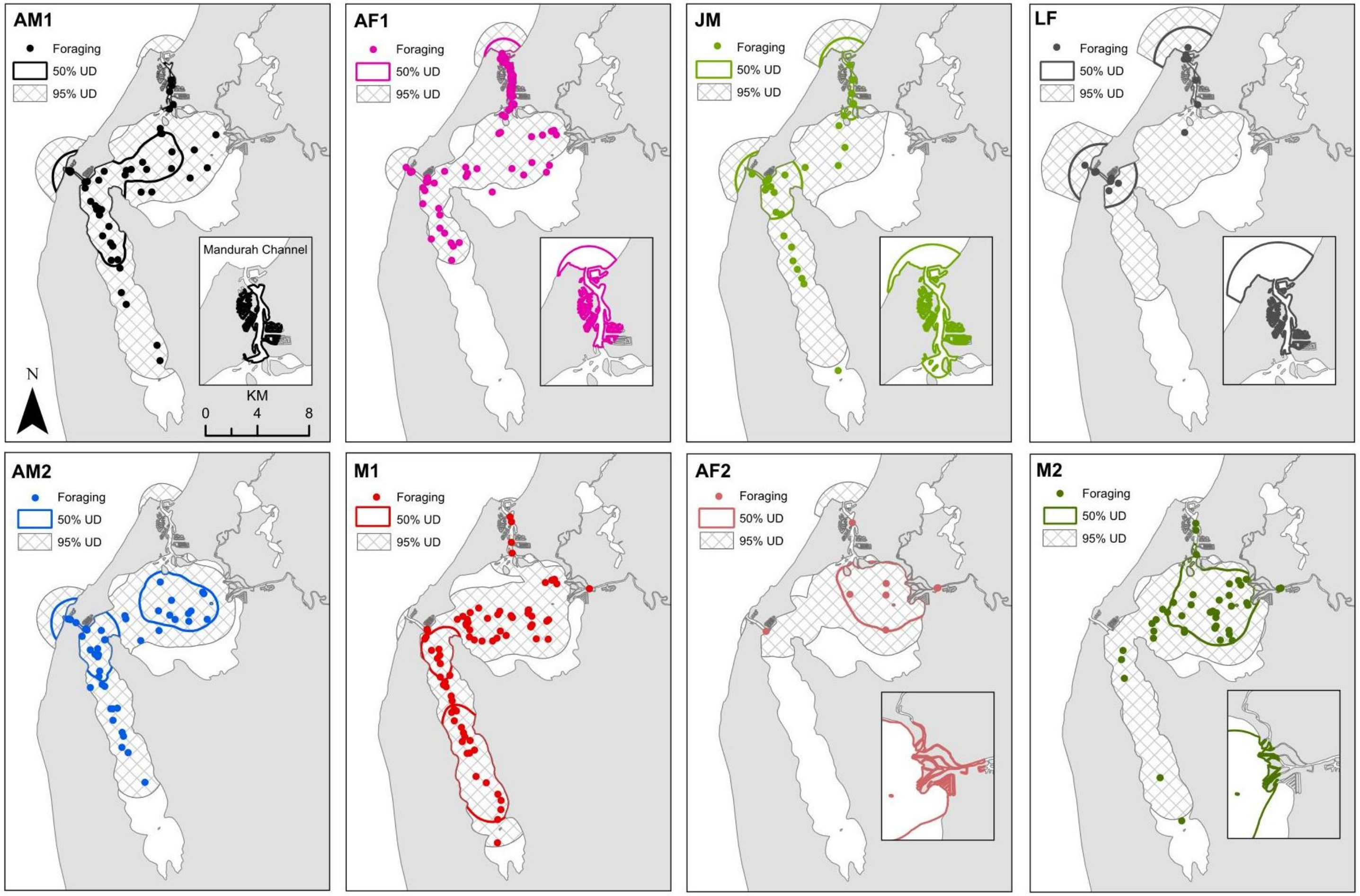


Figure 4.2. Core (i.e., 50%) and full (i.e., 95%) utilization distributions (UD) for Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) social clusters and a lone adult female, resident to the Peel-Harvey Estuary in Western Australia. Points show locations of observed foraging/feeding behavior. Social Clusters: AM1 = Adult Males Cluster 1, AM2 = Adult Males Cluster 2, AF1 = Adult Females Cluster 1, AF2 = Adult Females Cluster 2, JM = Juvenile Males, M1 = Mixed Sex/Age Cluster 1, M2 = Mixed Sex/Age Cluster 2, LF = Lone Adult Female

Table 4.4. Probability of overlap in utilization distribution (UD) of social clusters (n = 7) of Indo-Pacific bottlenose dolphins (*Tursiops aduncus)* within the Peel-Harvey Estuary, Western Australia. The full UD is a 95% kernel density estimate and the core UD (probability of overlap inside brackets) a 50% kernel density estimate. Notations: AM = Adult Males, AF = Adult Females, JM = Juvenile Males, M = Mix of Adult Females and Juveniles

Social cluster	**AM1**	**AM2**	**AF1**	**AF2**	**JM**	**M1**	**M2**	**LF**
AM1	-	0.93 (0.33)	0.87 (0.21)	0.78 (0.02)	0.88 (0.35)	0.90 (0.04)	0.84 (0.09)	0.70 (0.23)
AM2	0.89 (0.33)	-	0.86 (0.00)	0.82 (0.24)	0.84 (0.29)	0.77 (0.03)	0.86 (0.34)	0.67 (0.19)
AF1	0.67 (0.02)	0.70 (0.00)	-	0.77 (0.00)	0.70 (0.13)	0.34 (0.00)	0.70 (0.00)	0.58 (0.13)
AF2	0.54 (0.01)	0.65 (0.14)	0.87 (0.00)	-	0.60 (0.01)	0.27 (0.00)	0.79 (0.33)	0.51 (0.00)
JM	0.86 (0.27)	0.81 (0.23)	0.89 (0.49)	0.54 (0.02)	-	0.79 (0.03)	0.59 (0.00)	0.81 (0.36)
M1	0.82 (0.06)	0.80 (0.05)	0.59 (0.00)	0.64 (0.00)	0.68 (0.06)	-	0.79 (0.00)	0.45 (0.00)
M2	0.74 (0.06)	0.77 (0.22)	0.65 (0.00)	0.90 (0.41)	0.64 (0.00)	0.79 (0.00)	-	0.42 (0.03)
LF	0.81 (0.21)	0.81 (0.18)	0.92 (0.48)	0.65 (0.00)	0.88 (0.38)	0.47 (0.02)	0.63 (0.00)	-

values (mean ± SD = 8.65 ± 0.34) for adults. The mean $\delta^{15}N$ values did not significantly differ between males and females ($T_{36} = -1.37$, $P > 0.05$), juveniles and adults ($W = 140$, $P > 0.05$) or between individuals sampled in spring and autumn ($W = 155$, $P > 0.05$; Table 4.3).

4.3.4. Dietary sources

The model most supported by the stable isotope data for dolphin and fish prey allowed variation in diet among social clusters (Table 4.5). Prey feeding guild contributions to dolphin diet were heterogeneous among social clusters (Table 4.6). The dietary sources of clusters AM1, AF1, JM and LF consisted mostly of benthic omnivores and carnivores (55.0%, 47.6%, 45.3% and 45.8%, respectively), while the diet of M2 and AF2 was largely dominated by benthic detritivores (60.9% and 65.4%, respectively).

Herbivores and omnivores contributed the second largest proportion to the diet of clusters AM1, AF1, JM and LF (23.4.%, 30.1%, 32.3% and 28.1%, respectively) while contributing equally with benthic omnivores and carnivores to the diet of clusters M2 and AF2 (herbivores and omnivores: 18.2% and 16.9%, benthic omnivores and carnivores: 16.3% and 14.5%, respectively). Dietary sources of AM2 and M1 consisted of approximately equal proportions of herbivores and omnivores (36.4% and 32.6%, respectively) and benthic omnivores and carnivores (33.9% and 35.5%, respectively) with slightly lower contribution by benthic detritivores (22.5% and 26.0, respectively). Water column species contributed < 11% to the diet of all social clusters (Table 4.6). The largest contributors to the diet of social clusters AM2, AF2, M1 and M2 were benthic detritivores caught in the Murray River.

Table 4.5. Mixing models fit with MixSIAR on Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) data with 38 consumers (i.e., adult and juvenile dolphins of both sexes) belonging to eight social clusters within an estuarine dolphin population. Covariates 'Sex', 'Age' and 'Sex:Age" (i.e., covariate created by combining sex and age) were included as fixed effects and 'Social cluster' as a random effect. The Deviance Information Criterion (DIC) was used to evaluate relative model fit.

Model covariate	DIC
Social cluster	594.49
Sex + Age	612.79
Age	613.04
Null	617.86
Sex	618.07
Sex:Age	619.28

4.3.5. Total food intake by the dolphin population

Considering the proportion of adults (*n* =39) and juveniles (*n* = 25) in this dolphin population, an average individual was estimated to weigh 179 kg and consume between 3,395 and 4,125 kg annually, with a daily intake of between 9.3 and 11.3 kg. The dolphin population (*n* = 64) was estimated to consume between 217,248 and 263,968 kg of fish annually. Taking into account the number of individuals and their age class and the proportional contribution of each feeding guild to the diet of each social cluster, the total annual food intake for the population was estimated to comprise 29% benthic detritivores, 29% herbivores and omnivores, 36% benthic omnivores and carnivores and 6% water column feeders, mostly piscivores.

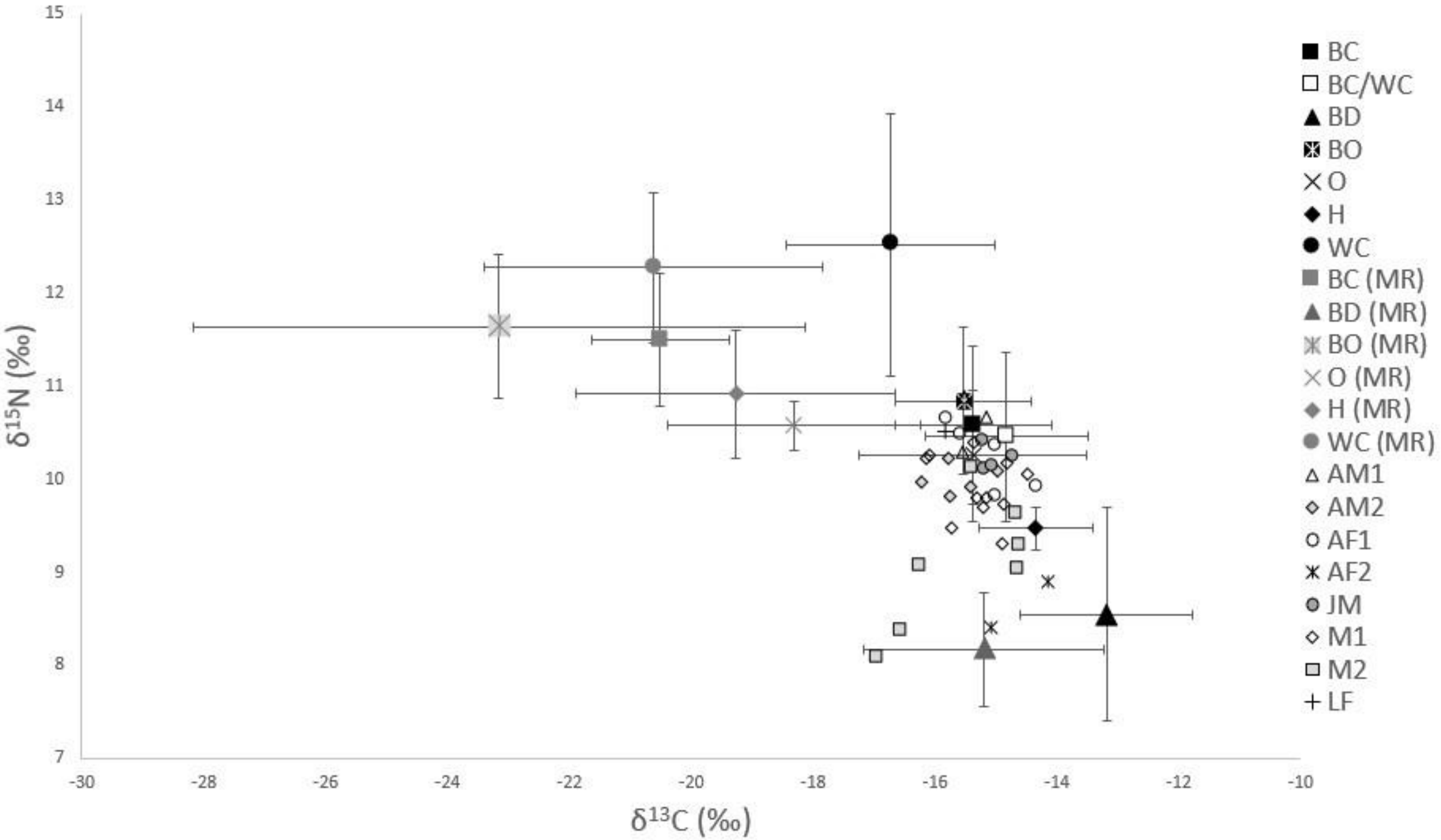


Figure 4.3. Carbon (δ^{13}C) and nitrogen (δ^{15}N) stable isotope ratios (mean ± SD, ‰) measured in skin of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary in Western Australia and in muscle of their potential prey species (fish) aggregated by feeding guild. Feeding guilds: BD = Benthic detritivore, H = Herbivore, O = Omnivore, BO = Benthic omnivore, BC = Benthic carnivore, WC =Water Column Feeder, MR = Murray River (i.e., fish caught in MR). Social Clusters: AM1 = Adult Males Cluster 1, AM2 = Adult Males Cluster 2, AF1 = Adult Females Cluster 1, AF2 = Adult Females Cluster 2, JM = Juvenile Males, M1 = Mixed Sex/Age Cluster 1, M2 = Mixed Sex/Age Cluster 2, LF = Lone Adult Female

Table 4.6. Proportional contribution (largest in bold) of different fish feeding guilds to the diet of eight social clusters of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary, Western Australia. Notations: Global = the overall dolphin population, SD = Standard Deviation, BD = Benthic Detritivore, H = Herbivore, O = Omnivore, BC = Benthic Carnivore, BO = Benthic Omnivore, WC = Water Column Feeder, AM = Adult Males, AF = Adult Females, JM = Juvenile Males, M = Mix of Adult Females and Juveniles, LF = Lone Female

Feeding guild	**Global Mean % (SD)**	**Dolphin social cluster**							
		AM1	**AM2**	**AF1**	**AF2**	**JM**	**M1**	**M2**	**LF**
		Mean % (SD)	**Mean % (SD)**	**Mean % (SD)**	**Mean % (SD)**	**Mean % (SD)**	**Mean % (SD)**	**Mean % (SD)**	**Mean % (SD)**
BD	7.9 (6.4)	5.1 (6.9)	6.8 (7.9)	7.4 (9.5)	11.2 (16.7)	7.9 (9.2)	8.4 (10.4)	3.6 (6.5)	6 (8.1)
BD (MR)	17.7 (8.6)	6.4 (6)	**15.7 (10.6)**	7.7 (7.3)	**54.2 (24.6)**	7.7 (7.2)	**17.6 (11.6)**	**57.3 (21.5)**	9.6 (9.5)
H	10.4 (8)	8.3 (10.5)	16 (17.8)	9.8 (12.6)	7.6 (13.1)	15 (15.9)	14.5 (18.8)	5.8 (12.7)	8.4 (11)
H (MR)	3.8 (4.1)	2.4 (4.6)	3.9 (6)	2.5 (4.7)	2 (4.9)	2.2 (3.4)	2.8 (4.4)	3.2 (7.6)	3.8 (7.5)
O	9.4 (7.6)	9.5 (14.5)	10.7 (14.3)	14.4 (21.1)	5.2 (9.8)	12 (16.3)	11.7 (16.8)	6.4 (14.3)	10.9 (16.5)
O (MR)	4.6 (4.9)	3.2 (5.6)	5.8 (8.6)	3.4 (6.9)	2.1 (4.4)	3.1 (5.7)	3.6 (6.3)	2.8 (6.2)	5 (9.5)
BC/WC	11.9 (8.6)	17.2 (20.2)	9.7 (10.7)	**21.7 (23.2)**	5 (7.2)	**17.9 (18.8)**	12.7 (15)	4.5 (5.7)	**13.9 (17.5)**
BC	10.3 (7.9)	16.3 (21.2)	10 (12)	14.6 (20.1)	4.1 (5.7)	12.9 (15.6)	11.7 (15.4)	4.4 (5.9)	13.8 (18.6)
BC (MR)	2.9 (3.3)	1.7 (2.6)	2.6 (3.7)	1.4 (2.2)	1.1 (2.1)	1.5 (2.1)	1.8 (2.7)	1.9 (3.6)	2.6 (4.5)
BO	9.6 (7.4)	**18.7 (22.6)**	9.6 (11.6)	8.8 (11.8)	3.4 (4.4)	12 (13.2)	8 (10.3)	4.2 (5.6)	13.5 (18)
BO (MR)	2.3 (2.9)	1.1 (1.7)	2 (2.9)	1.1 (1.6)	0.9 (1.6)	1 (1.4)	1.3 (2)	1.3 (2.3)	2 (3.7)
WC	5.9 (5)	7.9 (9.8)	4.2 (4.9)	5.1 (6.8)	2 (2.8)	5.1 (6.2)	3.9 (5.2)	2.8 (3.8)	7.2 (9.8)
WC (MR)	3.2 (3.5)	2.2 (3.4)	3.0 (4.2)	2.0 (3.5)	1.2 (2.0)	1.8 (2.6)	2.0 (3.0)	1.8 (3.0)	3.4 (5.6)

4.4. Discussion

This study demonstrated spatial and isotopic niche partitioning among social clusters of a population of Indo-Pacific bottlenose dolphins residing in the Peel-Harvey Estuary (PHE) in Western Australia. Dolphins foraged throughout the PHE using different foraging tactics depending on the prey species they targeted. Both behavioral observations and stable isotope analyses identified demersal fish species as the most important food source for dolphins. Dolphin social clusters varied in their space use within the estuary. Similarity in clusters' core habitat reflected similarity in their diet. Overall, the annual food intake of the dolphin population was estimated to be >200,000 kg, with detritivores, omnivores and herbivores and benthic omnivores and carnivores each contributing approximately a third and water column species the remainder of the biomass.

4.4.1. Intra-population partitioning in space use and dietary sources

Detritivores were proportionately the largest (~60%) dietary sources for social clusters AF2 (consisting of adult females) and M2 (consisting of adult females and juveniles of both sexes). Detritivores, particularly the cosmopolitan sea mullet (Whitfield et al. 2012), are commonly reported as bottlenose dolphin prey (Gunter 1942; Barros and Odell 1990; Barros and Wells 1998; Simões-Lopes 1998; Fury and Harrison 2011). In this study, sea mullet and Perth herring (*Nematalosa vlaminghi*) represented detritivores in the stable isotope analyses, with sea mullet being targeted more often based on behavioral observations. In the PHE these species travel up the rivers during the dry season and return to the lower reaches during the wet season (Potter et al. 1983; Loneragan et al. 1986; 1987; Valesini et al. 2009; Gibbs 2011). Both species are found in lower numbers in the estuary basins (Potter et al. 2016). The core activity space of social clusters AF2 and M2 extended from the eastern Peel Inlet into the rivers (Fig 4.2., Appendix C Fig. C.3) suggesting that overlap in habitat use and the relative abundance of sea mullet in the rivers, resulted in high proportional contribution of detritivores to the diet of these two clusters.

Mandurah Channel was part of the core activity space for social clusters AF1, AM1, JM and LF (Fig. 4.2). The core activity space of clusters AM1, JM and LF also included the Dawesville Channel. Results from the stable isotope mixing model showed that benthic omnivores and carnivores contributed the most to the diet of these four clusters, which had significantly higher $\delta^{15}N$ values than AF2 and M2. Estuary mouths and entrance channels are commonly used by dolphins (e.g., Wilson *et al*. 1997; Harzen 1998; Stockin et al. 2006; Chabanne et al. 2012) and often host a high diversity and abundance of fish (Loneragan et al. 1986; 1989; Valesini et al. 2009; Potter et al. 2016). The channel habitats in the PHE are highly modified by structures (e.g., jetties, canals and breakwalls) that function as barriers against which dolphins herd fish, mainly yelloweye and sea mullet (Table 4.1, Appendix C Fig. C.2). Such barriers likely improve foraging efficiency by aiding in prey detection, herding and manipulation (Heimlich-Boran, 1988; Hastie et al. 2003). Given the core activity space of these four clusters also extended slightly to coastal areas, it is likely that their diet is supplemented by prey from the marine food web.

Dietary sources for social clusters AM2 and M1 consisted of approximately equal proportions of herbivores and omnivores and benthic omnivores and carnivores with slightly lower contribution by detritivores. The core activity spaces of these clusters were in the estuary basins with the activity space of AM2 extending to Dawesville Channel. Unlike clusters AM1, JM and LF, which also occupied

Dawesville Channel, AM2 did not have significantly higher $\delta^{15}N$ values than the river-going social clusters. Both AM2 and M1 had a low probability of occupying the core space of AF1, which is effectively the Mandurah Channel (Fig. 4.2). As such, dietary source partitioning in this population corresponds to the degree to which individuals use the Mandurah Channel or the eastern shores of the estuary including the Serpentine and Murray rivers. Individuals frequenting the rivers feed at the lowest trophic position for the dolphins, indicating a shorter detritus-based food chain in these regions (i.e., detritus – sea mullet – dolphins). In contrast, individuals using the Mandurah Channel feed at the highest trophic position with several consumer trophic interactions having taken place prior to prey being consumed by dolphins. Individuals that primarily use the estuary basins (i.e., AM2 and M1) fall in between these two opposing trophic positions and reflect the estimated 'global' mean dietary source proportions in this population (i.e., an average individual's dietary proportions).

The observed spatial partitioning may lead to individuals being exposed to different pressures and threats which may affect their fitness and consequently population viability. For example, through trophic interactions, dolphins that frequent the riverine habitat (i.e., 19% of the population and 27% of the mature females) may be more exposed to algal toxins based on potentially harmful algae recorded in the Serpentine and Murray rivers (Thomson 2019). Biotoxins may cause immunomodulation in dolphins (Twiner et al. 2011) with harmful algal blooms linked to unusual mortality events (Lefebvre et al. 1999; Flewelling et al. 2005; Fire et al. 2011). In contrast, individuals showing high site fidelity to areas with greater human use (e.g., boating and fishing) such as the Mandurah and Dawesville Channels (i.e., 30% of the population and 30% of the mature females) may be more susceptible to disturbance and fishing line entanglements. These individuals also face higher predation risk as they visit coastal waters (Nicholson, unpublished data).

This study did not detect differences in mean isotopic values in dolphin skin tissue between seasons, sexes or age classes. Nor did it find support for these factors driving diet variability in this population. Fish abundance and species richness, however, changes spatio-temporally within the estuary in response to water quality parameters (e.g., salinity, temperature and dissolved oxygen: Loneragan et al. 1986; 1987; Valesini *et al*. 2009), shifts in macroalgal habitat and external influences from the marine environment (Potter et al. 2016; Valesini et al. 2019). Consequently, dolphin space use and diet may also vary spatio-temporally (e.g., Heithaus and Dill 2002; Zanardo et al. 2017). Given the complexity of trophic interactions and unquantified variation in each individual's resource use over time, the data collected (i.e., individuals were sampled only once) may not detect seasonal variation, even if it existed. Similarly, although $\delta^{15}N$ values between juveniles and adults did not differ statistically, ontogenetic shifts in diet and foraging strategies/tactics occur, at least to a degree: juveniles were not observed feeding on adult estuary catfish or Western Australian salmon (*A. truttacea*) and did not engage in tail-whacking behavior (Nicholson, personal observation).

4.4.2. Resource sharing with fishers

The estimated minimum annual food intake of the resident Peel-Harvey Estuary dolphin population (~200,000kg) exceeds the mean annual finfish biomass removed by commercial fishers in the estuary (Gaughan et al. 2019; Government of Western Australia 2020). Commercial fishers target sea mullet (~50–70% of catch), yellowfin whiting (*S. schomburgkii*), yelloweye mullet, and to a lesser extent Australian herring

(*Arripis georgianus*), Perth herring, tailor (*Pomatus saltatrix*) and estuary catfish, while recreational fishers whose total catch is less than commercial landings mainly target Australian herring, tailor, tarwhine (*Rhabdosargus sarba*), black bream (*Acanthopagrus butcheri*), king george whiting (*Sillago punctatus*) and other whiting species (Gaughan et al. 2019; Government of Western Australia, 2015; 2020). Of these species, sea mullet, yelloweye mullet, estuary catfish and whiting species (*Sillago* spp.) were identified as common dolphin prey, with sea mullet (and potentially Perth herring) contributing ~30% to the overall dolphin diet. Western striped grunter was a commonly foraged species by dolphins, however, is not targeted by either commercial or recreational fishers. As such, dolphins target some species that are not taken by fishers while sharing resources to a greater extent with commercial rather than recreational fishers given < 11% of dolphin dietary sources comprised water column species.

Competition between fishers and dolphins, however, may only exist if they overlap spatio-temporally and take the same species at the same life cycle stage. Approximately 14% of the estuary, including Mandurah Channel and the rivers, are closed to commercial fisheries (Government of Western Australia, 2015). This reduces potential competition between fishers and dolphins occupying mainly these areas (49% of the population). Although the size of fish taken by dolphins and fishers vary, the overall take of sea mullet, yelloweye mullet and whiting species, based on observations and life history of the species (Potter et al. 2016), consists largely of immature fish or maturing fish migrating to sea. In contrast, given the legal catch size limits (*Fish Resources Management Regulations 1995*) for estuary catfish and as all individuals caught by dolphins were >40 cm (size estimated from photographs against approximate size of dolphin’s features such as rostrum or dorsal fin), both fishers and dolphins are primarily removing mature individuals of this species (Nel et al. 1985). Thus, it can be concluded that dolphins and fishers target prey species at the same life cycle stage.

Most fish species targeted by dolphins in the PHE are part of defined stocks that extend outside the estuary and are considered stable and sustainably harvested (Gaughan et al. 2019). An exception may be estuary catfish for which the PHE is considered a discrete stock from coastal and other estuarine stocks (Nel et al. 1983; Potter et al. 1983; Ayvazian et al. 1994; Gaughan et al. 2019). Given that this species was most commonly observed being caught by dolphins, dolphins and fishers targeting similarly sized individuals and dolphins being the only known predator of adult estuary catfish in the estuary, incorporating mortality due to predation by dolphins in fish population models should be considered to improve fisheries management for this species (Tyrrell et al. 2011; Smith and Lenanton 2021).

The estimated amount of food intake by the dolphin population and the proportional feeding guild contributions to it, should be treated as an approximate minimum as not all sources of variability or uncertainty were accounted for. For example, it was not considered that food intake may vary seasonally and among individuals (Cheal and Gales 1992). Energetic demands of lactating females are higher than that of non-lactating females (Cheal and Gales 1991; Bejarano et al. 2017) and males may feed on wider variety of species (Hernandez-Milian, 2015) and have consistently higher food intakes than females (Cheal and Gales 1992) and bioenergetic requirements than females (Bejarano et al. 2017). Prey species also vary in their caloric content (McCluskey et al. 2016) with prey selection influencing the amount of fish individuals need to consume to meet their energy demands. Future work should consider applying a bioenergetic model (e.g., Bejarano et al. 2017; Reed et al. 2020) that incorporates uncertainty and variability in individuals' energy demands as well as energy content of prey to refine the estimated annual fish biomass removed by dolphins from the estuary. The prey species and heterogeneity in diet among social clusters identified in the current study can be used to inform such a model.

4.4.3. Ecological role of dolphins in the estuary

Dolphins occupy the role of an apex predator (as defined by Sergio et al. 2014) within the PHE as they feed on fish at all consumer levels while being free from predation risk effects themselves (large sharks are thought to be mostly absent from the estuary). As such, they have the potential to exert top-down pressure on prey populations through both consumption (Leopold 1943; Estes et al. 1995; 1998; Williams et al. 2004; Ripple and Beschta 2012; Ripple et al. 2014) and as agents of intimidation (Lima 1998; Abrams 2000; Brown and Kotler 2004; Morosinotto et al. 2010). Any decline or increase in dolphin abundance, or changes in their foraging behavior and diet may influence the trophic structure in the estuary. It is unlikely that dolphins can, through consumption, deplete fish species from this permanently open estuary as the presence and abundance of the main dolphin prey species in the PHE is directly linked to recruitment from the marine environment (Potter et al. 2016). Exceptions are the estuary catfish and black bream which complete their lifecycle in the estuary (Potter et al. 2016), although the latter was not considered an important dietary source for dolphins. Declines in dolphin abundance may lead to greater food availability for open and deeper water (>1m) avian piscivores, which at least partially occupy the same foraging niche to dolphins (Trayler et al. 1988; Stockwell et al. 2021) and consequently their increased abundance. Bottom-grubbing, by which dolphins mechanically disturb sediments, was the most observed foraging tactic. Through this behavior dolphins may influence the benthic microbial and faunal communities (Findlay et al. 1990a; 1990b; Cross and Curran 2000; 2004) and release nutrients into the water column further promoting anoxic conditions (Almroth et al. 2009). However, in comparison to re-suspension of sediments caused by abiotic (e.g., river flow, tidal currents, wind and waves) and anthropogenic (e.g., dredging) factors (Tweedley et al. 2016), bioturbation by dolphins is likely to be negligible.

4.4.4. Conclusions

This study confirmed spatial and isotopic niche partitioning according to social structure within a resident estuarine bottlenose dolphin population. The heterogeneity in social clusters' space use and diet indicates that individuals may be exposed differently to threats and extrinsic pressures. This has implications for conservation management as maintaining the collective niche of individuals requires consideration of impacts on individuals across social clusters. The annual food intake across consumer trophic levels, and the year-round presence of dolphins throughout the estuary has the potential to suppress prey populations and affect community structure through consumptive and non-consumptive pressures. As apex predators, dolphins collectively remove a substantial amount of demersal fish from the system and should be recognized as an important component of the estuarine ecosystem.

Chapter 5

General Discussion and conclusions

5.1. Dolphins as part of the ecological character of the Peel-Yalgorup Ramsar site

Research for this thesis provides the scientific basis for recognizing the Peel-Harvey Estuary (PHE) dolphin community as a biological component involved in ecosystem processes of the Peel-Yalgorup system (PYS) and for considering this community as part of the ecological character of the Peel-Yalgorup Ramsar-listed wetland. This conclusion is based on my studies of social structure, spatial distribution, foraging behavior and feeding ecology as well as the demographics and current population status of the resident community of dolphins.

Several findings support recognizing dolphins as a biological component of the wetland. First, the estuary is occupied by a year-round resident community of ~90 dolphins (Chapter 3). Second, the estuarine community is socially, spatially and isotopically distinct from dolphin communities in adjacent coastal waters (Chapter 2). Social analyses revealed extremely weak association relationships between members of different social communities, while high association relationships were detected within communities (Chapter 2). The study area encompassed the full coastal range of the estuarine community, with the community range extending slightly outside the estuary (Chapter 2). Intracommunity heterogeneity, however, was detected in individuals' space use patterns, suggesting that ~44% of independent individuals (i.e., juveniles and adults) in the estuarine community may venture out into coastal waters occasionally (Chapter 4). Regardless, stable isotope analyses confirmed the estuarine community to be dependent on wetland (i.e., PHE) fish resources (Chapters 2 and 4), while other identified social communities relied on coastal resources (Chapter 2).

The estuarine dolphin community was defined as a closed population where population changes are largely determined by birth and death processes (Chapter 3).

No immigration was observed into the community during this study and, although not confirmed, it is likely that some juvenile males permanently emigrate from the system. Therefore, from here onward, I refer to the estuarine community as a population.

Third, dolphins were found to be involved in ecosystem processes within the PHE, which constitutes approximately a half of the Peel-Yalgorup Ramsar site's total area. Stable isotope analyses confirmed dolphins to be reliant on estuarine food sources (Chapter 2) and were identified to occupy the role of an apex predator in the estuary (Chapter 4). As such, they likely contribute to consumer (i.e., top-down) control in the system (Leopold 1943; Estes and Duggins 1995; Bowen 1997; Schmitz 2010).

Based on the estuarine population's current age structure (Chapter 3) and heterogeneous diet among social clusters (Chapter 4), individuals were collectively estimated to remove >200,000 kg of finfish annually from the system. This exceeds the finfish biomass removed annually by commercial fishers in the estuary (~100,000 kg, Gaughan et al. 2019; Government of Western Australia 2020). The estimated annual food intake of the population comprised 29% detritivores, 29% herbivores and omnivores, 36% benthic omnivores and carnivores and 6% water column feeders (Chapter 4). Observations of foraging behavior and feeding events indicated some fish species to be consumed frequently and therefore deemed as important prey for dolphins (e.g., *Cnidoglanis macrocephalus*, *Mugil cephalus*, *Rhabdosargus sarba*, *Sillago* spp. and *Pelates octolineatus*), while other species were only observed to be consumed or targeted occasionally (e.g., *Hyporhampus* spp., *Platycephalus laevigatus*, *Octopus tetricus* and *Arripis truttacea*). The estimated volume of finfish consumption by dolphins indicates that they are an important consumer and may suppress prey populations within the estuary while the year-round presence of dolphins throughout the system has the potential to produce a 'landscape of fear' (Laundré et al. 2010) where predation risk influences prey distribution and behavior (Lima and Dill 1990; Brown et al. 1999; Heithaus and Dill 2002; Wirsing et al. 2007; Ale and Whelan 2008; Heithaus et al. 2009). There are no absolute abundance or biomass estimates for fish stocks of species that utilize the Peel-Harvey Estuary and the available density estimates are highly variable (Valesini et al. 2009; Potter et al. 2016). Further information is therefore required to confirm whether, or to what degree, dolphins suppress prey populations within the estuary.

Fish are considered a critical component of the ecological character of the Peel-Yalgorup Ramsar-site as they sustain piscivorous birds and fish (Hale and Butcher 2007; Stockwell et al. 2020) as well as dolphins (Chapter 4), and may as predators themselves influence the structure of fish, plant and invertebrate communities (e.g., Batzer et al. 2000; Hindell et al. 2000; Bessey et al. 2016). As such, changes in the dolphin population may influence the species community structure in the estuary and, for example, lead to simplification and shortening of the food web (Estes et al. 2011). Changes in the availability of fish species identified as regularly consumed dolphin prey (Chapter 4), however, are hypothesized to have less of an impact on the dolphin population. This is because dolphins generally show high behavioral plasticity and would likely switch between prey species in response to their availability and abundance (Radeloff et al. 2015).

5.2. Dolphins' contribution to the Peel-Yalgorup site meeting the Ramsar Convention listing criteria

The Peel-Harvey dolphin population rely on wetland resources with individuals, apart from juvenile males who may permanently emigrate (Chapter 3), spending their whole life cycle in the estuary. As such, dolphins contribute to the Peel-Yalgorup site meeting the Ramsar Convention listing criterion 4, by which ‘a wetland should be considered internationally important if it supports plant and/or animal species at a critical stage in their life cycles or provides refuge during adverse conditions’. Dolphins do not contribute to the Peel-Yalgorup Ramsar site meeting other listing criteria that may be relevant to dolphins in other wetlands (i.e., criterion 2, 3 and 9, see Table 1.1). For example, as Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) are classified globally ‘near threatened’ (IUCN Red List, Braulik et al. 2019), are considered data deficient in Australia (Woinarski et al. 2014) and are not listed as threatened or a priority species under State legislation in Western Australia, their conservation status does not contribute to the site meeting criterion 2. Also, the size of the estuarine population (i.e., ~90 individuals) does not constitute >1% of global abundance for this species (Braulik et al. 2019) and hence does not satisfy criterion 9 (Table 1.1.).

5.3. Baseline information and Limit of Acceptable Change (LAC)

This thesis provides a robust baseline on structure, abundance and demographics for the dolphin population residing in the PHE (Table 5.1). Although baselines may shift over time (e.g., Newsome et al. 2007a), they provide a standard against which future changes can be assessed and are therefore important for triggering management action to ensure population or species persistence (e.g., Nicholson et al. 2012, Palmer et al. 2014, Methion and Diaz López 2018; Martin et al. 2020).

Dolphins have used the PHE at least to some extent for decades (Hale and Butcher 2007; Groom and Coughran 2012), although it is likely they have been present in the estuary since its formation 8000 - 4000 years ago (Brearley, 2005). It is likely that the dolphin population size, residency and individuals’ space use

Table 5.1. Description of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) as a component of the ecological character of the Ramsar-listed Peel-Yalgorup wetland in Western Australia. Information is based on a data collected between 2016 and 2020.

Component	**Species**	**Description**	**Measurable baseline parameters**	**Threats**
Marine mammals	Indo-Pacific bottlenose dolphin (*Tursiops aduncus*)	The Peel-Harvey Estuary supports a resident population of ~90 dolphins. This population is socially, spatially and isotopically distinct from dolphin communities in adjacent coastal waters (Chapter 2 and 3) Coastal dolphins use the entrance channels (Mandurah and Dawesville Channels) particularly in autumn (Chapter 2) The resident dolphins rely on estuarine food sources and show niche partitioning according to social structure in their diet (Chapters 2 and 4) Collectively the resident dolphins remove a minimum of 200,000 kg of finfish annually from the Estuary (Chapter 4) As top predators in the system, they likely supress prey populations through consumption and as agents of intimidation (Chapter 4)	Dolphins use the full extent of the Peel-Harvey Estuary year-round Population size fluctuated between 84 and 94 individuals Mean annual apparent survival rates (%): Adults 94.6 (SD 2.02) Juveniles 88.2 (SD 2.54) Calves 100.0 (SD 0.00) Yearlings 75.4 (SD 17.50) Annual reproductive rate from 0.22 to 0.67 (with current population structure this equates to between 5 and 16 calves born each year) was recorded with an average of 0.39 over a 4-year period. Carbon and nitrogen stable isotope values: δ^{15}N: – 17.94 to – 14.15 (mean – 15.41, SD 0.74) δ^{13}C: 8.09 to 10.88 (mean 9.86, SD 0.65) Dolphins are dependent on estuarine food sources (i.e., carbon stable isotope values, δ^{13}C, measured overlap with those of potential prey species' inhabiting the Estuary)	Water quality (e.g., algal toxins) Commercial and urban development (habitat modification and/or loss) Entanglement in fishing gear Live strandings Disease outbreaks (e.g., cetacean morbillivirus)

patterns have changed with time. For example, the opening of the additional connection, the Dawesville Channel, to the Indian Ocean in 1995 resulted in changes to the ecological character of the estuary (e.g., hydrology and water quality have changed significantly and had effects on the biotic components such as decrease in phytoplankton and macroalgal biomass and increase in marine fish species, Hale and Butcher 2007; Potter et al. 2016) and likely influenced how dolphins have used the waterways since. Given the anecdotal nature of dolphin observations in the estuary prior to the present study, this thesis provides the first baseline for the status of the dolphin population.

In the context of the Ramsar Convention, the baseline information provided from the research in this thesis contributes to setting management goals to increase population growth rate to enable an appropriate LAC to be set for dolphins. To reverse the forecast decline in population size over time, management should prioritize action that reduces adult female mortality by at least 10%, or by 5% if yearling mortality is also reduced by 10% while maintaining the current high reproductive output. The baseline information also allows for a focused monitoring program to be developed and when established this allows decision makers and managers to confirm management actions to have a desired outcome over time or to take further action when required to ensure the dolphin population is maintained as part of the ecological character of the Peel-Yalgorup Ramsar site.

It is important to acknowledge that the baseline (Table 5.1) is based on only four years of dedicated research effort. This is a relatively short time given the longevity of dolphins (e.g., Connor and Krützen 2015; Wells 2014; Manlik et al. 2016). Future monitoring is recommended not only to ensure changes in the population are detected, but also to establish whether the baseline from this thesis has adequately captured natural variation in the measured demographic parameters for the population. The baseline also only considers dolphins as biological components of the ecosystem and their involvement in ecosystem processes, not their contribution to ecosystem benefits and services (e.g., value to indigenous culture, aesthetics and tourism, DEWHA 2008). The latter is an equally important consideration when evaluating whether dolphins are part of the ecological character of a wetland and whether they should be considered a critical component of it (DEWHA 2008). Further study is required to evaluate the cultural, aesthetic and economic value of dolphins in the Peel-Yalgorup Ramsar site. Together, the results from this thesis and an evaluation of ecosystem benefits and services provided by dolphins will form the basis for a fully informed development of a LAC.

5.4. Monitoring program

Recognizing dolphins as part of the ecological character of the Peel-Yalgorup Ramsar site implies they should also become a feature of monitoring and reporting in the wetland's ecological character (DEWHA 2008). Although future work is required to evaluate dolphins' contribution to ecosystem benefits and services, a monitoring program may be developed prior to this information being available. This is to evaluate whether management action has desired outcomes and to ensure dolphins are maintained as functional biological components of the wetland as described in this thesis (Table 5.1).

The main objective of the suggested monitoring program (Table 5.2) is to detect any changes in the population size and demographic parameters over time. Changes should be measured against parameter values reported in this thesis (see Table 5.1), with measured parameter values outside the observed variation triggering management to consider whether further intervention is needed (DEWHA 2008). Dedicated monitoring ensures information is available for decision makers to evaluate and guide management action and to enable consideration of adverse impacts to the dolphin population from human activities. A monitoring program further ensures a precautionary approach is taken to maintain the dolphin population for their contribution to ecosystem benefits and services that are yet to be fully identified, for example, their availability to tourism (Thompson et al. 2000; Hawkins et al. 2017).

Several studies have shown that there is generally low statistical power to detect population declines for delphinid species, with the amount of survey effort influencing the ability to detect population changes and demographic events such as calving (Taylor and Gerrodette 1993; Taylor et al. 2007; Tyne et al. 2016; Symons et al. 2018). It is therefore important to discuss the appropriateness of the suggested three surveys to be conducted in the estuary in each Austral season. A minimum of three surveys (i.e., sampling occasions) during primary sampling periods (i.e., seasons) are required to analyze the collected data in the Pollock's Closed Robust Design capture-recapture framework (Pollock 1982; Kendall and Nichols 1995; Kendall et al. 1995, 1997). This analytical approach is valuable for monitoring how many dolphins (i.e., including coastal individuals in the entrance channels) use the estuary over time, although the suggested amount of research effort is unlikely to result in enough power to, in an appropriate time frame, detect statistically significant decline in coastal dolphins using the estuary (Tyne et al. 2016). The suggested research effort is deemed sufficient, however, to specifically monitor changes in demographic parameters of the estuarine population, given all individuals in the population are currently known. Based on individual sighting frequencies during this study, three surveys per season resulted in >70% of individuals being encountered within a season and 100% within

Table 5.2. Components of a suggested monitoring program for Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) population resident to the Peel-Harvey Estuary, which is part of the Peel-Yalgorup Ramsar-site in Western Australia.

What to monitor	Objective of monitoring	Method	Frequency
Residency, abundance, apparent survival and reproductive rate	To detect changes in apparent survival and reproductive rates as measured against baseline information To ensure the estuarine population remains stable To monitor the use of the estuary entrances by coastal dolphins Ensure a proportion of resident mature females are reproducing each year	Boat based photo-identification surveys	At minimum 3 surveys covering the Peel-Harvey waterways each Austral season Additional survey days are recommended during autumn when there are likely to be more births occurring and a higher number of individuals using the estuary entrances Additional survey days are also recommended when an independent individual has not been sighted for 6 months. These surveys should target known high use areas by that particular individual
Reliance on estuarine food sources	Investigate whether resident dolphins are still reliant on Estuarine food sources	Stable isotope analyses of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in dolphin skin tissue	If the monitoring efforts indicate reduced use of the estuary by resident individuals

two seasons (Nicholson, unpublished data). As such, to ensure effective monitoring, each individual should be sighted periodically to confirm they are alive and present in the estuary. Only doing systematic sampling (i.e., transect design described in Chapters 2 and 3) is not likely to be sufficient for detecting births quickly enough to ensure calves that die soon after birth are also detected. Therefore, additional dedicated survey effort is recommended during the main calving season between March and May. Planning for a monitoring budget should allow for six days of monitoring per season and an additional ten days of monitoring in autumn. This monitoring program should be re-evaluated periodically to ensure sufficient sighting frequency of individuals to detect change in demographic parameters.

5.5. Note on dolphin protection and management in Western Australia

Including dolphins in the ecological character description and monitoring framework for the Peel-Yalgorup Ramsar site and them being managed as part of the Ramsar framework, does not conflict or overlap with any State legislation or management obligation for dolphins in Western Australia but rather complements existing framework for their protection.

All cetaceans (i.e., whales, dolphins and porpoises) are protected in Australian waters. The *EPBC Act* provides for their protection in Commonwealth waters (3-200nm) while corresponding State legislation applies in the waters under State jurisdiction (i.e., up to 3 nm). Thus, although the Commonwealth Government is ultimately responsible for conserving species under the *Convention on Biological Diversity*, an international agreement, the protection and management of the Peel-Harvey dolphin population rests with the State Government and State legislation.

In Western Australia, the *Biodiversity Conservation Act 2016* (WA*; BC Act*) provides for the protection mainly from immediate and measurable threats (e.g., individual incidents of interference with dolphins, for detail see 5.5. below) that may result in death or in accumulative sublethal impacts on an individual or the population (e.g., Wells et al. 2008; Pirotta et al. 2015). Under the *BC Act*, it is an offence to take (i.e., kill, injure, harvest or capture), disturb (i.e., chase, drive, follow, harass, herd or hunt), possess, deal in, process, import or export a cetacean. The success of controlling these actions depends on their adequate detection and enforcement. The second piece of important legislation for protecting dolphins is the *Environmental Protection Act 1986* (WA; *EP Act*), which provides for Environmental Impact Assessments (EIA) to be conducted to evaluate impacts of developments on the environment, including dolphins. Unfortunately, however, coastal dolphins are often not included in the EIA process due to lack of information or reliable data on dolphin populations being available for an impact assessment (Bejder et al. 2012).

Several dolphin populations in Australian waters are monitored inadvertently through research programs, EIAs and their potential follow-up monitoring/reporting requirements (e.g., Connor and Krützen 2014; Chabanne et al. 2017a; Brooks et al. 2017; Raudino et al. 2018; Sprogis et al. 2018; Bouchet et al. 2021). There, however, is no obligation on the Commonwealth or State governments to conduct surveys to identify the extent and range of cetacean species in Australian waters, nor is there any requirements to define populations for management purposes or to monitor identified populations over time. As such, managing the PHE dolphin population under the Ramsar framework (DEWHA 2008) offers it increased protection.

5.6. Threats and their potential consequences to the Peel-Harvey dolphin population

Signatories to the Ramsar Convention are expected to identify actual and likely threats to the ecological character of listed sites and to incorporate their mitigation in management planning (Ramsar Convention Article 3, COP8, Resolution VIII.14, 2002; DEWHA 2008). The slightly negative population growth rate projected for the Peel-Harvey dolphin population (Chapter 3) makes it vulnerable to external stressors and warrants management action to be taken to reverse the forecast decline in population size. Any human activity, event or environmental variable that may lead to decrease in survival and/or reproductive rates in this population may be considered a threat to the population's persistence. The effect of some threats (e.g., live strandings, entanglements, disease outbreaks) are more obvious, while the effect of others (e.g., climate change, habitat modification, disturbance, pollution) may be difficult to identify and quantify (Simmonds and Isaac 2007; Wells et al. 2008; Hollyoke et al. 2010; Schumann et al. 2013; Pirotta et al. 2015).

The more quantifiable and direct causes of mortality in this population are related to live strandings (Groom and Coughran 2012) and entanglements (Chapter 3). Approximately a third of the current population have live stranded at least once, some individuals on multiple occasions (Nicholson, unpublished data). Individuals who strand during the summer months face a risk of getting badly sunburnt, which may lead to further health complications and death. At least 21% percent of dolphin deaths recorded during this study were attributed to live stranding events (Chapter 3). Four individuals in the estuarine population have also been recorded with fishing line entanglements (Nicholson, unpublished data), which may result in death of individuals (Wells et al. 2008). Mortality due to live strandings and entanglements can impact the population trajectory and/or make the population more vulnerable to other external stressors especially if reproductive females are lost from the population. In addition, both live stranding and entanglement events need to be considered from an animal welfare perspective (Beausoleil et al. 2018).

Stochastic events, such as disease outbreaks may also be catastrophic for the Peel-Harvey dolphin population given the projected negative population growth rate. For example, cetacean morbillivirus (CeMV) has affected several dolphin populations and been linked to unusual mortality events (e.g., Holyoake et al. 2010; Kemper et al. 2016; Batley et al. 2019). In Western Australia, CeMV was linked to a dolphin mortality event where a third of an estuarine community of dolphins was lost (Holyoake et al. 2010; Chabanne et al. 2012; Stephens et al. 2014). Such loss in the Peel-Harvey dolphin population would likely lead to severe decline in reproductive output, depending on how many females are lost. As these outbreaks cannot be prevented, it is important to mitigate other external stressors on the population's health.

Climate change has been recognized both as a factor that may alter the ecological character of wetland ecosystems (Erwin et al. 2009; Finlayson et al. 2013) and driver of changes in abundance and distribution of marine mammals (Simmonds and Isaac 2007; Schumann et al. 2013). Climate change impacts on estuaries of south-western Australia include progressive warming and drying (Hallett et al. 2018). This leads to declines in freshwater flows with permanently open systems, such as the Peel-Harvey Estuary, becoming more marine and likely experiencing an increase in species diversity (Hallett et al. 2018). It is likely that climate driven changes in the abundance and distribution of dolphins using the estuary reflect changes in fish biomass and distribution in the system (Simmonds and Isaac 2007).

Human activities have also had negative consequences (e.g., biodiversity loss, decline in habitat quality and ecosystem services) on wetlands globally (Junk et al. 2013; Gardner and Finlayson 2018), while also leading to direct and indirect impacts on dolphins (e.g., animals moving temporarily or permanently away from an area, Watson-Capps et al. 2005; Bejder et al. 2006; Pirotta et al. 2013). Population level consequences from human impacts (e.g., boating, dredging, construction, noise, pollution) may be detected through observation of lowered reproductive success (Schwacke et al. 2002; Wells et al. 2005; Kemper et al. 2019; Senigaglia et al. 2019), increased mortality (Wells and Scott 1997; Wells et al. 2008; 2013) and decreased health of individuals (Wells et al. 2005; Twiner et al. 2011), making these parameters important to monitor.

The health of the Peel-Harvey dolphin population may also be impacted by water quality parameters indirectly, through trophic interactions (e.g., Chapter 4; Fire et al. 2008). The Serpentine and Murray Rivers currently show signs of significant eutrophication with potentially harmful algae dominating the phytoplankton communities (Thomson 2019). The identified algae may produce toxins (e.g., cyanotoxins, karlotoxins, domoic acid) that are associated with immunosuppression and modulation in dolphins (Twiner et al. 2011). The effects of climate change on reducing rainfall and river flow in south-western Australia are likely to cause a further increase in retention of nutrients in the estuary (Hallett et al. 2018), which may result in increased frequency of phytoplankton blooms. Further study is therefore warranted to investigate the impact of algal toxins to the estuarine dolphin population.

Should any, or a combination of external stressors lead to the extinction of the Peel-Harvey dolphin population, as defined in this thesis, it is possible that as newly available habitat the estuary would be re-colonized by coastal dolphins (e.g., Silliman et al. 2018; Chabanne et al. 2020). However, should the impacts of external stressors on dolphins not be managed appropriately, the estuary could become a sink habitat where a population may or may not persist without reproductive surpluses from productive source habitats (e.g., Pulliam 1988; Jansen and Yoshimura 1998; Chabanne et al. 2020). Given no immigration was observed into the estuary, it is difficult to hypothesize the degree of decline in population abundance that would trigger possible immigration or recolonization.

5.7. Management recommendations and future research

The inclusion of the Peel-Harvey dolphin population in the ecological character description of the Peel-Yalgorup Ramsar site and the baseline information provided in this thesis, facilitates the population being considered in future development planning and justifies the need for the population to be monitored to ensure its persistence.

Management should consider the Peel-Harvey dolphin population separate to dolphin communities in adjacent coastal waters with a primary goal of increasing adult female and yearling survival and ensuring that the reproductive rates reported in this thesis do not decline over time. Management should aim for zero human caused mortality (i.e., from entanglements) and survival of live stranded individuals, especially mature females to ensure the reproductive output of this population is maintained. This requires the government to build local capacity to detect and quickly respond to dolphin incidents in the estuary. Currently, the State government of Western Australia follows the national guidance on the management of dolphin incidents (DSEWPC 2013) and has not developed State-specific dolphin incident response protocols. These protocols are necessary to guide consistent decision making based on best available knowledge and to ensure adequate resources are strategically allocated within the State to areas with known high frequency of dolphin incidents (e.g., the PHE, Groom and Coughran 2012). I recommend developing these protocols and allocating sufficient resources to dolphin incident response within the State as a priority action.

Future research should evaluate the estuarine dolphins’ contribution to the Peel-Yalgorup Ramsar site ecosystem services and benefits (e.g., cultural, aesthetic and economic value, DEWHA 2008). This will allow a full assessment to be made on the importance of dolphins as part of the ecological character of the site. Additionally, this enables a comprehensive Limit of Acceptable Change to be set for the dolphin population. For better informed management, the natural progression of research to that detailed in this thesis, is to investigate the genetic population structure and connectivity to adjacent coastal communities. This would allow consideration of management of the estuarine dolphin population at a metapopulation scale and in the context of preserving genetic diversity within the species.

References

Abrams, P. A. 2000. The evolution of predator-prey interactions: theory and evidence. *Annual Review of Ecology and Systematics*, 31, 79-105.

Ale, S. B. and Whelan, C. J. 2008. Reappraisal of the role of big, fierce predators! *Biodiversity and Conservation*, 17, 685-690.

Allen, S. J., Bejder, L. and Krützen, M. 2011. Why do Indo-Pacific bottlenose dolphins (*Tursiops* sp.) carry conch shells (*Turbinella* sp.) in Shark Bay, Western Australia? *Marine Mammal Science*, 27, 449-454.

Almroth, E., Tengberg, A. andersson, J. H., Pakhomova, S. and Hall, P. O. 2009. Effects of resuspension on benthic fluxes of oxygen, nutrients, dissolved inorganic carbon, iron and manganese in the Gulf of Finland, Baltic Sea. *Continental Shelf Research*, 29, 807-818.

Alves, R. R. and Rosa, I. L. 2008. Use of tucuxi dolphin Sotalia fluviatilis for medicinal and magic/religious purposes in north of Brazil. *Human Ecology*, 36, 443-447.

Amir, O. A., Berggren, P., Ndaro, S. G. and Jiddawi, N. S. 2005. Feeding ecology of the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) incidentally caught in the gillnet fisheries off Zanzibar, Tanzania. *Estuarine, Coastal and Shelf Science*, 63, 429-437.

Ansmann, I. C., Parra, G. J., Chilvers, B. L. and Lanyon, J. M. 2012. Dolphins restructure social system after reduction of commercial fisheries. *Animal Behaviour*, 84, 575-581.

Araújo, C. C., Wang, J. Y., Hung, S. K., White, B. N. and Brito, D. 2014. Viability of the Critically Endangered eastern Taiwan Strait population of Indo-Pacific humpback dolphins Sousa chinensis. *Endangered Species Research*, 24, 263-271.

Arso Civil, M., Cheney, B., Quick, N. J., Islas-Villanueva, V., Graves, J. A., Janik, V. M., . . . Hammond, P. S. 2019. Variations in age- and sex-specific survival rates help explain population trend in a discrete marine mammal population. *Ecology and Evolution*, 9, 533-544.

Atkins, S., Cantor, M., Pillay, N., Cliff, G., Keith, M. and Parra, G. J. 2016. Net loss of endangered humpback dolphins: integrating residency, site fidelity and bycatch in shark nets. *Marine Ecology Progress Series*, 555, 249-260.

Auditor General for Western Australia. 2006. Auditor General’s Report. Management of Ramsar Wetlands in Western Australia. https://audit.wa.gov.au/wp-content/uploads/2013/05/report2006_09.pdf

Aureli, F., Schaffner, C. M., Boesch, C., Bearder, S. K., Call, J., Chapman, C. A., . . . Henzi, S. P. 2008. Fission-fusion dynamics: new research frameworks. *Current Anthropology*, 49, 627-654.

Ayvazian, S., Johnson, M. and Mcglashan, D. 1994. High levels of genetic subdivision of marine and estuarine populations of the estuarine catfishCnidoglanis macrocephalus (Plotosidae) in southwestern Australia. *Marine Biology*, 118, 25-31.

Bailey, H. and Thompson, P. 2010. Effect of oceanographic features on fine-scale foraging movements of bottlenose dolphins. *Marine Ecology Progress Series*, 418, 223-233.

Baird, R. W. and Whitehead, H. 2000. Social organization of mammal-eating killer whales: group stability and dispersal patterns. *Canadian Journal of Zoology*, 78, 2096-2105.

Baker, I., O'brien, J., Mchugh, K. and Berrow, S. 2020. Fine-scale sociality reveals female–male affiliations and absence of male alliances in bottlenose dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland. *Marine Mammal Science*, 36, 66-88.

Barros, N. B., Ostrom, P. H., Stricker, C. A. and Wells, R. S. 2010. Stable isotopes differentiate bottlenose dolphins off west-central Florida. *Marine Mammal Science*, 26, 324-336.

Barros, N. B. and Wells, R. S. 1998. Prey and feeding patterns of resident bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Journal of Mammalogy*, 79, 1045-1059.

Barry, R. P. and Mcintyre, J. 2011. Estimating animal densities and home range in regions with irregular boundaries and holes: A lattice-based alternative to the kernel density estimator. *Ecological Modelling*, 222, 1666-1672.

Batley, K. C., Sandoval-Castillo, J., Kemper, C. M., Attard, C. R., Zanardo, N., Tomo, I., . . . Möller, L. M. 2019. Genome-wide association study of an unusual dolphin mortality event reveals candidate genes for susceptibility and resistance to cetacean morbillivirus. *Evolutionary applications*, 12, 718-732.

Batzer, D. P., Pusateri, C. R. and Vetter, R. 2000. Impacts of fish predation on marsh invertebrates: Direct and indirect effects. *Wetlands*, 20, 307-312.

Bax, N. 1991. A comparison of fish biomass flow to fish, fisheries and marine mammals for six marine ecosystems. Pages 217-224 ICES marine science symposia.

Beausoleil, N. J., Mellor, D. J., Baker, L., Baker, S. E., Bellio, M., Clarke, A. S., . . . Harvey, A. 2018. “Feelings and Fitness” Not “Feelings or Fitness”–The Raison d'être of Conservation Welfare, Which Aligns Conservation and Animal Welfare Objectives. *Frontiers in veterinary science*, 5, 296.

Bejder, L., Fletcher, D. and Brager, S. 1998. A method for testing association patterns of social animals. *Animal Behaviour*, 56, 719-725.

Bejder, L., Hodgson, A., Loneragan, N. and Allen, S. 2012. Coastal dolphins in North-Western Australia: The need for re-evaluation of species listings and short-comings in the Environmental Impact Assessment process. *Pacific Conservation Biology*, 18, 22-25.

Bejder, L., Samuels, A., Whitehead, H., Gales, N., Mann, J., Connor, R., . . . Krützen, M. 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. *Conservation Biology*, 20, 1791-1798.

Bessey, C., Heithaus, M., Fourqurean, J., Gastrich, K. and Burkholder, D. 2016. Importance of teleost macrograzers to seagrass composition in a subtropical ecosystem with abundant populations of megagrazers and predators. *Marine Ecology Progress Series*, 553, 81-92.

Bianchi, T. S. 2006. Biochemistry of Estuaries. Oxford University Press, Oxford, United Kingdom.

BirdLife International. 2018. Sternula nereis. The IUCN Red List of Threatened Species 2018: e.T22694691A132568135. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22694691A132568135.en. Downloaded on 20 March 2021.

Blázquez, M., Baker, I., O'brien, J. M. and Berrow, S. D. 2020. Population Viability Analysis and Comparison of Two Monitoring Strategies for Bottlenose Dolphins (*Tursiops truncatus*) in the Shannon Estuary, Ireland, to Inform Management. *Aquatic Mammals*, 46, 307-325.

BMT WBM. 2010. Ecological Character Description of the Shoalwater and Corio Bays Area Ramsar Site. Prepared for the Australian Government Department of the Environment, Water, Heritage and the Arts. Canberra, Australia.

BMT WBM. 2011. Ecological Character Description of the Corner Inlet Ramsar Site – Final Report. Prepared for the Australian Government Department of Sustainability, Environment, Water, Population and Communities. Canberra, Australia.

Bolnick, D. I. 2001. Intraspecific competition favours niche width expansion in Drosophila melanogaster. *Nature*, 410, 463-466.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. and Forister, M. L. 2003. The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, 161, 1-28.

Bouchet, P. J., Thiele, D., Marley, S. A., Waples, K., Weisenberger, F., , B. R., . . . Williams, D. 2021. Regional Assessment of the Conservation Status of Snubfin Dolphins (Orcaella heinsohni) in the Kimberley Region, Western Australia. *Frontiers in Marine Science*, 7.Original Research

Bowen, W. 1997. Role of marine mammals in aquatic ecosystems. *Marine Ecology Progress Series*, 158, 267-274.

Braulik, G. T., I. Archer, F., Khan, U., Imran, M., Sinha, R. K., Jefferson, T. A., Donovan, C. and Graves, J. A. 2021. Taxonomic revision of the South Asian River dolphins (Platanista): Indus and Ganges River dolphins are separate species. Marine Mammal Science, https://doi.org/10.1111/mms.12801

Braulik, G. T., Arshad, M., Noureen, U. and Northridge, S. P. 2014. Habitat Fragmentation and Species Extirpation in Freshwater Ecosystems; Causes of Range Decline of the Indus River Dolphin (Platanista gangetica minor). *PLOS ONE*, 9, e101657.

Braulik, G., Natoli, A., Kiszka, J., Parra, G., Plön, S. and Smith, B.D. 2019. *Tursiops aduncus*. The IUCN Red List of Threatened Species 2019: e.T41714A50381127. https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T41714A50381127.en. Downloaded on 24 March 2021.

Braulik, G.T., Smith, B.D. and Chaudhry, S. 2012. Platanista gangetica ssp. minor. The IUCN Red List of Threatened Species 2012: e.T41757A17628296. https://doi.org/10.2305/IUCN.UK.2012.RLTS.T41757A17628296.en. Downloaded on 20 March 2021.

Brearley, A. 2005. Ernest Hodgkin's Swanland Estuaries and Coastal Lagoons of South-western Australia. UWA Publishing, Western Australia.

Bridge, P. D. 1993. Classification. Pages 219-242 *in* J. C. Fry ed. *Biological data analysis.* Oxford University Press, Oxford, U.K.

Brook, F., Kinoshita, R., Brown, B. and Metreweli, C. 2000. Ultrasonographic imaging of the testis and epididymis of the bottlenose dolphin, *Tursiops truncatus aduncas*. *Journal of Reproduction and Fertility*, 119, 233-240.

Brooks, L., Palmer, C., Griffiths, A. D. and Pollock, K. H. 2017. Monitoring variation in small coastal dolphin populations: an example from Darwin, Northern Territory, Australia. *Frontiers in Marine Science*, 4, 94.

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.

Brown, J. S. and Kotler, B. P. 2004. Hazardous duty pay and the foraging cost of predation. *Ecology Letters*, 7, 999-1014.

Brown, J. S., Laundré, J. W. and Gurung, M. 1999. The ecology of fear: optimal foraging, game theory and trophic interactions. *Journal of Mammalogy,* 80, 385-399.

Bruck, J. N. 2013. Decades-long social memory in bottlenose dolphins. *Proceedings of the Royal Society B: Biological Sciences,* 280, 20131726.

Buckland, S. T., Rexstad, E. A., Marques, T. A. and Oedekoven, C. S. 2015. Distance sampling: methods and applications. Springer.

Cagnazzi, D. D. B., Harrison, P. L., Ross, G. J. B. and Lynch, P. 2011. Abundance and site fidelity of Indo-Pacific Humpback dolphins in the Great Sandy Strait, Queensland, Australia. *Marine Mammal Science*, 27, 255-281.

Cairns, J. S. and Schwager, S. J. 1987. A comparison of association indices. *Animal Behaviour*, 35, 1454-1469.

Calenge, C. 2015. Home range estimation in R: the adehabitatHR package. . Pages 1-60.

Chabanne, D., Finn, H., Salgado-Kent, C. and Bedjer, L. 2012. Identification of a resident community of bottlenose dolphins (*Tursiops aduncus*) in the Swan Canning Riverpark, Western Australia, using behavioural information. *Pacific Conservation Biology*, 18, 247-262.

Chabanne, D. B., Finn, H. and Bejder, L. 2017a. Identifying the relevant local population for Environmental Impact Assessments of mobile marine fauna. *Frontiers in Marine Science*, 4, 148.

Chabanne, D. B., Pollock, K. H., Finn, H. and Bejder, L. 2017b. Applying the multistate capture–recapture robust design to characterize metapopulation structure. *Methods in ecology and evolution*, 8, 1547-1557.

Chabanne, D. B. H., Allen, S. J., Sherwin, W. B., Finn, H. C. and Krützen, M. 2020. Inconsistency between socio-spatial and genetic structure in a coastal dolphin population. Frontiers in Marine Science, 7, 1217.

Charlton-Robb, K., Taylor, A. and Mckechnie, S. 2015. Population genetic structure of the Burrunan dolphin (Tursiops australis) in coastal waters of south-eastern Australia: conservation implications. *Conservation Genetics*, 16, 195-207.

Cheal, A. J. and Gales, N. J. 1991. Body mass and food intake in captive, breeding bottlenose dolphins, *Tursiops truncatus*. *Zoo Biology*, 10, 451-456.

Cheal, A. J. and Gales, N. J. 1992. Growth, Sexual Maturity and Food-Intake of Australian Indian-Ocean Bottle-Nosed Dolphins, Tursiops-*Truncatus*, in Captivity. *Australian Journal of Zoology*, 40, 215-223.

Cheney, B., Wells, R., Barton, T. and Thompson, P. 2018. Laser photogrammetry reveals variation in growth and early survival in free-ranging bottlenose dolphins. *Animal Conservation*, 21, 252-261.

Cockcroft, V. and Ross, G. 1990a. Age, growth and reproduction in bottlenose dolphins from the east coast of southern Africa. *Fish. Bull*, 88, 289-302.

Cockcroft, V. and Ross, G. 1990. Food and feeding of the Indian Ocean bottlenose dolphin off southern Natal, South Africa. Pages 295-308 in S. Leatherwood and R. R. Reeves eds. The bottlenose dolphin. Academic Press, Inc., San Diego, U.S.A.

Committee on Taxonomy. 2021. List of marine mammal species and subspecies. Society for Marine Mammalogy. Available at https://marinemammalscience.org/science-and-publications/list-marine-mammal-species-subspecies (Accessed on 28 June 2021)

Conference of the Parties (COP), Convention on Wetlands (Ramsar, Iran, 1971), Proceedings of the 6th Meeting of the Conference of the Contracting Parties (Brisbane, Australia, 19-27 March 1996). Resolution VI.1: Working definitions of ecological character, guidelines for describing and maintaining the ecological character of listed sites and guidelines for operation of the Montreux record.

Conference of the Parties (COP), Convention on Wetlands (Ramsar, Iran, 1971), Proceedings of the 6th Meeting of the Conference of the Contracting Parties (Brisbane, Australia, 19-27 March 1996). Resolution VI.2: Adoption of specific criteria based on fish for identifying wetlands of international importance.

Conference of the Parties (COP), Convention on Wetlands (Ramsar, Iran, 1971), Proceedings of the 7th Meeting of the Conference of the Contracting Parties (San José, Costa Rica, 10-18 May 1999). Resolution VII.10: Wetland risk assessment framework.

Conference of the Parties (COP), Convention on Wetlands (Ramsar, Iran, 1971), Proceedings of the 8th Meeting of the Conference of the Contracting Parties (Valencia, Spain, 18-26 November 2002). Resolution VIII.14: New Guidelines for management planning for Ramsar sites and other wetlands.

Conference of the Parties (COP), Convention on Wetlands (Ramsar, Iran, 1971), Proceedings of the 9th Meeting of the Conference of the Contracting Parties (Kampala, Uganda, 8-15 November 2005). DOC. 17: Rationale for the proposed changes to the Strategic Framework and guidelines for the selection of Ramsar sites.

Conference of the Parties (COP), Convention on Wetlands (Ramsar, Iran, 1971), Proceedings of the 9th Meeting of the Conference of the Contracting Parties (Kampala, Uganda, 8-15 November 2005). Resolution IX.1: Additional scientific and technical guidance for implementing the Ramsar wise use concept

Conference of the Parties (COP), Convention on Wetlands (Ramsar, Iran, 1971), Proceedings of the 9th Meeting of the Conference of the Contracting Parties (Kampala, Uganda, 8-15 November 2005). Resolution IX.1 Annex A: A Conceptual Framework for the wise use of wetlands and the maintenance of their ecological character

Conference of the Parties (COP), Convention on Wetlands (Ramsar, Iran, 1971), Proceedings of the 11th Meeting of the Conference of the Contracting Parties (Bucharest, Romania, 6-13 July 2012). DOC. 24: Limits of Acceptable Change - The definition and operation of concepts and approaches for “limits of acceptable change” which may be applicable to the Ramsar context of defining and detecting change in the ecological character of wetlands.

Conference of the Parties (COP), Convention on Wetlands (Ramsar, Iran, 1971), Proceedings of the 12th Meeting of the Conference of the Contracting Parties (Punta del Este, Uruguay, 1-9 June 2015). Resolution XII.2: The Ramsar Strategic Plan 2016-2024.

Connor, R. C., Heithaus, M. R. and Barre, L. M. 2001. Complex social structure, alliance stability and mating access in a bottlenose dolphin ‘super-alliance’. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268, 263-267.

Connor, R. C. and Krützen, M. 2015. Male dolphin alliances in Shark Bay: changing perspectives in a 30-year study. *Animal Behaviour*, 103, 223-235.

Connor, R. C., Richards, A. F., Smolker, R. A. and Mann, J. 1996. Patterns of Female Attractiveness in Indian Ocean Bottlenose Dolphins. *Behaviour*, 133, 37-69.

Connor, R. C., Smolker, R. A. and Richards, A. F. 1992. Two levels of alliance formation among male bottlenose dolphins (*Tursiops* sp.). *Proceedings of the National Academy of Sciences - PNAS*, 89, 987-990.

Connor, R. C., Watson-Capps, J. J., Sherwin, W. B. and Krützen, M. 2011. A new level of complexity in the male alliance networks of Indian Ocean bottlenose dolphins (*Tursiops* sp.). *Biology Letters*, 7, 623-626.

Connor, R. C., Wells, R. S., Mann, J. and Read, A. J. 2000. The bottlenose dolphin: Social relationships in a fission-fusion society. Pages 91-126 *in* J. Mann, R. C. Connor, P. L. Tyack and H. Whitehead eds. *Cetacean societies: Field studies of dolphins and whales.* The University of Chicago Press, Chicago.

Convention on Wetlands (Ramsar, Iran, 1971), Ramsar Information Paper no. 5: The criteria for identifying wetlands of international importance (1 January 2007).

Corkeron, P. J., Bryden, M. and Hedstrom, K. 1990. Feeding by bottlenose dolphins in association with trawling operations in Moreton Bay, Australia. Pages 329-336 in S. Leatherwood and R. R. Reeves eds. The bottlenose dolphin. Academic Press, Inc., San Diego, U.S.A.

Coulson, T., Mace, G. M., Hudson, E. and Possingham, H. 2001. The use and abuse of population viability analysis. *Trends in Ecology & Evolution*, 16, 219-221.

Cross, R. and Curran, M. 2000. Effects of feeding pit formation by rays on an intertidal meiobenthic community. *Estuarine, Coastal and Shelf Science*, 51, 293-298.

Cross, R. E. and Curran, M. C. 2004. Recovery of meiofauna in intertidal feeding pits created by rays. *Southeastern Naturalist*, 3, 219-230.

Darimont, C., Price, M., Winchester, N., Gordon-Walker, J. and Paquet, P. 2004. Predators in natural fragments: foraging ecology of wolves in British Columbia's central and north coast archipelago. *Journal of Biogeography*, 31, 1867-1877.

da Silva, V., Martin, A., Fettuccia, D., Bivaqua, L. and Trujillo, F. 2020. Sotalia fluviatilis. The IUCN Red List of Threatened Species 2020: e.T190871A50386457. https://dx.doi.org/10.2305/IUCN.UK.2020-3.RLTS.T190871A50386457.en. Downloaded on 28 March 2021.

da Silva, V., Trujillo, F., Martin, A., Zerbini, A.N., Crespo, E., Aliaga-Rossel, E. and Reeves, R. 2018. Inia geoffrensis. The IUCN Red List of Threatened Species 2018: e.T10831A50358152. https://dx.doi.org/10.2305/IUCN.UK.2018-2.RLTS.T10831A50358152.en. Downloaded on 28 March 2021.

de Lecea, A. M. and De Charmoy, L. 2015. Chemical lipid extraction or mathematical isotope correction models: should mathematical models be widely applied to marine species? *Rapid Communications in Mass Spectrometry*, 29, 2013-2025.

Deniro, M. J. and Epstein, S. 1978. Influence of diet on the distribution of carbon isotopes in animals. *Geochimica et Cosmochimica Acta*, 42, 495-506.

Department of the Environment and Energy (DEE). 2018. Australia’s Ramsar implementation plan 2016-2018. Implementation Plan for First Triennium of Ramsar Strategic Plan 2016-2024. Report against indicators. Australian Government Department of the Environment and Energy. Canberra, Australia.

Department of the Environment, Water, Heritage and the Arts (DEWHA). 2008. National frameworkand guidance for describing the ecological character of Australian Ramsar wetlands. Module 2 of the National Guidelines for Ramsar Wetlands - Implementing the Ramsar Convention in Australia. Australian Government Department of the Environment, Water, Heritage and the Arts, Canberra, Australia

Department od Sustainability, Environment, Water, Population and Communities (DSEWPC). 2013. National Guidance on the Management of Whale and Dolphin Incidents in Australian Waters. Canberra, Australia

Department of Water and Environmental Regulation (DWER). 2020. Bindjareb Djilba A plan for the protection of the Peel-Harvey estuary. Government of Western Australia.

Diaz-Aguirre, F., Parra, G. J., Passadore, C. and Möller, L. 2018. Kinship influences social bonds among male southern Australian bottlenose dolphins (Tursiops cf. australis). *Behavioral Ecology and Sociobiology*, 72, 190.

Diaz-Aguirre, F., Parra, G. J., Passadore, C. and Möller, L. 2020. Kinship and reproductive condition correlate with affiliation patterns in female southern Australian bottlenose dolphins. *Scientific Reports*, 10, 1891.

Dobson, F. S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behaviour*, 30, 1183-1192.

Donaldson, R., Finn, H. and Calver, M. 2010. Illegal feeding increases risk of boat-strike and entanglement in bottlenose dolphins in Perth, Western Australia. *Pacific Conservation Biology*, 16, 157-161.

East Gippsland Catchment Management Authority (EGCMA). 2015. Gippsland Lakes Ramsar Site Management Plan. Bairnsdale, Australia

Efron, B. and Stein, C. 1981. The Jackknife Estimate of Variance. *The Annals of Statistics*, 9, 586-596.

Elliott, M., Mander, L., Mazik, K., Simenstad, C., Valesini, F., Whitfield, A. and Wolanski, E. 2016. Ecoengineering with ecohydrology: successes and failures in estuarine restoration. *Estuarine, Coastal and Shelf Science*, 176, 12-35.

Elton, C. 1927. Animal ecology: London. *Sidgwick and Jackson, Ltd*,

Emlen, S. T. 1976. Lek organization and mating strategies in the bullfrog. *Behavioral Ecology and Sociobiology*, 1, 283-313.

Epanechnikov, V. A. 1969. Non-parametric estimation of a multivariate probability density. *Theory of Probability & Its Applications*, 14, 153-158.

Ermak, J., Brightwell, K. and Gibson, Q. 2017. Multi-level dolphin alliances in northeastern Florida offer comparative insight into pressures shaping alliance formation. *Journal of Mammalogy,* 98, 1096-1104.

Erwin, K. L. 2009. Wetlands and global climate change: the role of wetland restoration in a changing world. *Wetlands Ecology and Management,* 17, 71.

Estes, J. A. and Duggins, D. O. 1995. Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecological Monographs,* 65, 75-100.

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., . . . Jackson, J. B. 2011. Trophic downgrading of planet Earth. *science,* 333, 301-306.

Estes, J. A., Tinker, M. T., Williams, T. M. and Doak, D. F. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *science,* 282, 473-476.

Farine, D. R., Montiglio, P.-O. and Spiegel, O. 2015. From individuals to groups and back: the evolutionary implications of group phenotypic composition. *Trends in Ecology & Evolution,* 30, 609-621.

Findlay, R. H., Trexler, M. B., Guckert, J. B. and White, D. C. 1990a. Laboratory study of disturbance in marine sediments: response of a microbial community. *Marine ecology progress series. Oldendorf,* 62, 121-133.

Findlay, R. H., Trexler, M. B. and White, D. C. 1990b. Response of a benthic microbial community to biotic disturbance. *Marine ecology progress series. Oldendorf,* 62, 135-148.

Finlayson, C., Davis, J. A., Gell, P. A., Kingsford, R. and Parton, K. 2013. The status of wetlands and the predicted effects of global climate change: the situation in Australia. *Aquatic Sciences*, 75, 73-93.

Finn, H., Donaldson, R. and Calver, M. 2008. Feeding flipper: a case study of a humandolphin interaction. *Pacific Conservation Biology*, 14, 215-225.

Fire, S. E., Wang, Z., Byrd, M., Whitehead, H. R., Paternoster, J. and Morton, S. L. 2011. Co-occurrence of multiple classes of harmful algal toxins in bottlenose dolphins (*Tursiops truncatus*) stranding during an unusual mortality event in Texas, USA. *Harmful Algae*, 10, 330-336.

Flewelling, L. J., Naar, J. P., Abbott, J. P., Baden, D. G., Barros, N. B., Bossart, G. D., . . . Heil, C. A. 2005. Red tides and marine mammal mortalities. *Nature,* 435, 755-756.

Frère, C. H., Krützen, M., Kopps, A. M., Ward, P., Mann, J. and Sherwin, W. B. 2010a. Inbreeding tolerance and fitness costs in wild bottlenose dolphins. *Proceedings of the Royal Society B: Biological Sciences*, 277, 2667-2673.

Frère, C. H., Krützen, M., Mann, J., Connor, R. C., Bejder, L. and Sherwin, W. B. 2010b. Social and genetic interactions drive fitness variation in a free-living dolphin population. *Proceedings of the national academy of sciences*, 107, 19949-19954.

Froese, R. and Pauly, D. 2019. Fishbase. www.fishbase.in. Retrieved,

Fry, B. 2006. Stable isotope ecology. Springer.

Fury, C. A. and Harrison, P. L. 2008. Abundance, site fidelity and range patterns of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in two Australian subtropical estuaries. *Marine and Freshwater Research*, 59, 1015-1027.

Galezo, A. A., Foroughirad, V., Krzyszczyk, E., Frère, C. H. and Mann, J. 2020. Juvenile social dynamics reflect adult reproductive strategies in bottlenose dolphins. *Behavioral Ecology*, 31, 1159–1171.

Gardner, R. C. and Finlayson, C. 2018. Global wetland outlook: state of the World’s wetlands and their services to people. Ramsar Convention Secretariat.

Gaughan, D., Molony, B. and Santoro, K. 2019. Status Reports of the Fisheries and Aquatic Resources of Western Australia 2017/18: The State of the Fisheries. *Department of Primary Industries and Regional Development, Western Australia*,

Gelman, A., Carlin, J. B., Stern, H. S., Dunson, D. B., Vehtari, A. and Rubin, D. B. 2013. Bayesian data analysis. CRC press.

Genov, T., Centrih, T., Kotnjek, P. and Hace, A. 2019. Behavioural and temporal partitioning of dolphin social groups in the northern Adriatic Sea. *Marine Biology*, 166, 11.

Genoves, R. C., Fruet, P. F., Di Tullio, J. C., Möller, L. M. and Secchi, E. R. 2018. Spatiotemporal use predicts social partitioning of bottlenose dolphins with strong home range overlap. *Ecology and Evolution*, 8, 12597-12614.

Gerber, L., Connor, R. C., King, S. L., Allen, S. J., Wittwer, S., Bizzozzero, M. R., . . . Krützen, M. 2019. Affiliation history and age similarity predict alliance formation in adult male bottlenose dolphins. *Behavioral Ecology*, 31, 361-370.

Gero, S., Bejder, L., Whitehead, H., Mann, J. and Connor, R. C. 2005. Behaviourally specific preferred associations in bottlenose dolphins, *Tursiops* spp. *Canadian Journal of Zoology*, 83, 1566-1573.

Gerrodette, T. 1996. A comparison of mortality limits for eastern tropical Pacific dolphins under the Declaration of Panama and under potential biological removal (PBR) management. *Southwest Fisheries Science Center Administrative Report*, LJ-96–18,

Chilvers, L.B. and Corkeron, P. J. 2001. Trawling and bottlenose dolphins' social structure. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 268, 1901-1905.

Gibbs, M. 2011. An Aboriginal fish trap on the Swan Coastal Plain: the Barragup mungah. *Records of the Western Australian Museum*, 004,

Gibbs, S. E., Harcourt, R. G. and Kemper, C. M. 2011. Niche differentiation of bottlenose dolphin species in South Australia revealed by stable isotopes and stomach contents. *Wildlife Research*, 38, 261-270.

Giménez, J., Louis, M., Barón, E., Ramírez, F., Verborgh, P., Gauffier, P., . . . G. Forero, M. 2018. Towards the identification of ecological management units: A multidisciplinary approach for the effective management of bottlenose dolphins in the southern Iberian Peninsula. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 28, 205-215.

Giménez, J., Ramírez, F., Almunia, J., Forero, M. G. and De Stephanis, R. 2016. From the pool to the sea: Applicable isotope turnover rates and diet to skin discrimination factors for bottlenose dolphins (*Tursiops truncatus*). *Journal of Experimental Marine Biology and Ecology*, 475, 54-61.

Gomon, M. F., Bray, D. J. and Kuiter, R. H. 2008. Fishes of Australia's southern coast. New Holland Chatswood, Australia.

Gowans, S. and Whitehead, H. 2001. Photographic identification of northern bottlenose whales (*Hyperoodon ampullatus*): Sources of heterogeneity from natural marks. *Marine Mammal Science*, 17, 76-93.

Grinell, J. 1917. The niche relationship of California. *Thrsher Auk*, 1, 64-82.

Groom, C. and Coughran, D. 2012. Three decades of cetacean strandings in Western Australia: 1981 to 2010. *Journal of the Royal Society of Western Australia*, 95, 63.

Gubbins, C. 2002. Association patterns of resident bottlenose dolphins (*Tursiops truncatus*) in a South Carolina estuary. *Aquatic Mammals*, 28, 24-31.

Gunter, G. 1942. Contributions to the natural history of the bottlenose dolphin, *Tursiops truncatus* (Montague), on the Texas coast, with particular reference to food habits. *Journal of Mammalogy*, 23, 267-276.

Hale, J. and Butcher, R. 2007. Ecological Character Description of the Peel-Yalgorup Ramsar Site. *Report to the Department of Environment and Conservation and the Peel-Harvey Catchment Council, Perth, Western Australia*,

Hale, J. and Kobryn, H. 2009. Peel-Yalgorup Ramsar wetlands monitoring: littoral & fringing vegetation mapping. *A report to Department of Environment and Conservation, Western Australia*,

Hallett, C., Valesini, F. and Yeoh, D. 2019. Assessing the health of the Peel-Harvey Estuary through its fish communities. *ARC Linkage Project LP150100451. Unpublished report, Murdoch University, Western Australia*,

Hallett, C. S., Hobday, A. J., Tweedley, J. R., Thompson, P. A., Mcmahon, K. and Valesini, F. J. 2018. Observed and predicted impacts of climate change on the estuaries of south-western Australia, a Mediterranean climate region. *Regional Environmental Change*, 18, 1357-1373.

Hansen, B. D., Fuller, R. A., Watkins, D., Rogers, D. I., Clemens, R. S., Newman, M., . . . Weller, D. R. 2016. Revision of the East Asian-Australasian Flyway population estimates for 37 listed migratory shorebird species. *Unpublished report for the Department of the Environment. BirdLife Australia, Melbourne*,

Harzen, S. 1998. Habitat use by the bottlenosed dolphin (*Tursiops truncatus*) in the Sado Estuary, Portugal. *Aquatic Mammals*, 24, 117-128.

Hastie, G. D., Wilson, B. and Thompson, P. M. 2003. Fine-scale habitat selection by coastal bottlenose dolphins: application of a new land-based video-montage technique. *Canadian Journal of Zoology*, 81, 469-478.

Hastie, G. D., Wilson, B., Wilson, L., Parsons, K. and Thompson, P. M. 2004. Functional mechanisms underlying cetacean distribution patterns: hotspots for bottlenose dolphins are linked to foraging. *Marine Biology*, 144, 397-403.

Hawkins, E. R., Harcourt, R., Bejder, L., Brooks, L. O., Grech, A., Christiansen, F., . . . Harrison, P. L. 2017. Best practice framework and principles for monitoring the effect of coastal development on marine mammals. *Frontiers in Marine Science*, 4, 59.

Hedrick, P. W. and Kalinowski, S. T. 2000. Inbreeding depression in conservation biology. *Annual Review of Ecology and Systematics*, 31, 139-162.

Heimlich-Boran, J. R. 1988. Behavioral ecology of killer whales (Orcinus orca) in the Pacific Northwest. *Canadian Journal of Zoology*, 66, 565-578.

Heithaus, M. R. and Dill, L. M. 2002. Food Availability and Tiger Shark Predation Risk Influence Bottlenose Dolphin Habitat Use. *Ecology*, 83, 480-491.

Hinde, R. A. 1976. Interactions, relationships and social structure. *Man*, 1-17.

Hindell, J. S., Jenkins, G. P. and Keough, M. J. 2000. Evaluating the impact of predation by fish on the assemblage structure of fishes associated with seagrass (Heterozostera tasmanica)(Martens ex Ascherson) den Hartog and unvegetated sand habitats. *Journal of Experimental Marine Biology and Ecology*, 255, 153-174.

Hohn, A. A., Scott, M. D., Wells, R. S., Sweeney, J. C. and Irvine, A. B. 1989. Growth layers in teeth from known-age, free-ranging bottlenose dolphins. *Marine Mammal Science*, 5, 315-342.

Holyoake, C., Finn, H., Stephens, N., Linke, T., Daniel, C., Allen , S., . . . Bejder, L. 2011. Toxicant exposure, population genetics and trophic associations of bottlnose dolphins (*Tursiops aduncus*) in the Swan River. Murdoch University Cetacean Research Unit, Murdoch University. pp.

Huisman, J. and Twomey, L. 2008. The black Swan: investigating the estuary after dark. *Landscope*, 23, 46-51.

Hutchinson, G. E. 1957. Cold spring harbor symposium on quantitative biology. *Concluding remarks*, 22, 415-427.

Jansen, V. A. and Yoshimura, J. 1998. Populations can persist in an environment consisting of sink habitats only. Proceedings of the National Academy of Sciences of the United States of America, 95, 3696-3698.

Jedensjö, M., Kemper, C. M. & Krützen, M. (2017). Cranial morphology and taxonomic resolution of some dolphin taxa (*Delphinidae*) in Australian waters, with a focus on the genus *Tursiops*. *Marine Mammal Science*, 33, 187-205.

Junk, W. J., An, S., Finlayson, C., Gopal, B., Květ, J., Mitchell, S. A., . . . Robarts, R. D. 2013. Current state of knowledge regarding the world's wetlands and their future under global climate change: a synthesis. *Aquatic Sciences*, 75, 151-167.

Katona, S. and Whitehead, H. 1988. Are cetacea ecologically important. *Oceanogr Mar Biol Annu Rev,* 26, 553-568.

Keller, L. F. and Waller, D. M. 2002. Inbreeding effects in wild populations. *Trends in Ecology & Evolution,* 17, 230-241.

Kellogg, Brown and Root. 2010. Western Port Ramsar wetland ecological character description. Report for Australian Government Department of Sustainability, Environment, Water, Population and Communities. Canberra, Australia.

Kemper, C., Talamonti, M., Bossley, M. and Steiner, A. 2019. Sexual maturity and estimated fecundity in female Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) from South Australia: Combining field observations and postmortem results. *Marine Mammal Science,* 35, 40-57.

Kemper, C., Tomo, I., Bingham, J., Bastianello, S., Wang, J., Gibbs, S., . . . Kelly, D. 2016. Morbillivirus-associated unusual mortality event in South Australian bottlenose dolphins is largest reported for the Southern Hemisphere. *Royal Society open science,* 3, 160838.

Kendall, W. L. and Nichols, J. D. 1995. On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics*, 22, 751-762.

Kendall, W. L., Nichols, J. D. and Hines, J. E. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology*, 78, 563-578.

Kendall, W. L., Pollock, K. H. and Brownie, C. 1995. A likelihood-based approach to capture-recapture estimation of demographic parameters under the robust design. *Biometrics,* 51, 293-308.

Kiszka, J., Simon-Bouhet, B., Gastebois, C., Pusineri, C. and Ridoux, V. 2012. Habitat partitioning and fine scale population structure among insular bottlenose dolphins (*Tursiops aduncus*) in a tropical lagoon. *Journal of Experimental Marine Biology and Ecology,* 416, 176-184.

Kogi, K., Hishii, T., Imamura, A., Iwatani, T. and Dudzinski, K. M. 2004. Demographic parameters of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around Mikura Island, Japan. *Marine Mammal Science,* 20, 510-526.

Kopps, A. M., Ackermann, C. Y., Sherwin, W. B., Allen, S. J., Bejder, L. and Krützen, M. 2014. Cultural transmission of tool use combined with habitat specializations leads to fine-scale genetic structure in bottlenose dolphins. Proceedings of the Royal Society B: Biological Sciences, 281, 20133245

Krumholz, O. 2019. Macrophyte communities in the Peel-Harvey Estuary: Historical trends and current patterns in biomass and distribution. Masters thesis. Murdoch University.

Krützen, M., Barré, L. M., Connor, R. C., Mann, J. and Sherwin, W. B. 2004a. 'O father: where art thou?'—Paternity assessment in an open fission–fusion society of wild bottlenose dolphins (Tursiops sp.) in Shark Bay, Western Australia. *Molecular Ecology*, 13, 1975-1990.

Krützen, M., Barré, L. M., Möller, L. M., Heithaus, M. R., Simms, C. and Sherwin, W. B. 2002. A biopsy system for small cetaceans: Darting success and wound healing in Tursiops spp. *Marine Mammal Science*, 18, 863-878.

Krützen, M., Kreicker, S., Macleod, C. D., Learmonth, J., Kopps, A. M., Walsham, P. and Allen, S. J. 2014. Cultural transmission of tool use by Indo-Pacific bottlenose dolphins (Tursiops sp.) provides access to a novel foraging niche. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20140374.

Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L., Sherwin, W. B. and Marler, P. 2005. Cultural Transmission of Tool Use in Bottlenose Dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 8939-8943.

Krützen, M., Sherwin, W. B., Berggren, P. and Gales, N. 2004b. Population structure in an inshore cetacean revealed by microsatellite and mtDNA analysis: Bottlenose dolphins (*Tursiops* sp.) in Shark Bay, Western Australia. *Marine Mammal Science*, 20, 28-47.

Krzyszczyk, E., Patterson, E. M., Stanton, M. A. and Mann, J. 2017. The transition to independence: sex differences in social and behavioural development of wild bottlenose dolphins. *Animal Behaviour*, 129, 43-59.

Lacy, R., Miller, P. and Traylor-Holzer, K. 2017. Vortex 10 user's Manual. 6 September 2017 update. *IUCN SSC Conservation Breeding Specialist Group and Chicago Zoological Society, Apple Valley, MN, USA*,

Lacy, R. and Pollak, J. 2017. Vortex: a stochastic simulation of the extinction process. Ver. 10.2. 17.0. *Chicago Zoological Society, Brookfield, IL, USA*,

Lacy, R. C. 1993. VORTEX: a computer simulation model for population viability analysis. *Wildlife Research*, 20, 45-65.

Lacy, R. C. 2000. Structure of the VORTEX simulation model for population viability analysis. *Ecological Bulletins*, 48, 191-203.

Laundré, J. W., Hernández, L. and Ripple, W. J. 2010. The landscape of fear: ecological implications of being afraid. *The Open Ecology Journal*, 3,

Lee Long, W. J. and O'reilly, W. K. 2009. Ecological character description for the Great Sandy Strait Ramsar site, July 2008, Report for the Environmental Protection Agency. pp. 171

Lefebvre, K. A., Powell, C. L., Busman, M., Doucette, G. J., Moeller, P. D., Silver, J. B., . . . Silver, M. W. 1999. Detection of domoic acid in northern anchovies and California sea lions associated with an unusual mortality event. *Natural Toxins*, 7, 85-92.

Leibold, M. A. 1995. The niche concept revisited: mechanistic models and community context. *Ecology*, 76, 1371-1382.

Leopold, A. 1943. Deer irruptions. Wis. Conserv. *Bull.(reprinted in Wis. Conserv. Dept. Publ. 321: 1–11),*

Lidicker, W. 1975. The role of dispersal in the demography of small mammals. Pages 103-128 *in* K. Petrusewicz, E. B. Golley and L. Ryszkowski eds. *Small mammals: productivity and dynamics of populations.* Cambridge University Press, London, U.K.

Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience*, 48, 25-34.

Lima, S. L. and Dill, L. M. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68, 619-640.

Logan, J. M., Jardine, T. D., Miller, T. J., Bunn, S. E., Cunjak, R. A. and Lutcavage, M. E. 2008. Lipid corrections in carbon and nitrogen stable isotope analyses: comparison of chemical extraction and modelling methods. *Journal of Animal Ecology*, 838-846.

Loneragan, N., Potter, I. and Lenanton, R. 1989. Influence of site, season and year on contributions made by marine, estuarine, diadromous and freshwater species to the fish fauna of a temperate Australian estuary. *Marine Biology*, 103, 461-479.

Loneragan, N., Potter, I., Lenanton, R. and Caputi, N. 1986. Spatial and seasonal differences in the fish fauna in the shallows of a large Australian estuary. *Marine Biology*, 92, 575-586.

Loneragan, N., Potter, I., Lenanton, R. and Caputi, N. 1987. Influence of environmental variables on the fish fauna of the deeper waters of a large Australian estuary. *Marine Biology*, 94, 631-641.

Lorrain, A., Graham, B. S., Popp, B. N., Allain, V., Olson, R. J., Hunt, B. P. V., . . . Ménard, F. 2015. Nitrogen isotopic baselines and implications for estimating foraging habitat and trophic position of yellowfin tuna in the Indian and Pacific Oceans. *Deep Sea Research Part II: Topical Studies in Oceanography*, 113, 188-198.

Lusseau, D. 2007. Why Are Male Social Relationships Complex in the Doubtful Sound Bottlenose Dolphin Population? *PLOS ONE*, 2, e348.

Lusseau, D., Schneider, K., Boisseau, O. J., Haase, P., Slooten, E. and Dawson, S. M. 2003. The bottlenose dolphin community of Doubtful Sound features a large proportion of long-lasting associations. *Behavioral Ecology and Sociobiology*, 54, 396-405.

Macarthur, R. H. and Pianka, E. R. 1966. On optimal use of a patchy environment. *The American Naturalist*, 100, 603-609.

Manlik, O., Mcdonald, J. A., Mann, J., Raudino, H. C., Bejder, L., Krützen, M., . . . Sherwin, W. B. 2016. The relative importance of reproduction and survival for the conservation of two dolphin populations. *Ecology and Evolution*, 6, 3496-3512.

Mann, J. 1999. Behavioral sampling methods for cetaceans: A review and critique. *Marine Mammal Science*, 15, 102-122.

Mann, J., Connor, R. C., Barre, L. M. and Heithaus, M. R. 2000. Female reproductive success in bottlenose dolphins (Tursiops sp.): life history, habitat, provisioning and group-size effects. *Behavioral Ecology*, 11, 210-219.

Mann, J. and Sargeant, B. 2003. Like mother, like calf: The ontogeny of foraging traditions in wild Indian Ocean bottlenose dolphins (*Tursiops* sp.). Pages 236-266 *in* D. M. Fragaszy and S. Perry eds. *The biology of traditions : models and evidence.* Cambridge University Press, Cambridge, UK ; New York.

Mann, J., Smolker, R. A. and Smuts, B. B. 1995. Responses to calf entanglement in free-ranging bottlenose dolphins. *Marine Mammal Science*, 11, 100-106.

Marks, W., Burton, S., Stratton, E., Zolman, E., Biedenbach, G. and Page-Karjian, A. 2020. A case study of monofilament line entanglement in a common bottlenose dolphin (*Tursiops truncatus*): entanglement, disentanglement and subsequent death. *BMC Veterinary Research*, 16, 1-7.

Martin, M. J., Gridley, T., Roux, J.-P. and Elwen, S. H. 2020. First abundance estimates of Heaviside's (Cephalorhynchus heavisidii) and dusky (Lagenorhynchus obscurus) dolphins off Namibia using a novel visual and acoustic line transect survey. *Frontiers in Marine Science*, 7, 800.

Matich, P. and Heithaus, M. R. 2014. Multi-tissue stable isotope analysis and acoustic telemetry reveal seasonal variability in the trophic interactions of juvenile bull sharks in a coastal estuary. *Journal of Animal Ecology*, 199-213.

McCabe, E. J. B., Gannon, D. P., Barros, N. B. and Wells, R. S. 2010. Prey selection by resident common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Marine Biology*, 157, 931-942.

McCluskey, S., Sprogis, K., London, J., Bejder, L. and Loneragan, N. 2020. Foraging preferences of an apex marine predator revealed through stomach content and stable isotope analyses. *Global Ecology and Conservation*, e01396.

McCluskey, S. M., Bejder, L. and Loneragan, N. R. 2016. Dolphin prey availability and calorific value in an estuarine and coastal environment. *Frontiers in Marine Science*, 3, 30.

McHugh, K. A., Barleycorn, A. A., Allen, J. B., Bassos-Hull, K., Lovewell, G., Boyd, D., . . . Mase, B. 2021. Staying Alive: Long-term success of bottlenose dolphin interventions in southwest Florida. *Frontiers in Marine Science*.

McLoughlin, P. D., Boyce, M. S., Coulson, T. and Clutton-Brock, T. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. *Proceedings of the Royal Society B: Biological Sciences*, 273, 1449-1454.

McLoughlin, P. D., Morris, D. W., Fortin, D., Vander Wal, E. and Contasti, A. L. 2010. Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology*, 79, 4-12.

Mead, J. and Potter, C. 1990. Natural history of bottle nose dolphins along the central Atlantic coast of the United States. Pp: 165-195. *The bottle nose dolphin (S Leatherwood and RR Reeves, eds.). Academic Press, San Diego, CA,*

Methion, S. and Díaz López, B. 2018. Abundance and demographic parameters of bottlenose dolphins in a highly affected coastal ecosystem. *Marine and Freshwater Research*, 69, 1355-1364.

Miketa, M. L., Krzyszczyk, E. and Mann, J. 2017. Behavioral responses to fishing line entanglement of a juvenile bottlenose dolphin in Shark Bay, Australia. *Matters*, 3, e201711000011.

Möller, L., Allen , S. and Harcourt , R. 2002. Group Characteristics, Site Fidelity And Seasonal Abundance Of Bottlenosed Dolphins (*Tursiops aduncus*) In Jervis Bay And Port Stephens, South-Eastern Australia. *Australian mammalogy*, 24, 11-22.

Möller, L. M. and Beheregaray, L. B. 2004. Genetic evidence for sex-biased dispersal in resident bottlenose dolphins (*Tursiops aduncus*). *Molecular Ecology*, 13, 1607-1612.

Möller, L. M. and Harcourt, R. G. 2008. Shared Reproductive State Enhances Female Associations in Dolphins. *Research Letters in Ecology*, 498390, 1-5.

Moore, E., Lyday, S., Roletto, J., Litle, K., Parrish, J. K., Nevins, H., . . . Piazza, M. 2009. Entanglements of marine mammals and seabirds in central California and the north-west coast of the United States 2001–2005. *Marine Pollution Bulletin*, 58, 1045-1051.

Moritz, C. 1994. Defining ‘Evolutionarily Significant Units’ for conservation. *Trends in Ecology & Evolution*, 9, 373-375.

Morosinotto, C., Thomson, R. L. and Korpimäki, E. 2010. Habitat selection as an antipredator behaviour in a multi-predator landscape: all enemies are not equal. *Journal of Animal Ecology*, 79, 327-333.

Nel, S., Potter, I. and Loneragan, N. 1985. The biology of the catfish Cnidoglanis macrocephalus (Plotosidae) in an Australian estuary. *Estuarine, Coastal and Shelf Science,* 21, 895-909.

Nerini, M. 1984. A review of gray whale feeding ecology. *The gray whale, Eschrichtius robustus,* 423-450.

Newman, M. E. 2004. Analysis of weighted networks. *Physical review E*, 70, 056131.

Newman, M. E. 2006. Modularity and community structure in networks. *Proceedings of the national academy of sciences*, 103, 8577-8582.

Newsome, S. D., Chivers, S. J. and Berman Kowalewski, M. 2018. The influence of lipid-extraction and long-term DMSO preservation on carbon (δ^{13}C) and nitrogen (δ^{15}N) isotope values in cetacean skin. *Marine Mammal Science*, 34, 277-293.

Newsome, S. D., Etnier, M. A., Gifford-Gonzalez, D., Phillips, D. L., Van Tuinen, M., Hadly, E. A., . . . Koch, P. L. 2007a. The shifting baseline of northern fur seal ecology in the northeast Pacific Ocean. *Proceedings of the national academy of sciences*, 104, 9709-9714.

Newsome, S. D., Koch, P. L., Etnier, M. A. and Aurioles-Gamboa, D. 2006. Using carbon and nitrogen isotope values to investigate maternal strategies in northeast Pacific otariids. *Marine Mammal Science*, 22, 556-572.

Newsome, S. D., Martinez Del Rio, C., Bearhop, S. and Phillips, D. L. 2007b. A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, 5, 429-436.

Newsome, S. D., Yeakel, J. D., Wheatley, P. V. and Tinker, M. T. 2012. Tools for quantifying isotopic niche space and dietary variation at the individual and population level. *Journal of Mammalogy*, 93, 329-341.

Nicholson, K., Bejder, L., Allen, S. J., Krützen, M. and Pollock, K. H. 2012. Abundance, survival and temporary emigration of bottlenose dolphins (Tursiops sp.) off Useless Loop in the western gulf of Shark Bay, Western Australia. *Marine and Freshwater Research*, 63, 1059-1068.

Nicholson, K., H. Finn, N. Loneragan and L. Bejder. 2019. Thirty years of records highlight an Australian stranding hotspot for a resident community of Indo-Pacific bottlenose dolphin within a microtidal estuary. Oral presentation. World Marine Mammal Conference, Spain, 9-12 December 2019

Obregón, C., Tweedley, J. R., Loneragan, N. R. and Hughes, M. 2020. Different but not opposed: perceptions between fishing sectors on the status and management of a crab fishery. *ICES Journal of Marine Science*, 77, 2354-2368.

Oliver, J. S., Kvitek, R. G. and Slattery, P. N. 1985. Walrus feeding disturbance: scavenging habits and recolonization of the Bering Sea benthos. *Journal of Experimental Marine Biology and Ecology*, 91, 233-246.

Oliver, J. S. and Slattery, P. N. 1985. Destruction and opportunity on the sea floor: effects of gray whale feeding. *Ecology*, 66, 1965-1975.

Ostfeld, R. S. 1986. Territoriality and mating system of California voles. *The Journal of Animal Ecology*, 691-706.

Owen, E. C. G. 2003. The reproductive and ecological functions of the pair-bond between allied, adult male bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida.

Owen, E. C. G., Wells, R. S. and Hofmann, S. 2002. Ranging and association patterns of paired and unpaired adult male Atlantic bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative male strategies. *Canadian Journal of Zoology*, 80, 2072-2089.

Palmer, C., Brooks, L., Parra, G. J., Rogers, T., Glasgow, D. and Woinarski, J. C. Z. 2014. Estimates of abundance and apparent survival of coastal dolphins in Port Essington harbour, Northern Territory, Australia. *Wildlife Research*, 41, 35-45.

Palsbøll, P. J., Bérubé, M. and Allendorf, F. W. 2007. Identification of management units using population genetic data. *Trends in Ecology & Evolution*, 22, 11-16.

Parra, G. J. and Cagnazzi, D. 2016. Chapter seven - conservation status of the Australian humpback dolphin (Sousa sahulensis) Using the IUCN Red List criteria. Pages 157-192 *in* T. A. Jefferson and B. E. Curry eds. *Advances in Marine Biology.* Academic Press.

Parra, G., Cagnazzi, D., Perrin, W. and Braulik, G.T. 2017. Sousa sahulensis. The IUCN Red List of Threatened Species 2017: e.T82031667A82031671. https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T82031667A82031671.en. Downloaded on 28 March 2021

Parra, G. J., Corkeron, P. J. and Marsh, H. 2006. Population sizes, site fidelity and residence patterns of Australian snubfin and Indo-Pacific humpback dolphins: Implications for conservation. *Biological Conservation*, 129, 167-180.

Passadore, C., Möller, L., Diaz-Aguirre, F. and Parra, G. J. 2017. Demography of southern Australian bottlenose dolphins living in a protected inverse estuary. *Aquatic Conservation: Marine and Freshwater Ecosystems,* 27, 1186-1197.

Patterson, E. M. and Mann, J. 2011. The ecological conditions that favor tool use and innovation in wild bottlenose dolphins (Tursiops sp.). *PLOS ONE,* 6, e22243.

Pauly, D., Trites, A., Capuli, E. and Christensen, V. 1998. Diet composition and trophic levels of marine mammals. *ICES Journal of Marine Science,* 55, 467-481.

Peel-Harvey Catchment Council (PHCC). 2009. Peel-Yalgorup Ramsar site management plan, Peel-Harvey Catchment Council. Mandurah, Western Australia

Peel-Harvey Catchment Council (PHCC). 2017. Wetlands and people plan Peel Yalgorup System - A CEPA action plan for Ramsar site 482. A report by Andrew Del Marco and Amanda Willmott to the Peel-Harvey Catchment Council. Mandurah, Western Australia.

Phillips, D. L. 2012. Converting isotope values to diet composition: the use of mixing models. *Journal of Mammalogy*, 93, 342-352.

Pirotta, E., Harwood, J., Thompson, P. M., New, L., Cheney, B., Arso, M., . . . Lusseau, D. 2015. Predicting the effects of human developments on individual dolphins to understand potential long-term population consequences. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20152109.

Pirotta, E., Laesser, B. E., Hardaker, A., Riddoch, N., Marcoux, M. and Lusseau, D. 2013. Dredging displaces bottlenose dolphins from an urbanised foraging patch. *Marine Pollution Bulletin*, 74, 396-402.

Pleslić, G., Rako-Gospić, N., Miočić-Stošić, J., Blazinić Vučur, T., Radulović, M., Mackelworth, P., . . . Holcer, D. 2019. Social structure and spatial distribution of bottlenose dolphins (*Tursiops truncatus*) along the Croatian Adriatic coast. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29, 2116-2132.

Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *The Journal of wildlife management*, 46, 752-757.

Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. *Ecology*, 83, 703-718.

Potter, I., Loneragan, N., Lenanton, R., Chrystal, P. and Grant, C. 1983. Abundance, distribution and age structure offish populations in a Western Australian estuary. *Journal of Zoology*, 200, 21-50.

Potter, I. C., Veale, L., Tweedley, J. R. and Clarke, K. R. 2016. Decadal changes in the ichthyofauna of a eutrophic estuary following a remedial engineering modification and subsequent environmental shifts. *Estuarine, Coastal and Shelf Science*, 181, 345-363.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. The American Naturalist, 132, 652-661.

Radeloff, V. C., Williams, J. W., Bateman, B. L., Burke, K. D., Carter, S. K., Childress, E. S., . . . Kraemer, B. M. 2015. The rise of novelty in ecosystems. *Ecological Applications*, 25, 2051-2068.

Raeside, J. 2012. The ecology of the bottlenose dolphin (*Tursiops aduncus*) in the Peel-Harvey Estuary. Honours thesis. Murdoch University, Western Australia.

Ramsar Information Sheet (RIS). 1998. Peel-Yalgorup system, Australia. https://rsis.ramsar.org/ris/482

Ramsar Information Sheet (RIS). 2001. Indus Dolphin Reserve, Pakistan. https://rsis.ramsar.org/ris/1065

Ramsar Information Sheet (RIS). 2012. Río Yata, Bolivia. https://rsis.ramsar.org/ris/2094

Ramsar Information Sheet (RIS). 2013. Dong dongting hu, China. https://rsis.ramsar.org/ris/551

Ramsar Information Sheet (RIS). 2018. Complejo de humedales Lagos de Tarapoto, Colombia. https://rsis.ramsar.org/ris/2336

Raudino, H. C., Douglas, C. R. and Waples, K. A. 2018. How many dolphins live near a coastal development? *Regional Studies in Marine Science*, 19, 25-32.

Read, A. J., Urian, K. W., Wilson, B. and Waples, D. M. 2003. Abundance of bottlenose dolphins in the bays, sounds and estuaries of North Carolina. *Marine Mammal Science*, 19, 59-073.

Read, A. J. and Wade, P. R. 2000. Status of Marine Mammals in the United States. *Conservation Biology*, 14, 929-940.

Reeves, R. R. 2003. Dolphins, whales and porpoises: 2002-2010 conservation action plan for the world's cetaceans. IUCN.

Ripple, W. J. and Beschta, R. L. 2012. Trophic cascades in Yellowstone: the first 15 years after wolf reintroduction. *Biological Conservation*, 145, 205-213.

Ripple, W. J., Estes, J. A., Beschta, R. L., Wilmers, C. C., Ritchie, E. G., Hebblewhite, M., . . . Nelson, M. P. 2014. Status and ecological effects of the world’s largest carnivores. *science*, 343,

Roman, J. and Mccarthy, J. J. 2010. The whale pump: marine mammals enhance primary productivity in a coastal basin. *PLOS ONE*, 5, e13255.

Rosel, P. E., Hohn, A. A., Mullin, K., Garrison, L. P., Schwacke, L. H., Adams, J., . . . Eguchi, T. 2011. Photo-identification capture-mark-recapture techniques for estimating abundance of bay, sound and estuary populations of Bottlenose dolphins along the US East Coast and Gulf of Mexico, a workshop report.

Rossman, S., Ostrom, P. H., Stolen, M., Barros, N. B., Gandhi, H., Stricker, C. A. and Wells, R. S. 2015. Individual specialization in the foraging habits of female bottlenose dolphins living in a trophically diverse and habitat rich estuary. *Oecologia*, 178, 415-425.

Rowe, L. E. and Dawson, S. M. 2009. Determining the sex of bottlenose dolphins from Doubtful Sound using dorsal fin photographs. *Marine Mammal Science*, 25, 19-34.

Royle, J. A., Chandler, R. B., Sollmann, R. and Gardner, B. 2013. Spatial capture-recapture. Academic Press.

Saltz, J. B., Geiger, A. P. anderson, R., Johnson, B. and Marren, R. 2016. What, if anything, is a social niche? *Evolutionary Ecology*, 30, 349-364.

Sargeant, B., Wirsing, A., Heithaus, M. and Mann, J. 2007. Can environmental heterogeneity explain individual foraging variation in wild bottlenose dolphins (*Tursiops* sp.)? *Behavioral Ecology and Sociobiology*, 61, 679-688.

Sargeant, B. L., Mann, J., Berggren, P. and Krützen, M. 2005. Specialization and development of beach hunting, a rare foraging behavior, by wild bottlenose dolphins (Tursiops sp.). *Canadian Journal of Zoology*, 83, 1400-1410.

Schmitz, O. J. 2010. Resolving ecosystem complexity (MPB-47). Princeton University Press. Princeton, NJ, U.S.A.

Schumann, N., Gales, N. J., Harcourt, R. G. and Arnould, J. P. 2013. Impacts of climate change on Australian marine mammals. *Australian Journal of Zoology*, 61, 146-159.

Schwacke, L. H., Voit, E. O., Hansen, L. J., Wells, R. S., Mitchum, G. B., Hohn, A. A. and Fair, P. A. 2002. Probabilistic risk assessment of reproductive effects of polychlorinated biphenyls on bottlenose dolphins (*Tursiops truncatus*) from the Southeast United States coast. *Environmental Toxicology and Chemistry*, 21, 2752-2764.

Scott, M. D., Wells, R. S. and Irvine, A. B. 1990. A Long-Term Study of Bottlenose Dolphins on the West Coast of Florida. Pages 235-244 *in* S. Leatherwood and R. R. Randall eds. *The bottlenose dolphin.* Academic Press, San Diego, U.S.A.

Semmens, B. X., Ward, E. J., Moore, J. W. and Darimont, C. T. 2009. Quantifying inter-and intra-population niche variability using hierarchical Bayesian stable isotope mixing models. *PLOS ONE,* 4, e6187.

Senigaglia, V., Christiansen, F., Sprogis, K. R., Symons, J. and Bejder, L. 2019. Food-provisioning negatively affects calf survival and female reproductive success in bottlenose dolphins. *Scientific Reports*, 9, 8981.

Shane, S. H. 1990. Behavior and ecology of the bottlenose dolphin at Sanibel Island, Florida. Pages 245-265 in S. Leatherwood and R. R. Reeves eds. The bottlenose dolphin. Academic Press, Inc., San Diego, U.S.A.

Silk, J. B. 2007. The adaptive value of sociality in mammalian groups. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 362, 539-559.

Silliman, B. R., Hughes, B. B., Gaskins, L. C., He, Q., Tinker, M. T., Read, A., . . . Stepp, R. 2018. Are the ghosts of nature’s past haunting ecology today? *Current Biology,* 28, R532-R537.

Silva, M. A., Magalhaes, S., Prieto, R., Santos, R. S. and Hammond, P. S. 2009. Estimating survival and abundance in a bottlenose dolphin population taking into account transience and temporary emigration. *Marine Ecology Progress Series*, 392, 263-276.

Silverman, B. W. 1986. Density estimation for statistics and data analysis. CRC press.

Simmonds, M. P. and Isaac, S. J. 2007. The impacts of climate change on marine mammals: early signs of significant problems. *Oryx*, 41, 19-26.

Simões-Lopes, P. C., Fabián, M. E. and Menegheti, J. O. 1998. Dolphin interactions with the mullet artisanal fishing on southern Brazil: a qualitative and quantitative approach. *Revista Brasileira de Zoologia*, 15, 709-726.

Skrzypek, G. and Paul, D. 2006. δ^{13}C analyses of calcium carbonate: comparison between the GasBench and elemental analyzer techniques. *Rapid Communications in Mass Spectrometry: An International Journal Devoted to the Rapid Dissemination of Up-to-the-Minute Research in Mass Spectrometry*, 20, 2915-2920.

Slooten, E. and Davies, N. 2012. Hector's dolphin risk assessments: old and new analyses show consistent results. *Journal of the Royal Society of New Zealand*, 42, 49-60.

Smith, B. D., Ahmed, B., Ali, M. E. and Braulik, G. 2001. Status of the Ganges river dolphin or shushuk Platanista gangetica in Kaptai Lake and the southern rivers of Bangladesh. *Oryx*, 35, 61-72.

Smith, H., Frère, C., Kobryn, H. and Bejder, L. 2016. Dolphin sociality, distribution and calving as important behavioural patterns informing management. *Animal Conservation*, 19, 462-471.

Smith, H. and Sprogis, K. 2016. Seasonal feeding on giant cuttlefish (Sepia apama) by Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in south-western Australia. *Australian Journal of Zoology*, 64, 8-13.

Smith, H. C., Pollock, K., Waples, K., Bradley, S. and Bejder, L. 2013. Use of the Robust Design to Estimate Seasonal Abundance and Demographic Parameters of a Coastal Bottlenose Dolphin (*Tursiops aduncus*) Population. *PLOS ONE*, 8, e76574.

Smolker, R., Richards, A., Connor, R., Mann, J. and Berggren, P. 1997. Sponge carrying by dolphins (*Delphinidae*, *Tursiops* sp.): A foraging specialization involving tool use? *Ethology*, 103, 454-465.

Smolker, R. A., Richards, A. F., Connor, R. C. and Pepper, J. W. 1992. Sex differences in patterns of association among Indian Ocean bottlenose dolphins. *Behaviour*, 123, 38-69.

Sprogis, K. R., Christiansen, F., Wandres, M. and Bejder, L. 2018. El Niño Southern Oscillation influences the abundance and movements of a marine top predator in coastal waters. *Global Change Biology*, 24, 1085-1096.

Sprogis, K. R., Pollock, K. H., Raudino, H. C., Allen, S. J., Kopps, A. M., Manlik, O., . . . Bejder, L. 2016a. Sex-Specific Patterns in Abundance, Temporary Emigration and Survival of Indo-Pacific Bottlenose Dolphins (*Tursiops aduncus*) in Coastal and Estuarine Waters. *Frontiers in Marine Science*, 3.Original Research

Sprogis, K. R., Raudino, H. C., Hocking, D. and Bejder, L. 2017. Complex prey handling of octopus by bottlenose dolphins (*Tursiops aduncus*). *Marine Mammal Science*, 33, 934-945.

Sprogis, K. R., Raudino, H. C., Rankin, R., Macleod, C. D. and Bejder, L. 2016b. Home range size of adult Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in a coastal and estuarine system is habitat and sex-specific. *Marine Mammal Science*, 32, 287-308.

Stelfox, M., Hudgins, J. and Sweet, M. 2016. A review of ghost gear entanglement amongst marine mammals, reptiles and elasmobranchs. *Marine Pollution Bulletin*, 111, 6-17.

Stephens, N., Duignan, P. J., Wang, J., Bingham, J., Finn, H., Bejder, L., . . . Holyoake, C. 2014. Cetacean morbillivirus in coastal Indo-Pacific bottlenose dolphins, Western Australia. *Emerging Infectious Diseases*, 20, 666.

Stock, B., Semmens, B. and Mixsiar, G. 2016. User Manual. Version 3.1.

Stock, B. C., Jackson, A. L., Ward, E. J., Parnell, A. C., Phillips, D. L. and Semmens, B. X. 2018. Analyzing mixing systems using a new generation of Bayesian tracer mixing models. *PeerJ*, 6, e5096.

Stockin, K. A., Weir, C. R. and Pierce, G. J. 2006. Examining the importance of Aberdeenshire (UK) coastal waters for North Sea bottlenose dolphins

(*Tursiops truncatus*). Journal of the Marine Biological Association of the United Kingdom, 86, 201-207.

Stockwell, S. 2019. The foraging ecology of Caspian Terns (Hydroprogne caspia) on Peel-Harvey Estuary, south-western Australia. Murdoch University.

Stockwell, S., Greenwell, C., Dunlop, N. and Loneragan, N. 2021. Distribution and foraging by non-breeding Caspian Terns on a large temperate estuary of south-western Australia - preliminary investigations. *Pacific Conservation Biology*

Stolen, M. K. and Barlow, J. 2003. A model life table for bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon system, Florida, U.S.A. *Marine Mammal Science,* 19, 630-649.

Sueur, C., King, A. J., Conradt, L., Kerth, G., Lusseau, D., Mettke-Hofmann, C., . . . Aureli, F. 2011. Collective decision-making and fission–fusion dynamics: a conceptual framework. *Oikos*, 120, 1608-1617.

Svanbäck, R. and Bolnick, D. I. 2007. Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences*, 274, 839-844.

Symons, J., Sprogis, K. R. and Bejder, L. 2018. Implications of survey effort on estimating demographic parameters of a long-lived marine top predator. *Ecology and Evolution*, 8, 10470-10481.

Taylor, B. L. 1995. The reliability of using population viability analysis for risk classification of species. *Conservation Biology*, 9, 551-558.

Taylor, B. L. and Dizon, A. E. 1999. First policy then science: why a management unit based solely on genetic criteria cannot work. *Molecular Ecology*, 8, S11-S16.

Taylor, B. L. and Gerrodette, T. 1993. The uses of statistical power in conservation biology: the vaquita and northern spotted owl. *Conservation Biology*, 7, 489-500.

Taylor, B. L., Martinez, M., Gerrodette, T., Barlow, J. and Hrovat, Y. N. 2007. Lessons from monitoring trends in abundance of marine mammals. *Marine Mammal Science*, 23, 157-175.

Thomas, C. D. and Kunin, W. E. 1999. The spatial structure of populations. *Journal of Animal Ecology*, 68, 647-657.

Thomas, L., Buckland, S. T., Rexstad, E. A., Laake, J. L., Strindberg, S., Hedley, S. L., . . . Burnham, K. P. 2010. Distance software: design and analysis of distance sampling surveys for estimating population size. *Journal of Applied Ecology*, 47, 5-14.

Thompson, P. M., Wilson, B., Grellier, K. and Hammond, P. S. 2000. Combining power analysis and population viability analysis to compare traditional and precautionary approaches to conservation of coastal cetaceans. *Conservation Biology*, 14, 1253-1263.

Thomson, C. 2019. Regional Estuaries Initiative, Estuary Condition Report: Peel-Harvey 2016/17. *Department of Water and Enviromental Regulation, Western Australia*,

Titcomb, E. M., O'corry-Crowe, G., Hartel, E. F. and Mazzoil, M. S. 2015. Social communities and spatiotemporal dynamics of association patterns in estuarine bottlenose dolphins. *Marine Mammal Science*, 31, 1314-1337.

Tollit, D. J., Pierce, G. J., Hobson, K. A., Bowen, W. D. and Iverson, S. J. 2010. Diet. *in* I. L. Boyd, W. D. Bowen and S. J. Iverson eds. *Marine mammal ecology and conservation: a handbook of techniques*. Oxford University Press.

Torres, L. G. and Read, A. J. 2009. Where to catch a fish? The influence of foraging tactics on the ecology of bottlenose dolphins (*Tursiops truncatus*) in Florida Bay, Florida. *Marine Mammal Science*, 25, 797-815.Article

Trayler, K., Brothers, D., Wooller, R. and Potter, I. 1989. Opportunistic foraging by three species of cormorants in an Australian estuary. *Journal of Zoology*, 218, 87-98.

Troina, G. C., Botta, S., Dehairs, F., Di Tullio, J. C., Elskens, M. and Secchi, E. R. 2020. Skin δ^{13}C and δ^{15}N reveal spatial and temporal patterns of habitat and resource use by free-ranging odontocetes from the southwestern Atlantic Ocean. *Marine Biology*, 167, 186.

Tsai, Y.-J. J. and Mann, J. 2013. Dispersal, philopatry and the role of fission-fusion dynamics in bottlenose dolphins. *Marine Mammal Science*, 29, 261-279.

Tweedley, J. R., Warwick, R. M. and Potter, I. C. 2016. The contrasting ecology of temperate macrotidal and microtidal estuaries. CRC Press.

Twiner, M. J., Fire, S., Schwacke, L., Davidson, L., Wang, Z., Morton, S., . . . Wells, R. S. 2011. Concurrent exposure of bottlenose dolphins (*Tursiops truncatus*) to multiple algal toxins in Sarasota Bay, Florida, USA. *PLOS ONE*, 6, e17394.

Tyne, J. A., Loneragan, N. R., Johnston, D. W., Pollock, K. H., Williams, R. and Bejder, L. 2016. Evaluating monitoring methods for cetaceans. *Biological Conservation*, 201, 252-260.

Tyne, J. A., Pollock, K. H., Johnston, D. W. and Bejder, L. 2014. Abundance and survival rates of the Hawai'i Island associated spinner dolphin (Stenella longirostris) stock. *PLOS ONE*, 9, e86132.

Tyrrell, M., Link, J. and Moustahfid, H. 2011. The importance of including predation in fish population models: implications for biological reference points. *Fisheries Research*, 108, 1-8.

Urian, K., Gorgone, A., Read, A., Balmer, B., Wells, R. S., Berggren, P., . . . Hammond, P. S. 2015. Recommendations for photo-identification methods used in capture-recapture models with cetaceans. *Marine Mammal Science*, 31, 298-321.

Urian, K., Hohn, A. A. and Hansen, L. J. 1999. Status of te photo-identification catalog of coastal bottlenose dolphins of the western North Atlantic. Report of a workshop of catalog contributors. *NOAA Technical Memorandum NMFS-SEFSC*, 425,

Urian, K. W., Hofmann, S., Wells, R. S. and Read, A. J. 2009. Fine-scale population structure of bottlenose dolphins (*Tursiops truncatus*) in Tampa Bay, Florida. *Marine Mammal Science*, 25, 619-638.

Urian, K. W., Waples, D. M., Tyson, R. B., Hodge, L. E. and Read, A. J. 2014. Abundance of bottlenose dolphins (*Tursiops truncatus*) in estuarine and near-shore waters of North Carolina, USA. *Journal of North Carolina Academy of Science*, 129, 165-171.

Valesini, F., Coen, N., Wildsmith, M., Hourston, M., Tweedley, J., Hallett, C., . . . Potter, I. 2009. Relationships between fish faunas and habitat type in south-western Australian estuaries. Fisheries Research and Development Corporation Final Report, July 2009.

Valesini, F., Hallett, C., Hipsey, M., Kilminster, K., Huang, P. and Hennig, K. 2019. Peel-Harvey Estuary, Western Australia. Pages 103-120 *in* E. Wolanski, J. W. Day, M. Elliott and R. Ramachandran eds. *Coasts and Estuaries.* Elsevier, Oxford, U.K.

van Aswegen, M., Christiansen, F., Symons, J., Mann, J., Nicholson, K., Sprogis, K. and Bejder, L. 2019. Morphological differences between coastal bottlenose dolphin (*Tursiops aduncus*) populations identified using non-invasive stereo-laser photogrammetry. *Scientific Reports*, 9, 1-14.

Veale, L. J., Coulson, P. G., Hall, N. G. and Potter, I. C. 2016. Biology of a marine estuarine-opportunist fish species in a microtidal estuary, including comparisons among decades and with coastal waters. *Marine and Freshwater Research*, 67, 1128-1140.

Vidal, O., Barlow, J., Hurtado, L. A., Torre, J., Cendón, P. and Ojeda, Z. 1997. Distribution and abundance of the Amazon river dolphin (Inia geoffrensis) and the tucuxi (Sotalia fluviatilis) in the upper Amazon River. *Marine Mammal Science*, 13, 427-445.

Wade, P. R. 1998. Calculating limits to the allowable human-caused mortality of cetaceans and pinnipeds. *Marine Mammal Science*, 14, 1-37.

Wallen, M. M., Krzyszczyk, E. and Mann, J. 2017. Mating in a bisexually philopatric society: bottlenose dolphin females associate with adult males but not adult sons during estrous. *Behavioral Ecology and Sociobiology*, 71, 1-12.

Wang, J.Y. and Reeves, R. 2017. Neophocaena phocaenoides. The IUCN Red List of Threatened Species 2017: e.T198920A50386795. https://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T198920A50386795.en. Downloaded on 28 March 2021.

Watson, J.J. 2005. Female mating behavior in the context of sexual coercion and female ranging behavior of Bottlenose dolphins (Tursiops sp.) in Shark Bay, Western Australia. PhD thesis. Georgetown University, U.S.A.

Watson-Capps, J. J. and Mann, J. 2005. The effects of aquaculture on bottlenose dolphin (Tursiops sp.) ranging in Shark Bay, Western Australia. *Biological Conservation*, 124, 519-526.

Webber, Q. M. and Vander Wal, E. 2018. An evolutionary framework outlining the integration of individual social and spatial ecology. *Journal of Animal Ecology*, 87, 113-127.

Weir, L. K., Grant, J. W. A. and Hutchings, J. A. 2011. The influence of operational sex ratio on the intensity of competition for mates. *The American Naturalist*, 177, 167-176.

Weiss, M. N., Franks, D. W., Croft, D. P. and Whitehead, H. 2019. Measuring the complexity of social associations using mixture models. *Behavioral Ecology and Sociobiology*, 73, 8.

Wells, R. 2000. Reproduction in wild bottlenose dolphins: overview of patterns observed during a long-term study. Pages 57-74 in D. Duffield and T. Robeck eds. Bottlenose dolphins reproduction workshop report. AZA marine mammal taxon advisory group, Silver Springs

Wells, R. S. 1991. The role of long-term study in understanding the social structure of a bottlenose dolphin community. Pages 199-225 *in* K. Pryor and K. S. Norris eds. *Dolphin societies: Discoveries and puzzles.* University of California Press, Berkeley, U.S.A.

Wells, R. S. 2003. Dolphin social complexity: lessons from long-term study and life history. Pages 57-74 *in* F. B. M. De Waal and P. L. Tyack eds. *Animal social complexity: Intelligence, culture and individualized societies.* Harvard University Press, Cambridge, MA, U.S.A.

Wells, R. S. 2014. Social structure and life history of bottlenose dolphins near Sarasota Bay, Florida: insights from four decades and five generations. Pages 149-172 *in* J. Yamagiwa and L. Karczmarski eds. *Primates and cetaceans.* Springer, Tokyo, Japan.

Wells, R. S., Allen, J. B., Hofmann, S., Bassos-Hull, K., Fauquier, D. A., Barros, N. B., . . . Scott, M. D. 2008. Consequences of injuries on survival and reproduction of common bottlenose dolphins (*Tursiops truncatus*) along the west coast of Florida. *Marine Mammal Science*, 24, 774-794.

Wells, R. S., Fauquier, D. A., Gulland, F. M., Townsend, F. I. and Digiovanni Jr, R. A. 2013. Evaluating postintervention survival of free-ranging odontocete cetaceans. *Marine Mammal Science*, 29, 463-483.

Wells, R. S., Natoli, A. and Braulik, G. 2019. *Tursiops truncatus* (errata version published in 2019). *The IUCN Red List of Threatened Species 2019*, e.T22563A156932432,

Wells, R. S., Rhinehart, H. L., Hansen, L. J., Sweeney, J. C., Townsend, F. I., Stone, R., . . . Rowles, T. K. 2004. Bottlenose dolphins as marine ecosystem sentinels: developing a health monitoring system. *EcoHealth*, 1, 246-254.

Wells, R. S. and Scott, M. D. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-release techniques. *Reports of the International Whaling Commission*, 12, 407-415.

Wells, R. S. and Scott, M. D. 1997. Seasonal incidence of boat strikes on bottlenose dolphins near Sarasota, Florida. *Marine Mammal Science*, 13, 475-480.

Wells, R. S., Scott, M. D. and Irvine, A. B. 1987. The social structure of free-ranging bottlenose dolphins. Pages 247-305 *in* H. H. Genoways ed. *Current mammalogy*. Springer, Boston, MA, U.S.A.

Wells, R. S., Tornero, V., Borrell, A., Aguilar, A., Rowles, T. K., Rhinehart, H. L., . . . Sweeney, J. C. 2005. Integrating life-history and reproductive success data to examine potential relationships with organochlorine compounds for bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Science of the Total Environment*, 349, 106-119.

Whitehead, H. 1995. Investigating structure and temporal scale in social organizations using identified individuals. *Behavioral Ecology*, 6, 199-208.

Whitehead, H. 1999. Testing association patterns of social animals. *Animal Behaviour*, 57, F26-F29.

Whitehead, H. 2008a. Analyzing animal societies: quantitative methods for vertebrate social analysis. University of Chicago Press.

Whitehead, H. 2008b. Precision and power in the analysis of social structure using associations. *Animal Behaviour*, 75, 1093-1099.

Whitehead, H. 2009. SOCPROG programs: analysing animal social structures. *Behavioral Ecology and Sociobiology*, 63, 765-778.

Whitehead, H., Bejder, L. and Ottensmeyer, C. A. 2005. Testing association patterns: issues arising and extensions. *Animal Behaviour*, 69, e1.

Whitehead, H. and Connor, R. 2005. Alliances I. How large should alliances be? *Animal Behaviour*, 69, 117-126.

Whitehead, H. and Rendell, L. 2014. The cultural lives of whales and dolphins. University of Chicago Press. Chicago, U.S.A.

Whitfield, A., Panfili, J. and Durand, J.-D. 2012. A global review of the cosmopolitan flathead mullet Mugil cephalus Linnaeus 1758 (Teleostei: Mugilidae), with emphasis on the biology, genetics, ecology and fisheries aspects of this apparent species complex. *Reviews in Fish Biology and Fisheries*, 22, 641-681.

Wildsmith, M., Rose, T., Potter, I., Warwick, R., Clarke, K. and Valesini, F. 2009. Changes in the benthic macroinvertebrate fauna of a large microtidal estuary following extreme modifications aimed at reducing eutrophication. *Marine Pollution Bulletin*, 58, 1250-1262.

Williams, T. M., Estes, J. A., Doak, D. F. and Springer, A. M. 2004. Killer appetites: assessing the role of predators in ecological communities. *Ecology*, 85, 3373-3384.

Wilson, B., Thompson, P. and Hammond, P. 1997. Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology*, 1365-1374.

Wiszniewski, J., Allen, S. J. and Möller, L. M. 2009. Social cohesion in a hierarchically structured embayment population of Indo-Pacific bottlenose dolphins. *Animal Behaviour*, 77, 1449-1457.

Wiszniewski, J., Brown, C. and Möller, L. M. 2012. Complex patterns of male alliance formation in a dolphin social network. *Journal of Mammalogy*, 93, 239-250.

Woinarski, J., Burbidge, A. and Harrison, P. 2014. The action plan for Australian mammals 2012. CSIRO publishing, Collingwood, Australia.

Worton, B. J. 1989. Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, 70, 164-168.

Würsig, B. and Jefferson, T. A. 1990. Methods of photo-identification for small cetaceans. *Report of the International Whalling Commision, Special Issue*, 12, 43-52.

Würsig, B. and Würsig, M. 1977. The photographic determination of group size, composition and stability of coastal porpoises (*Tursiops truncatus*). *science*, 198, 755-756.

Yordy, J. E., Wells, R. S., Balmer, B. C., Schwacke, L. H., Rowles, T. K. and Kucklick, J. R. 2010. Life history as a source of variation for persistent organic pollutant (POP) patterns in a community of common bottlenose dolphins (*Tursiops truncatus*) resident to Sarasota Bay, FL. *Science of the Total Environment*, 408, 2163-2172.

Young, R. F. and Phillips, H. D. 2002. Primary production required to support bottlenose dolphins in a salt marsh estuarine creek system. *Marine Mammal Science*, 18, 358-373.

Zanardo, N., Parra, G. J. and Möller, L. M. 2016. Site fidelity, residency and abundance of bottlenose dolphins (Tursiops sp.) in Adelaide's coastal waters, South Australia. *Marine Mammal Science*, 32, 1381-1401.

Zanardo, N., Parra, G. J., Passadore, C. and Möller, L. M. 2017. Ensemble modelling of southern Australian bottlenose dolphin Tursiops sp. distribution reveals important habitats and their potential ecological function. *Marine Ecology Progress Series*, 569, 253-266.

Zhang, X., Wang, D., Liu, R., Wei, Z., Hua, Y., Wang, Y., . . . Wang, L. 2003. The Yangtze River dolphin or baiji (Lipotes vexillifer): population status and conservation issues in the Yangtze River, China. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 13, 51-64.

Zolman, E. S. 2002. Residence patterns of bottlenose dolphins (*Tursiops truncatus*) in the Stono River estuary, Charleston County, South Carolina, USA. *Marine Mammal Science*, 18, 879-892.

Appendix A

Table A.1. Results of post-hoc Dunn test to determine which Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) social communities/groups had significantly different mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotope values from each other. Stable isotope composition was measured in skin of dolphins sampled in the Peel-Harvey Estuary and adjacent coastal waters in Western Australia.

Dolphin community	**Carbon**			**Nitrogen**		
	Z-Score	**P unadjusted**	**P adjusted**	**Z-Score**	**P unadjusted**	**P adjusted**
Offshore - Peel-Harvey	-5.8534761	0.00	0.0000001	5.816383	0.00	0.0000001
Peel-Harvey - Shoalwater	3.6801435	0.00	0.0034965	-5.27592	0.00	0.0000020
Coastal unknown - Peel-Harvey	-5.7884553	0.00	0.0000001	4.891774	0.00	0.0000150
Dawesville Cut - Peel-Harvey	-4.8412292	0.00	0.0000194	4.673918	0.00	0.0000443
Comet Bay - Peel-Harvey	-3.8263372	0.00	0.0019510	4.328085	0.00	0.0002256
Dawesville Cut - Offshore	2.3687102	0.02	0.2677535	-2.44245	0.01	0.2188209
Comet Bay - Coastal unknown	0.8266401	0.41	1.0000000	0.251951	0.80	1.0000000
Comet Bay - Dawesville Cut	-0.3040632	0.76	1.0000000	0.883124	0.38	1.0000000
Coastal unknown - Dawesville Cut	-1.3880466	0.17	1.0000000	0.719537	0.47	1.0000000
Comet Bay - Offshore	1.7759714	0.08	1.0000000	-1.36741	0.17	1.0000000
Coastal unknown - Offshore	1.1682727	0.24	1.0000000	-1.75108	0.08	1.0000000
Comet Bay - Shoalwater	-0.3804478	0.70	1.0000000	-0.4011	0.69	1.0000000
Coastal unknown - Shoalwater	-1.3121512	0.19	1.0000000	-0.72149	0.47	1.0000000
Dawesville Cut - Shoalwater	-0.1338961	0.89	1.0000000	-1.4397	0.15	1.0000000
Offshore - Shoalwater	-2.2313367	0.03	0.3848825	1.049994	0.29	1.0000000

Appendix B

Table B.1. Population growth rate (r) and probability of extinction in 100 years estimated by an age-based Monte Carlo simulation of stochastic and deterministic effects on the viability of an Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) population resident to the Peel-Harvey Estuary in Western Australia. All model parameters were kept the same apart from standard deviation due to environmental variance (e.g., weather, prey availability, predation pressure).

Model	**SD_{EV}**	***r* (SD)**	**Probability of extinction (SE)**
PVA_1	0.10	- 0.004 (0.059)	0.005 (0.002)
PVA_2	0.50	- 0.004 (0.059)	0.004 (0.002)
PVA_3	1.00	- 0.004 (0.060)	0.005 (0.002)
PVA_4	1.51	- 0.004 (0.062)	0.01 (0.003)
PVA_5	2.00	- 0.004 (0.064)	0.009 (0.0039)
PVA_6	2.50	- 0.004 (0.066)	0.008 (0.003)

Table B.2. Effects of parameter variation on mean population growth rate (*r*), probability of extinction (*PE*) and population size in 100 years forecast for an Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) population resident to the Peel-Harvey Estuary in Western Australia. Notations: *K* = carrying capacity, AFm = adult female mortality rate, Ym = yearling (i.e., individuals < 1 years old) mortality rate, RR = reproductive rate, SD = standard deviation.

Model description	***K***	**AFm**	**Ym**	**RR**	***r* (SD)**	**PE (SE)**	**Extant N (SD)**
PVA_base	150	5.05	24.76	38.53	- 0.0044 (0.0619)	0.0100 (0.0032)	65 (33)
PVA_stable_age	150	5.05	24.76	38.53	- 0.0044 (0.0620)	0.0110 (0.0033)	65 (34)
PVA_RR_+1%	150	5.05	24.76	38.92	- 0.0036 (0.0604)	0.0060 (0.0024)	69 (35)
PVA_RR_+5%	150	5.05	24.76	40.03	- 0.0020 (0.0590)	0.0030 (0.0017)	79 (36)
PVA_RR_+10%	150	5.05	24.76	41.52	- 0.0001 (0.0567)	0.0020 (0.0014)	90 (37)
PVA_AFm_-1%	150	5.00	24.76	38.53	- 0.0039 (0.0615)	0.0100 (0.0032)	69 (36)
PVA_AFm_-5%	150	4.80	24.76	38.53	- 0.0024 (0.0594)	0.0030 (0.0017)	76 (35)
PVA_AFm_-10%	150	4.55	24.76	38.53	- 0.0001 (0.0570)	0.0000 (0.0000)	89 (36)
PVA_Ym_-1%	150	5.05	24.33	38.53	- 0.0035 (0.0612)	0.0040 (0.0020)	70 (35)
PVA_Ym_-5%	150	5.05	23.35	38.53	- 0.0033 (0.0611)	0.0070 (0.0026)	71 (35)
PVA_Ym_-10%	150	5.05	22.13	38.53	- 0.0021 (0.0597)	0.0060 (0.0024)	79 (36)
PVA_AFm_5%_Ym_10%	150	4.80	22.13	38.53	0.0000 (0.0406)	0.0010 (0.0010)	90 (37)
PVA_AFm_10%_Ym_10%	150	4.55	22.13	38.53	0.0016 (0.0563)	0.0000 (0.0000)	99 (35)
PVA_AFm_10%_Ym_10%_K86	86	4.55	22.13	38.53	0.0012 (0.0620)	0.0050 (0.0022)	60 (19)
PVA_K_86	86	5.05	24.76	38.53	-0.0045 (0.6710)	0.0120 (0.0034)	48 (22)
PVA_K_100	100	5.05	24.76	38.53	-0.0037 (0.0616)	0.0070 (0.0026)	68 (33)

Table B.3. Reproductive success of sexually mature females in the population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary, Western Australia. Notations: n/a = no age estimate, ° = age estimated using stereo-laser photogrammetry methods, * = age estimated from the animal being six years old (average age juvenile) or 10 years old if with a calf at the time of first known live stranding, W = weaned, O = orphaned, D = deceased/disappeared, FC = first calf, - = immature, M = mature, X = no longer in the breeding population, (?) = available to have a calf but no calf recorded, three letter codes = individual identification code, (NA) = with dependent calf

Social cluster		**AF1**							**AF2**		**M1**										**M2**							**CA**	**L1**
Female ID		CMS	GNW	HAT	LBL	NKY	TNT	TWT	BDW	HNA	TON	SEA	MLK	PRN	MWG	ZET	DER	LUC	BOW	HAY	ANN	COL	FRL	SQC	SWP	TOM	RVR	SCR	ANG
Estimated age (2016)		8 - 9.5°	n/a	11°	19°	20*	19°	29*	n/a	n/a	21*	14°	16°	n/a	12°	12°	12°	16°	13°	11°	14°	15°	n/a	35°	17°	4°	6°	n/a	12°
Year calf was born	2016	EST (FC,D)	NGT (O)	HAL (D)	(NA)	(NA)	(NA)	(NA)	PAN (W,D)	(NA)	(NA)	(NA)	(NA)	(NA)	CTH (D)	LIT (W)	SCB	LNA (W)	ZIG (W)	CMT (W)	(NA)	(NA)	(NA)	(NA)	(NA)	-	-	(NA)	-
	2017	(NA)	X	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	X	NIK	BRZ (W)	SLH	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	X	AND (D)	(NA)	-	-	SPC (D)	-
	2018	SPI	X	(NA)	(NA)	DJN (O,D)	CAR	(NA)	(NA)	X	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	(NA)	KIM (D)	STY	X	POM (D)	(NA)	-	-	X	-
	2019	(NA)	X	HLI	AOR (D)	SOL	(NA)	TSW	TNK (D)	X	TAL (D)	CCC	(NA)	PPR	MPL	(NA)	(NA)	DMN	SRD	HRB (D)	(?)	(NA)	X	KLN (D)	RYD	(M)	MER (FC)	X	BRV (FC)

Table B.4. Approximate age of adult males in a population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary, Western Australia. Notations: n/a = no age estimate, ° = age estimated using stereo-laser photogrammetry methods, * = age estimated from the animal being at least six years old (average age juvenile) at the time of first known live stranding

Social cluster	**AM1**						**AM2**						**L2**
Male ID	ZNE	FTN	BLK	FRS	HOK	BTS	YOY	LMY	TRB	THT	RBY	CRK	SQK
Estimated age (2016)	29*	28*	31°	29*	15°	31°	29°	24°	22	n/a	n/a	10-17°	n/a

Table B.5. Sex and approximate age of juveniles in a population of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary, Western Australia. Notations: m = male, f = female, n/a = no age estimate, ° = age estimated using stereo-laser photogrammetry methods, ^ = known age from birth records, * = first calf born in 2020

Social cluster	JM					CA	M2		M1											
Juvenile ID	GGL	LIO	LNK	KDB	BKY	ELV	SPK	HTY	TGG	BTL	PRJ	SRY	CPR	SPO	KRS	HNH	DOR	ERC	BUD	BOR
Sex	m	m	m	m	m	f	f	f	m	m	m	m	m	f	m	m	m	f	f	f
Estimated age (2016)	4^	5°	5^	4°	5^	n/a	n/a	n/a	n/a	n/a	8°	7°	n/a	n/a	4°	6°	4°	6°	4°	6*

Figure B.1. Age distribution used as initial population structure for a Population Viability Analysis for a community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary, Western Australia.

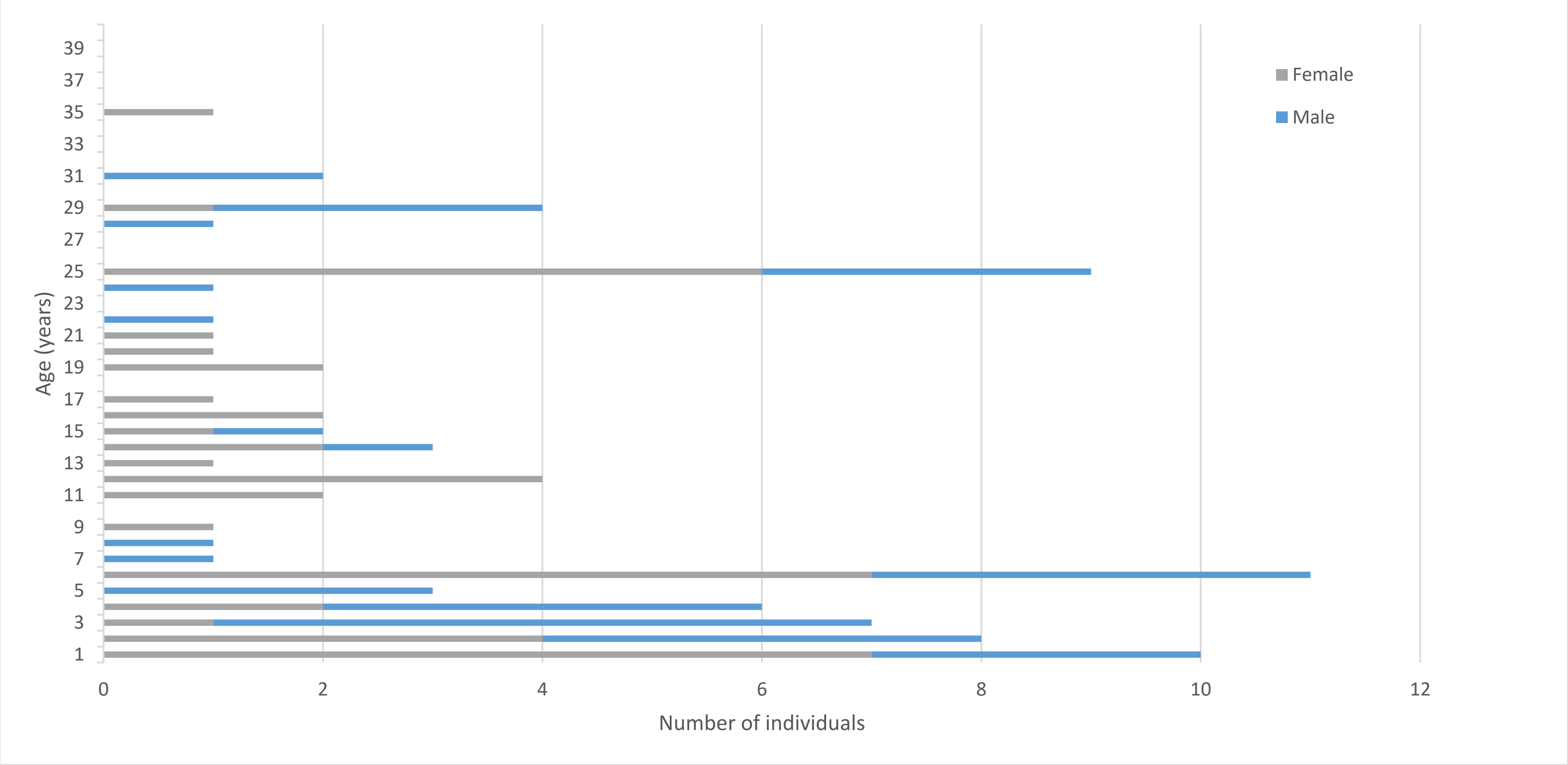
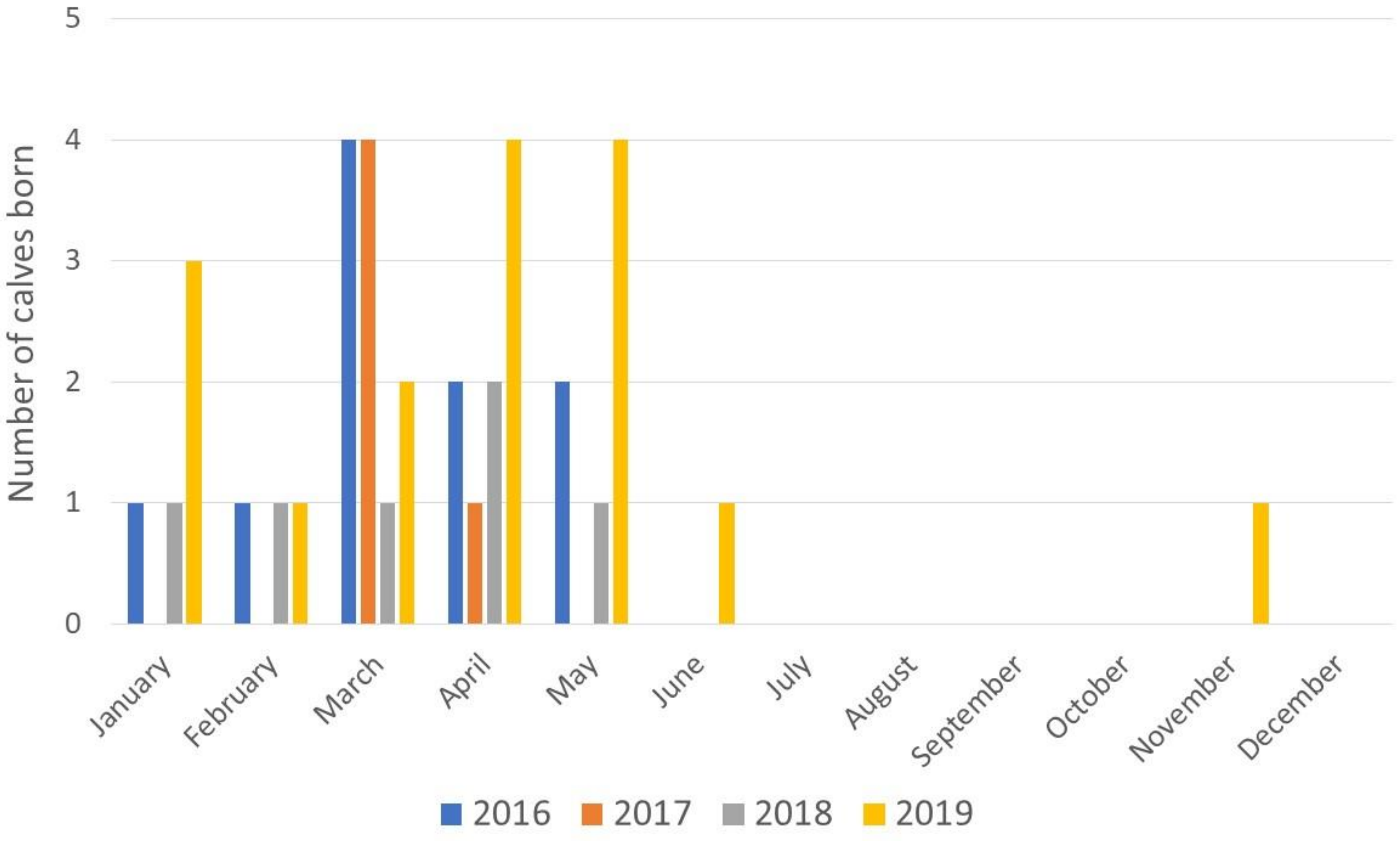


Figure B.2. Number of calves born to a community of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) resident to the Peel-Harvey Estuary, Western Australia.



Appendix C

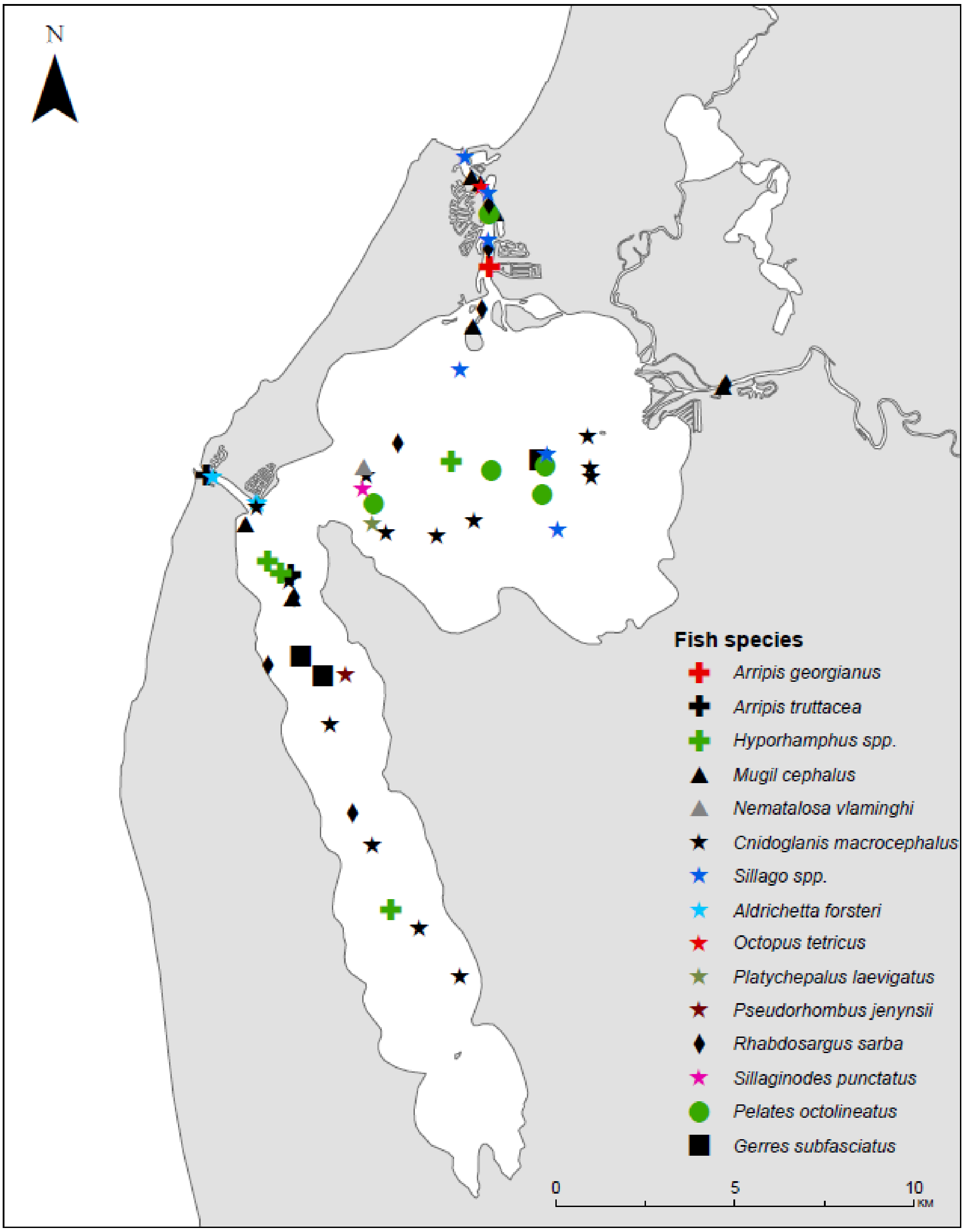


Figure C.1. Location of prey species (n = 17) observed to be targeted by Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the Peel-Harvey Estuary, Western Australia

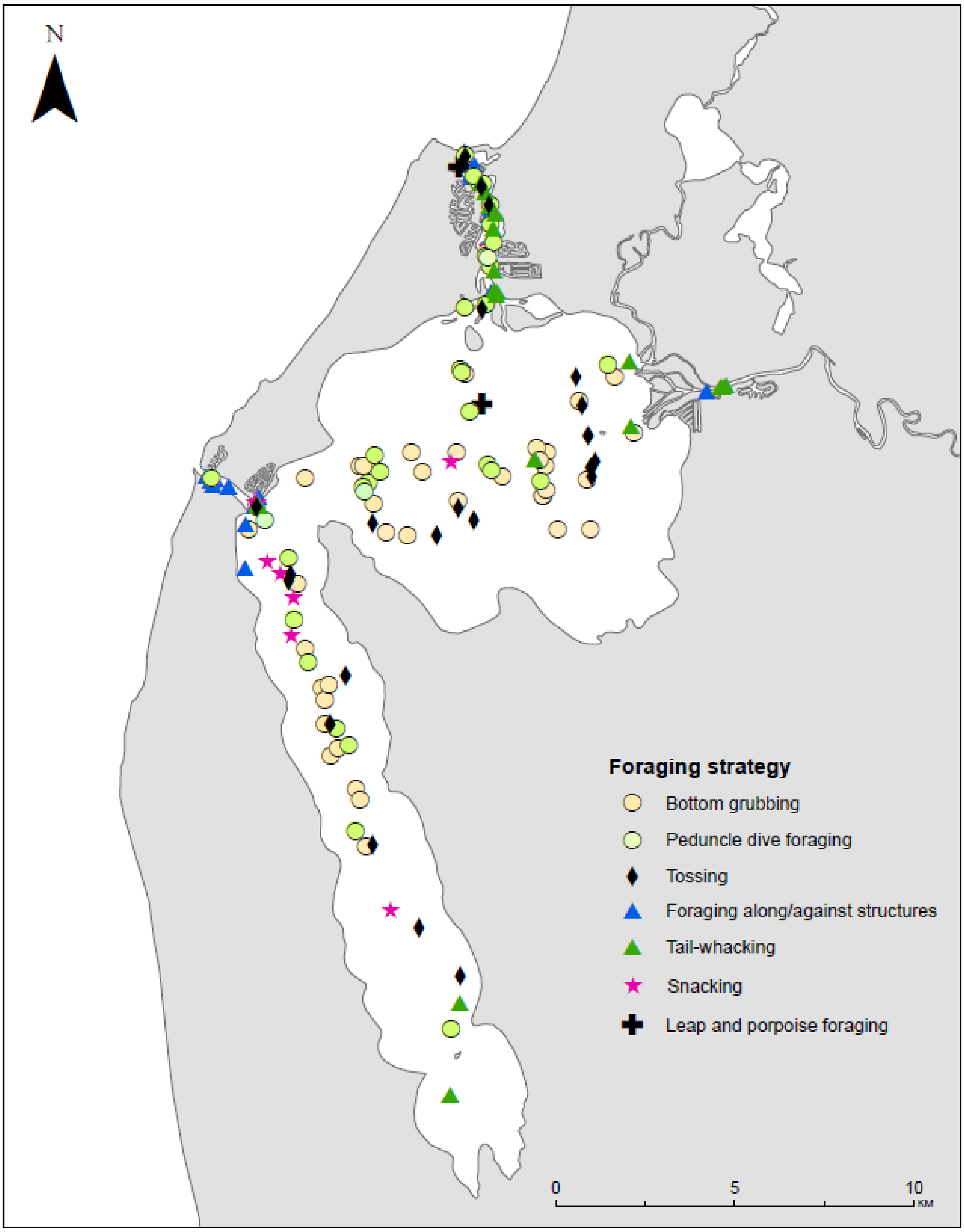


Figure C.2. Location of foraging strategies observed to be used by Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the Peel-Harvey Estuary, Western Australia

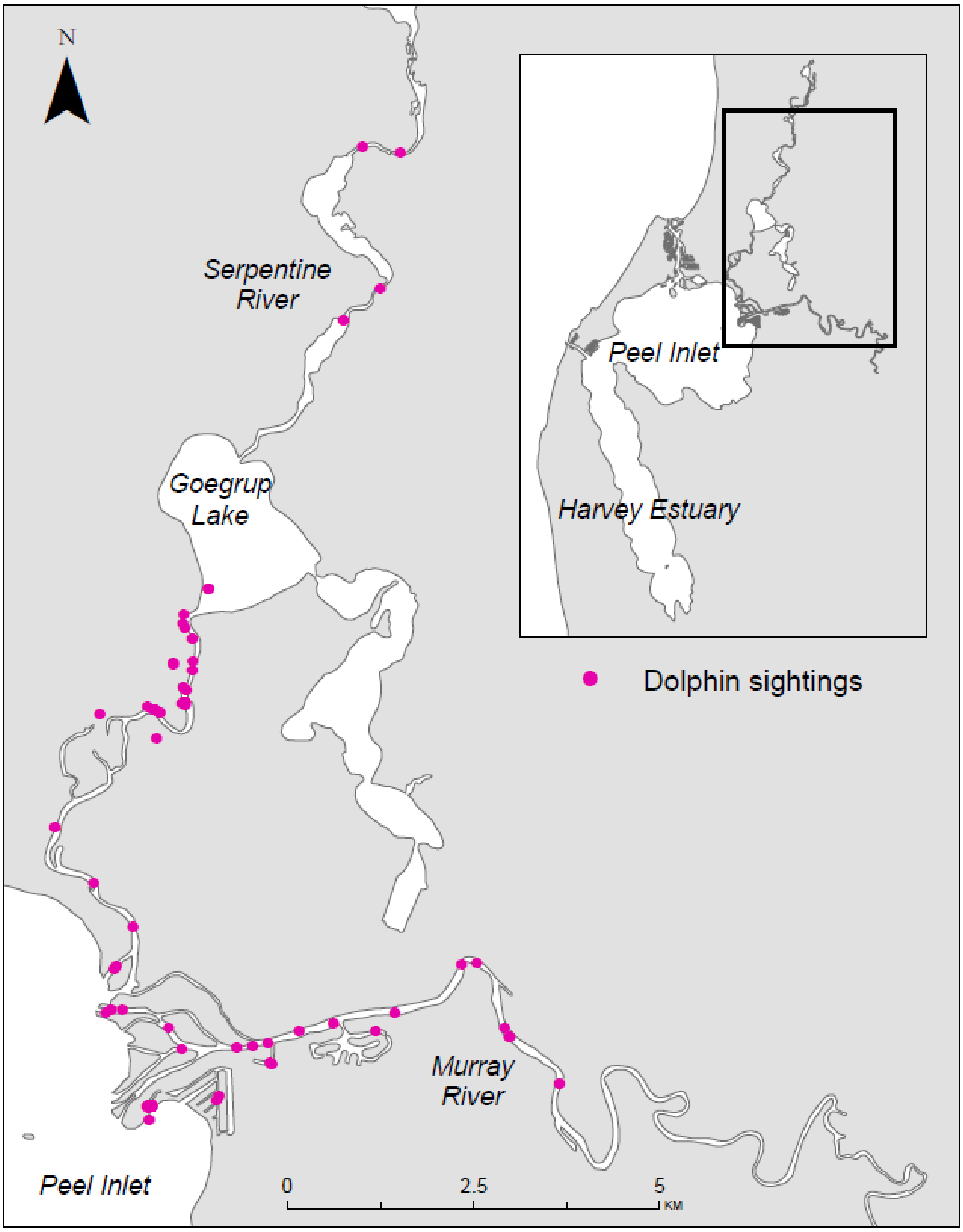


Figure C.3. Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) sighting locations (n = 43) recorded by the public via a mobile application, Dolphin Watch between December 2015 and August 2020. Dolphin Watch is a citizen science initiative which allows people to participate in dolphin monitoring in the Peel-Harvey Estuary, Western Australia