The behavioural ecology of mixed-species groups of delphinids

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Summary

Many species form mixed-species groups to gain antipredator, foraging, and/or social benefits. Amongst delphinids, mixed-species groups appear to be widespread, however, in most cases their functions remain unknown. Moreover, research has been hindered by several shortcomings, notably inconsistent terminology, the lack of a conceptual framework for assessing their functions, and a limited number of targeted studies. In this thesis, I review the current knowledge on delphinid mixed-species groups (Chapter 2), address inconsistencies in how mixed-species groups are defined (Chapters 2 and 3), and develop a conceptual framework for their study (Chapter 2). I then apply this framework on a model system of Australian humpback, *Sousa sahulensis* (hereafter "humpback dolphin"), and Indo-Pacific bottlenose dolphins, *Tursiops aduncus* (hereafter "bottlenose dolphin"), around the North West Cape, Western Australia, to: assess habitat partitioning and co-occurrence patterns with a joint species distribution model and a temporal analysis (Chapter 4); compare the characteristics of single- and mixed-species sightings to determine the possible functions of these mixed-species groups (Chapter 5); and evaluate behavioural patterns using Markov chain analysis to better understand coexistence mechanisms and the functions of these mixed-species groups (Chapter 6). From the review in Chapter 2, I found reports of 54 cetacean species from five families apparently forming mixed-species groups. Most reports, however, were brief observational accounts and only 27 studies proposed and discussed potential functions. By combining the results of this review with broader theory, I constructed a framework for assessing the functions of cetacean mixed-species groups (Chapter 2). In Chapter 3, I used the results of a review and survey on how the terms *group*, *school*, *party*, and *pod* are defined in delphinid studies to make the recommendation that the term *group*, defined with spatial proximity criteria, be used exclusively for sampling units of dolphins observed in the field. Additionally, I propose a process for formulating biologically meaningful definitions by analysing interindividual distances (Chapter 3). From my study of the model system, I found that humpback and bottlenose dolphins around the North West Cape displayed habitat and temporal niche partitioning: humpback dolphins preferred shallower and more nearshore waters, bottlenose dolphins were sighted more often during the afternoon, and interspecific behavioural patterns indicated that the species differed in their use of the study area (Chapters 4 and 6). Despite this partitioning, the species co-occurred more often than expected by chance, indicating attraction between them and the active formation of mixed-species groups (Chapter 4). Both species displayed varied interspecific behavioural interactions, from aggressive and sexual behaviours to neutral and affiliative behaviours, suggesting that a variety of social benefits may be relevant, depending on the individuals involved and their traits (Chapter 5). Furthermore, when in mixed-species groups, humpback and bottlenose dolphins were more likely to transition to socialising from other behaviours and both species socialised more and travelled and foraged less, further indicating that the benefits that they gain are social (Chapter 6). This study advances our understanding of delphinid mixed-species groups and provides a solid platform for future studies of other populations and species.

Declaration

I certify that this thesis does not incorporate without acknowledgment any material previously submitted for a degree or diploma in any university and that, to the best of my knowledge and belief, it does not contain any material previously published or written by another person except where due reference is made in the text.

Signed: J Syme

Date: 2022-12-02

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Statement of authorship

I, Jonathan Syme, am the principal contributor to each chapter of this thesis. My primary supervisor, Associate Professor Dr Guido J Parra, and my associate supervisor, Assistant Professor Dr Jeremy J Kiszka, are co-authors of the manuscripts derived from this thesis due to their significant contribution, advice, and guidance to the concept and study design, data collection and processing, statistical analysis, and manuscript writing and editing. The specific contributions for each chapter are as follows.

Chapter 1: General introduction

Manuscript writing: JS with critical review and editorial input from GJP and JJK

Chapter 2: Dynamics of cetacean mixed-species groups: A review and conceptual framework for assessing their functional significance

Concept and study design: JS, JJK, and GJP

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Statistical analysis: JS with advice from GJP and JJK

Manuscript writing: JS with critical review and editorial input from GJP and JJK

Chapter 3: How to define a dolphin “group”? Need for consistency and justification based on objective criteria

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Chapter 4: Habitat partitioning, co-occurrence patterns, and mixed-species group formation in sympatric delphinids

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Chapter 5: Multiple social benefits drive the formation of mixed-species groups of Australian humpback and Indo-Pacific bottlenose dolphins

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Chapter 6: Variation in behavioural patterns furthers our understanding of coexistence mechanisms and the function of mixed-species groups in sympatric delphinids

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Chapter 1

General introduction

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General introduction

1.1 Mixed-species groups

Grouping is an integral part of the behavioural ecology of many species belonging to diverse taxa, from insects, to fishes, to mammals (Krause & Ruxton 2002, Majolo & Huang 2018). The theoretical basis for group living has been well established – individuals that form groups gain benefits, including reduced predation risk, improved feeding rates, and enhanced reproductive opportunities, that outweigh the costs, such as increased interindividual competition and disease transmission (Krause & Ruxton 2002, Ward & Webster 2016, Majolo & Huang 2018). Groups can also be formed, however, by individuals of different species. Mixed-species groups, also called interspecific, heterospecific, or polyspecific associations, have been observed amongst diverse taxa, including fishes, birds, ungulates, primates, and cetaceans (Lukoschek & McCormick 2000, Stensland et al. 2003, Goodale et al. 2017, Sridhar & Guttal 2018, Syme et al. 2021). The theoretical basis of mixed-species group formation largely follows that of single-species groups – the benefits of grouping outweigh the costs (Stensland et al. 2003, Sridhar et al. 2009, Goodale et al. 2017, Syme et al. 2021). These benefits are typically summarised by three non-mutually exclusive hypotheses – the antipredator, foraging, and social advantage hypotheses – which are considered to be the functional explanations for mixed-species group formation (Stensland et al. 2003, Goodale et al. 2017, Sridhar & Guttal 2018, Syme et al. 2021).

The antipredator advantage hypothesis states that individuals experience reduced predation risk when in mixed-species groups due to the dilution and confusion effects, improved defence against predators, or increased group vigilance (Stensland et al. 2003, Sridhar et al. 2009, Goodale et al. 2017, Syme et al. 2021). For example, saddleback (*Saguinus fuscicollis*) and moustached tamarins (*Saguinus mystax*) may experience reduced predation risk when in mixed-species groups due to their complementary vigilance strategies – saddleback tamarins scan primarily for terrestrial and scansorial predators while moustached tamarins scan primarily for aerial and arboreal ones (Peres 1993). In the Eastern Tropical Pacific and the western Indian Ocean, spinner dolphins (*Stenella longirostris*) may form groups with pantropical spotted dolphins (*Stenella attenuata*) to reduce the risk of predation by benefiting from the daytime vigilance of the latter (Scott & Cattanach 1998, Kiszka et al. 2011a).

The foraging advantage hypothesis contends that individuals improve their ability to detect and obtain food resources by mutual or non-mutual exchange of information, by gaining access to new resources, or by cooperatively foraging with heterospecifics (Stensland et al. 2003, Sridhar et al. 2009, Goodale et al. 2017, Syme et al. 2021). For example, in central Namibia, rock kestrels (*Falco rupicolus*) follow chacma baboons (*Papio ursinus*) that are "travel foraging" (i.e., searching for food while moving) and catch insects (*Orthoptera* sp.) that are flushed by the primates' movements (King & Cowlishaw 2009). Off the California coast, common bottlenose dolphins (*Tursiops truncatus*) may take advantage of the diving and food-finding abilities of short-finned pilot whales (*Globicephala macrorhynchus*) and Risso's dolphins (*Grampus griseus*) by following and joining them when they forage (Shane 1994, Bacon et al. 2017).

Finally, according to the social advantage hypothesis, individuals gain social benefits from interacting with heterospecifics by practicing a variety of social behaviours, from those involved in alloparenting and play to those involved in courtship and infanticide (Herzing & Johnson 1997, Spinka et al. 2001, Stensland et al. 2003, Parra 2005, Melillo et al. 2009, Syme et al. 2021). For example, interspecific play behaviour, such as has been observed between tropical rainforest primates (*Colobus* and *Cercopithecus* sp.) in the Kibale Forest, Uganda (Struhsaker 2010), may provide young individuals with the opportunity to practice skills with stronger or more experienced partners (Spinka et al. 2001). Off Zanzibar, East Africa, young male Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) may practice socio-sexual behaviours by interacting with Indian Ocean humpback dolphins (*Sousa plumbea*) (Stensland et al. 2003).

As a result of these antipredator, foraging, and social benefits, the formation of mixed-species groups can influence the behaviour, diet, and habitat use of the species involved (Peres 1992b, Heymann & Buchanan-Smith 2000, Wolters & Zuberbühler 2003, Sridhar et al. 2009). For example, Diana monkeys (*Cercopithecus diana*) utilise lower forest strata when in mixed-species groups with sooty mangabeys (*Cercocebus atys*), as the latter are effective sentinels and so reduce ground predator pressure (McGraw & Bshary 2002). When in association with saddleback and red-chested tamarins (*Saguinus labiatus*), Goeldi's monkeys (*Callimico goeldii*) expand their dietary niche and acquire a broader, higher quality diet (Porter & Garber 2007). Understanding the functions of mixed-species groups and the changes that they bring about is important as they may, in turn, affect the fitness and survival of participating individuals and populations and, thus, have conservation value (Goodale et al. 2017, Zou et al. 2018).

Numerous species of delphinids have been observed in mixed-species groups with other delphinids as well as with other cetaceans (Stensland et al. 2003, Cords & Würsig 2014, Syme et al. 2021). The species, frequency, and characteristics of delphinid mixed-species groups indicate that they vary greatly amongst species and habitats. Nevertheless, the majority of accounts of delphinid mixed-species groups are brief observational reports and few studies have, firstly, established if these observations truly represent mixed-species groups or are simply chance encounters that result from the coincidental meeting of co-occurring species or aggregations of animals that are attracted to a common resource and, secondly, investigated the potential functions of the formation of mixed-species groups (Stensland et al. 2003, Cords & Würsig 2014, Syme et al. 2021).

1.2 Shortcomings and key aspects of investigating the functions of delphinid mixed-species groups

Understanding the potential functions of mixed-species groups requires, firstly, distinguishing mixed-species groups from chance encounters and aggregations and, secondly, assessing the potential evolutionary benefits that animals may gain (Waser 1982, Stensland et al. 2003, Syme et al. 2021). Research into these aspects of delphinid mixed-species groups has been hindered by several theoretical and analytical limitations, notably the lack of a conceptual framework, inconsistent terminology, and the lack of targeted and comprehensive investigations. A conceptual framework would begin to overcome these limitations by providing guidance for future studies on the scope and focus of the problems to address, the terminology to use, and the steps to take to investigate any potential functions. The theoretical basis for mixed-species group formation applies across taxa (Stensland et al. 2003, Sridhar et al. 2009, Heymann & Hsia 2015, Goodale et al. 2017) and studies of species as diverse as rainforest primates, woodland birds, and oceanic dolphins have applied similar methods to investigate their functions, such as comparisons of behaviour and habitat use of single- and mixed-species groups (e.g., Wolters & Zuberbühler 2003, Thomson & Ferguson 2007, Kiszka et al. 2011). Thus, although any conceptual framework for assessing the functions of delphinid mixed-species groups should be based primarily on studies of delphinids, it should also incorporate information on other taxa. As a result, despite the unique challenges presented by studying highly-mobile, marine species, such as delphinids, the framework, and the terminology and steps contained within it, could be applied to other taxa that form mixed-species groups.

1.2.1 Defining mixed-species groups

A primary shortcoming of distinguishing mixed-species groups from chance encounters and aggregations concerns the fundamental question of what constitutes a mixed-species group. In ecology, confusion and inconsistency surrounding key concepts (e.g., population, community, or interaction) has hindered the advancement of study and limited the widespread understanding of ideas and phenomena (Jax 2006, Viscido & Shrestha 2015, Nakazawa 2020). The study of mixed-species groups is no exception – various terms (e.g., *mixed-species group* and *interspecific association*) are used and are not consistently defined. Broadly speaking, a mixed-species group can be described as a group containing individuals from multiple species (Stensland et al. 2003, Syme et al. 2021). Thus, at the heart of the issues concerning the definition of a mixed-species group is the matter of defining a group. This, however, is deceptively complex. To effectively fulfil their central role in studies of ecology and behaviour, groups should ideally be operationally defined in a way that is biologically meaningful, practical to identify in the field, and comparable between studies (Krause & Ruxton 2002, Whitehead 2008, Croft et al. 2008, Viscido & Shrestha 2015, Syme et al. 2022). Thus, any solutions to the issues concerning terminology and definitions require a multi-faceted approach that not only evaluates the biological relevance of definitions to the study populations, but that also considers the current practices and opinions of researchers. Greater clarity regarding what constitutes a group would facilitate the study of mixed-species groups, as well as comparative socio-ecological research on these group-living species, by reducing the current inconsistency and confusion.

1.2.2 Distinguishing mixed-species groups from chance encounters and aggregations

When studying mixed-species groups, there is one fundamental aspect that operational group definitions employed in the field are typically unable to assess – whether species are found together in close spatiotemporal proximity as a result of chance, aggregation to shared resources, or attraction between species. This step is critical because, unlike chance encounters and aggregations, mixed-species groups are the result of an attraction between species that stems from the evolutionary benefits that individuals gain by associating with heterospecifics (Waser 1984, Whitesides 1989).

Researchers have developed various analytical methods to test whether species are found together in close spatiotemporal proximity because of attraction between them, because of chance, or because of a shared attraction to a resource or habitat. However, techniques that have been used previously mainly in the study of terrestrial species, such as ideal gas models and null models (Waser 1982, Whitesides 1989, Gotelli 2000, Hutchinson & Waser 2007, Astaras et al. 2011), have certain drawbacks. For example, ideal gas models, which simulate the movement of groups through space to generate expected encounter rates, require detailed data on group travel speed and diameter that are not readily available for highly-mobile marine species (Cords & Würsig 2014, Syme et al. 2021). Null models, on the other hand, do not account for the influence of shared habitat preferences (Pollock et al. 2014, Ovaskainen et al. 2017). Consequently, no studies, to my knowledge, of apparent delphinid mixed-species groups have used such models to conduct this key analytical step, with most studies instead making the assumption that whenever two or more species of delphinids are observed together frequently or for extended periods of time they constitute a mixed-species group (Cords & Würsig 2014, Goodale et al. 2017, Syme et al. 2021). To overcome this barrier and advance our understanding of the dynamics and function of mixed-species groups, we must investigate the co-occurrence patterns of the species involved and assess if their co-occurrence is the result of attraction, or if they simply represent chance encounters or aggregations of animals.

1.2.3 Assessing the benefits of mixed-species groups

If there is attraction between species that results in the formation of mixed-species groups, then, it follows that there are evolutionary benefits (e.g., antipredator, foraging, or social) that one or more of the species gains (Heymann & Buchanan-Smith 2000, Stensland et al. 2003, Goodale et al. 2017, Syme et al. 2021). Previous studies of primate and avian mixed-species groups have used a variety of techniques to determine the benefits that species may gain, from observational studies to playback experiments (Heymann & Buchanan-Smith 2000, Sridhar et al. 2009, Cords & Würsig 2014, Goodale et al. 2017). The key in these analyses is to compare single- and mixed-species groups to determine how key characteristics change with heterospecific presence (Sridhar & Guttal 2018, Syme et al. 2021). For example, racket-tailed drongos (*Dicrurus paradiseus*) adjust the height at which they perch when in mixed-species flocks and capture insects disturbed by heterospecifics, resulting in a higher rate of foraging and foraging success (Satischandra et al. 2007). These differences in behaviour indicate a foraging benefit for the racket-tailed drongos (Satischandra et al. 2007), as is the case for the many bird species that increase their rate of foraging when in mixed-species flocks (Sridhar et al. 2009). The benefits that dolphins may gain from their participation in mixed-species groups are not so well understood. The few studies available have typically inferred potential benefits from observations and comparative analyses of the characteristics (e.g., number of individuals, behaviour, and age and sex composition) of single- and mixed-species groups to determine how these characteristics change with heterospecific presence (Stensland et al. 2003, Cords & Würsig 2014, Sridhar & Guttal 2018, Syme et al. 2021). For example, mixed-species groups of pantropical spotted and spinner dolphins around the western Indian Ocean island of Mayotte are larger, occur in deeper water, and travel more frequently than single-species groups of either species (Kiszka et al. 2011a). Moreover, it appears that spinner dolphins initiate these mixed-species groups by seeking pantropical spotted dolphins when in deeper water where the latter preferentially occur, suggesting antipredator benefits for the spinner dolphins (Kiszka et al. 2011a). For many delphinids, however, the drivers behind the formation of mixed-species groups remain unclear or unknown (Stensland et al. 2003, Cords & Würsig 2014, Syme et al. 2021).

1.2.4 The influence of ecological, morphological, and behavioural traits on mixed-species groups

Various aspects of mixed-species groups, such as their frequency, stability, and benefits, can be influenced by the ecological, morphological, and behavioural traits of the participating species. Sympatric species partition resources and habitats, spatially and/or temporally, to avoid competitive interactions (Grinnell 1924, Pianka 1974, Chesson 2000, Tokeshi 2009). For example, amongst large carnivores in western Zambia, African wild dogs (*Lycaon pictus*) avoid areas heavily used by lions (*Panthera leo*) while cheetahs (*Acinonyx jubatus*) mainly hunt during daylight hours to avoid lions which hunt primarily at night (Dröge et al. 2017). Amongst species that form mixed-species groups, the degree of niche partitioning can influence the dynamics of mixed-species groups. Differences in dietary niche can reduce interspecific competition and contribute to the frequency and stability of mixed-species groups (Heymann & Buchanan-Smith 2000, Sridhar & Guttal 2018). For example, the very high stability of mixed-species groups of saddle-back and moustached tamarins in the Amazon can be partially explained by differences in foraging behaviour, with saddle-back tamarins foraging at lower heights on concealed prey and moustached tamarins foraging in midstorey foliage on well-exposed prey (Peres 1992b). On the other hand, dietary overlap can improve the quality of the benefits that species gain from forming mixed-species groups as heterospecifics with similar diets can provide more relevant information on, for example, the location of food resources (Sridhar & Guttal 2018, Goodale et al. 2020).

When in mixed-species groups, some species are able to utilise new habitats and, thus, expand their niches (McGraw & Bshary 2002, Wolters & Zuberbühler 2003, Porter & Garber 2007). For example, cryptic Campbell's monkeys (*Cercopithecus campbelli*) use higher, more exposed forest strata when in association with conspicuous Diana monkeys, potentially as the result of experiencing reduced predation risk (Wolters & Zuberbühler 2003). Moreover, the benefits gained from mixed-species groups can also counterbalance the costs of competition. For example, despite having high dietary overlap and feeding competition, Diana monkeys form mixed-species groups with putty-nosed monkeys (*Cercopithecus nictitans*) seemingly because of the latter's valuable role in defence against predators, such as crowned eagles (*Stephanoaetus coronatus*) (Eckardt 2004). Thus, niche partitioning and mixed-species group formation influence each other and the interplay between them should be considered when investigating mixed-species groups.

The behaviour and morphology of the participating species can also influence the dynamics of mixed-species groups. For example, the social organisation of participating species may influence the stability of mixed-species groups (Buchanan-Smith 1999) and, alongside individual intraspecific social status, may influence how individuals interact with heterospecifics (Melillo et al. 2009). The quality of antipredator benefits, such as those obtained from collective vigilance, mobbing, and the confusion effect, tends to be higher if heterospecifics experience a substantial predation threat and share predators (Goodale et al. 2017, 2020, Sridhar & Guttal 2018). For example, Gunther's dik-diks (*Madoqua guentheri*), which are vulnerable to predation, can benefit from eavesdropping on the alarm calls of white-bellied go-away birds (*Corythaixoides leucogaster*) because they share certain predators (e.g., raptors) (Lea et al. 2008). For some species, the quality of antipredator benefits can also improve with greater behavioural and morphological differences, as in the previous example, however, for other species, such as stoplight (*Sparisoma viride*) and striped parrotfishes (*Scarus iserti*), potential antipredator benefits decrease with increased morphological difference due to the oddity effect (Wolf 1985).

Given that the similarities and differences between species in various ecological, morphological, and behavioural traits can influence the dynamics of their mixed-species groups, I now review the relevant available knowledge of the two study species that I use in this thesis as a model system in order to lay the foundations for my study questions and hypotheses.

1.3 Study species: The Australian humpback dolphin and the Indo-Pacific bottlenose dolphin

The Australian humpback dolphin (*Sousa sahulensis*, hereafter "humpback dolphin") and the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*, hereafter "bottlenose dolphin") occur sympatrically across northern Australia (Parra et al. 2004, Jefferson et al. 2015, Beasley et al. 2016, Parra & Cagnazzi 2016, Wang 2018) where they have been reported to form mixed-species groups (Corkeron 1990, Ansmann 2011, Brown et al. 2012, Hunt 2018). The dynamics of these mixed-species groups, however, have not been investigated and, although certain aspects of their sympatric ecology have been studied (Corkeron 1990, Hanf et al. 2022), it is unclear how niche partitioning influences mixed-species group formation. Humpback and bottlenose dolphins form an interesting model system for assessing the potential functions of mixed-species groups and investigating coexistence mechanisms as they show both similarities and differences in key traits pertaining to morphology, habitat, predators, diet, and social structure.

1.3.1 Description

Humpback and bottlenose dolphins are similar in body size, with adult humpback dolphins reaching a maximum length of 2.7 m and a maximum weight of 240-280 kg and adult bottlenose dolphins averaging 2.7 m and 200 kg (Jefferson & Rosenbaum 2014, Parra &

Jefferson 2018, Wang 2018). The species do, however, display certain morphological differences. The humpback dolphin has a robust body, a low triangular dorsal fin, broad flippers and flukes, and a long, narrow rostrum, although it lacks the namesake prominent dorsal hump (Jefferson & Rosenbaum 2014, Parra & Jefferson 2018) (Figure 1.1). It has a darker upper body and a lighter underside separated diagonally from above the eye to the urogenital area with some individuals exhibiting sexually dimorphic white patches and spotting, particularly on the dorsal fin, peduncle, and flukes (Jefferson & Rosenbaum 2014, Brown et al. 2016a). The bottlenose dolphin has a tall, falcate dorsal fin, light to dark grey colouration, and a moderate length beak separated from the melon by a distinct crease (Wang 2018) (Figure 1.1). It also has fins, flippers, and flukes that are large and broad relative to its body size, a long and narrow rostrum, and, frequently, the presence of ventral spotting (Wang et al. 2000, Jefferson et al. 2015, Wang 2018).

Figure 1.1 Photo of an Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) and an Australian humpback dolphin (*Sousa sahulensis*) in a mixed-species group near the North West Cape, Western Australia, displaying some of their characteristic morphological traits: bottlenose dolphin – grey colour and tall, falcate dorsal fin; humpback dolphin – pale grey colour and low, triangular dorsal fin.

1.3.2 Habitat

Both humpback and bottlenose dolphins typically inhabit shallow, protected, coastal waters, including lagoons, inshore reefs, and estuaries, although the humpback dolphin has a stricter preference for shallower water (<20 m deep) than the bottlenose dolphin which is found in water up to 100 m deep (Parra & Jefferson 2018, Wang 2018, Hanf et al. 2022).

1.3.3 Predators

The natural predators of humpback and bottlenose dolphins are few, with bite marks indicating that large (>3 m) sharks, including white (*Carcharodon carcharias*), bull (*Carcharhinus leucas*), tiger (*Galeocerdo cuvier*), and dusky sharks (*Carcharhinus obscurus*), are their main threat (Heithaus 2001, Heithaus et al. 2017, Parra & Jefferson 2018, Wang 2018, Smith et al. 2018). Rates of predation are difficult to measure, however predator presence, along with food availability, is known to affect the behaviour and habitat use of inshore dolphins (Heithaus & Dill 2002, 2006).

1.3.4 Diet

Both humpback and bottlenose dolphins feed in shallow, inshore waters, often near estuaries and reefs (Parra 2006, Cagnazzi et al. 2011, Wang 2018). Stomach content analyses of stranded humpback dolphins in Queensland revealed a diet of various benthic and pelagic fish, indicating that humpback dolphins are opportunistic, generalist feeders (Parra & Jedensjö 2014). Like humpback dolphins, bottlenose dolphins have a varied diet that consists primarily of benthic and pelagic fish species from a range of trophic levels, but that also includes cephalopods (Amir et al. 2005, Kiszka et al. 2014, Smith & Sprogis 2016, Wang 2018).

1.3.5 Social structure

Short-term relationships between individuals form the basis of humpback dolphin social structure, which is fluid and has a high degree of fission-fusion dynamics (Parra et al. 2011, Brown et al. 2012). Group size is typically small (i.e., one to 15 individuals), with mean group sizes at various study sites around Australia ranging from two to five individuals (Cagnazzi 2010, Parra et al. 2011, Brown et al. 2012, Hunt et al. 2017). Similarly, bottlenose dolphins are typically found in small groups of up to 20 individuals, although larger groups of hundreds of individuals have been observed in Japan and South Africa (Jefferson et al. 2015, Wang 2018). Bottlenose dolphins also live in high fission-fusion societies with groups that vary in size and composition according to ecological factors such as food availability and predation (Connor et al. 2000, Heithaus & Dill 2002). The social structure of bottlenose dolphins is highly complex and has been particularly well studied in Shark Bay, Western Australia, where adult males form alliances to gain access to reproductive females and multiple alliances may cooperate to form second- and third-order alliances (Connor & Krützen 2015). Pairs of large male humpback dolphins have been observed in close association on multiple occasions, suggesting that they too may, at least temporarily, form alliances (Allen et al. 2017).

1.3.6 Sympatric ecology and mixed-species groups

Humpback and bottlenose dolphins co-occur throughout the shallow, coastal waters of northern Australia and southern Papua, from southeast Queensland to Shark Bay (Parra et al. 2004, Jefferson et al. 2015, Beasley et al. 2016, Parra & Cagnazzi 2016, Wang 2018). Where they occur sympatrically, previous research has found that bottlenose dolphins tend to occur further from the shore and in deeper water than humpback dolphins (Corkeron 1990, Hanf et al. 2022). Despite any apparent niche partitioning, humpback and bottlenose dolphins appear to regularly form mixed-species groups. During opportunistic boat-based surveys around the North West Cape, Western Australia, Brown et al. (2012) recorded that 24% of humpback dolphin groups also contained bottlenose dolphins. Mixed-species groups of humpback and bottlenose dolphins species were observed in the same location by Hunt (2018) and have also been recorded in Moreton Bay, Queensland (Parra, GJ personal observations, Corkeron 1990, Ansmann 2011).

Mixed-species groups of bottlenose and Indian Ocean humpback dolphins (*Sousa plumbea*) have been recorded at several locations on the east African coast and around western Indian Ocean islands (Stensland et al. 1998, 2003, Kiszka 2007, Cerchio et al. 2015, Koper & Plön 2016, Braulik et al. 2018). Humpback dolphins have also been observed to interact with Australian snubfin dolphins (*Orcaella heinsohni*) in Queensland (Parra 2005, Cagnazzi 2010) and in northwestern Australia (Brown et al. 2014) while bottlenose dolphins are known to interact with Australian snubfin dolphins in northwestern Australia (Allen et al. 2012) and with spinner dolphins around La Réunion in the Indian Ocean (Dulau-Drouot et al. 2008). The other members of the *Tursiops* and *Sousa* genera, particularly the common bottlenose dolphin, have also been recorded in mixed-species groups with a variety of delphinid species (Cords & Würsig 2014, Syme et al. 2021).

The proposed functional explanations for mixed-species groups involving humpback and bottlenose dolphins are diverse. In Algoa Bay, South Africa, small groups of Indian Ocean humpback dolphins may join larger groups of bottlenose dolphins to reduce their predation risk from sharks or to obtain information regarding food resources (Koper & Plön 2016) while in Zanzibar, male bottlenose dolphins harass female Indian Ocean humpback dolphins during aggressive and sexual interactions, possibly to practice social behaviours (Stensland et al. 2003). Previous to this study, however, no investigation had, firstly, established if humpback and bottlenose dolphins do actually form mixed-species groups and not aggregations or chance encounters and, secondly, assessed the potential functions underlying the formation of their mixed-species groups. Humpback and bottlenose dolphins are often found in potential mixed-species groups around the North West Cape, Western Australia, providing a unique opportunity to study the nature and dynamics of their interspecific interactions.

1.4 Study site: The North West Cape, Western Australia

The North West Cape lies in the Pilbara Region of Western Australia and is bounded to the west and to the north by the Ningaloo Reef and to the east by Exmouth Gulf (Figure 1.2). This area is rich in biodiversity and supports a variety of biological communities, including reef flats, patch reefs, sandflats, mangroves, and mudflats (Cassata & Collins 2008, Kobryn et al. 2013, Wilson 2013a).

The North West Cape was described as a "hotspot" for humpback dolphins by Brown et al. (2012) who, in only 18 days of survey effort, recorded 42 groups and identified 54 individuals. The importance of the North West Cape for humpback dolphins was confirmed by Hunt et al. (2017), who estimated that the population contains between 65 and 102 animals and, at approximately one dolphin per km^2, has the highest recorded density for this species. Furthermore, the humpback dolphins of the North West Cape display high levels of site fidelity and residency (Hunt et al. 2017). The North West Cape also contains a large population of bottlenose dolphins with an estimated resident population of 141 and a super-population (i.e., resident and transient individuals) of 370 (Haughey et al. 2020).

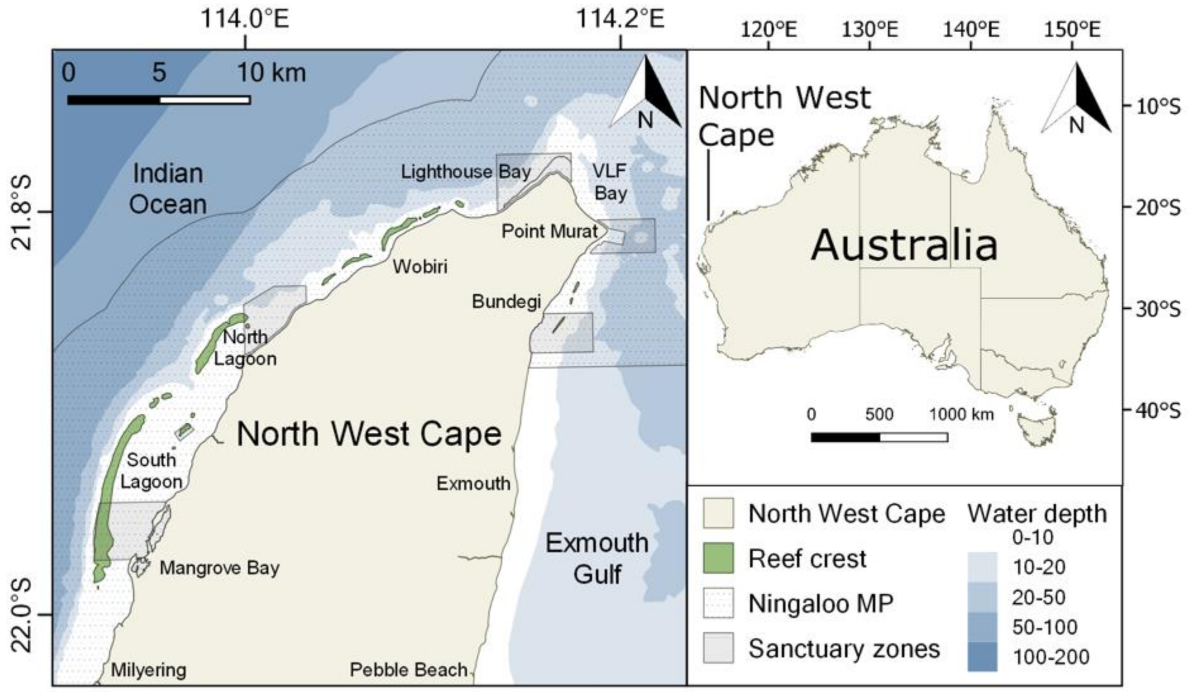

Figure 1.2 Map of the study area – the North West Cape, Western Australia – showing the locations of the reef crests and the water depth as well as Ningaloo Marine Park, including sanctuary zones. Inset shows the location of the North West Cape within Australia.

1.5 Aims and research objectives

In this thesis, I pursued two overall aims. Firstly, to review existing knowledge on mixed-species groups and perceptions of what constitutes a group to provide clarity about the definitions of key terms and to develop a conceptual framework for assessing the functions of mixed-species groups of delphinids. Secondly, to apply this framework on a model system consisting of sympatric humpback and bottlenose dolphins around the North West Cape to investigate their spatial and temporal co-occurrence patterns, to assess the functions of their mixed-species groups, and to evaluate the impact of mixed-species group formation on their behaviour. The specific objectives of this study, each corresponding to a thesis chapter, are as follows.

Objective 1. Review the literature on cetacean mixed-species groups (Chapter 2)

In Chapter 2, I conduct a literature review on cetacean mixed-species groups to: 1) address any inconsistencies in terminology and definitions; 2) assess their characteristics (i.e., the species involved, occurrence, and distribution); 3) evaluate what is known about their potential functions; and 4) use the results to propose standardised terminology and a conceptual framework to assist future studies with characterising their dynamics and functions.

Objective 2. Assess how delphinid groups are termed and defined (Chapter 3)

In Chapter 3, I examine the issues concerning how delphinid groups are termed and defined by conducting a literature review of published studies on delphinids and an online survey of the delphinid research community to: 1) determine which terms (i.e., *group*, *school*, *party*, and *pod*) are most commonly used, compare how they are defined, and propose recommendations for their future use; 2) assess the criteria in group definitions in terms of their use, relevance, and applicability; 3) identify issues associated with current group definitions as well as their potential solutions; and 4) propose a process for formulating biologically meaningful group definitions.

Objective 3. Investigate spatial and temporal occurrence patterns of humpback and bottlenose dolphins around the North West Cape (Chapter 4)

In Chapter 4, I assess spatial habitat partitioning between humpback and bottlenose dolphins around the North West Cape and determine whether these species occur together more or less often than expected by chance given their responses to environmental factors. Additionally, I analyse sighting data to elucidate temporal habitat partitioning and any temporal patterns in the occurrence of mixed-species groups. These analyses serve to elucidate coexistence mechanisms and to determine whether humpback and bottlenose dolphins truly form mixed-species groups as opposed to chance encounters or aggregations.

Objective 4. Investigate the potential benefits of mixed-species groups of humpback and bottlenose dolphins around the North West Cape (Chapter 5)

In Chapter 5, I analyse the characteristics (e.g., number of individuals, age composition, and behaviour) of single- and mixed-species sightings of humpback and bottlenose dolphins around the North West Cape to characterise their mixed-species groups in more detail and to evaluate which of three non-mutually exclusive hypotheses – the antipredator, foraging, and social advantage hypotheses – is most congruent with recorded observations. In doing so, I provide insight into the potential functions and evolutionary benefits of mixed-species groups of humpback and bottlenose dolphins.

Objective 5. Evaluate behavioural coexistence mechanisms of humpback and bottlenose dolphins around the North West Cape and further investigate the functions of their mixed-species groups (Chapter 6)

In Chapter 6, I use focal follow data to create Markov chain models of the behaviour of humpback and bottlenose dolphins observed around the North West Cape in order to compare the behavioural transitions (i.e., the probability that dolphins in a given behavioural state will transition to another behavioural state within a predetermined time step), behavioural bout lengths (i.e., the average amount of time that dolphins spend in a given behavioural state before transitioning to another), and behavioural budgets of the two species in single- and mixed-species sightings. These comparisons serve to elucidate potential behavioural coexistence mechanisms and to provide further insight into the benefits and costs of mixed-species group formation.

1.6 Thesis structure

This thesis consists of seven chapters. Each chapter, except for Chapters 1 (General introduction) and 7 (General discussion), was prepared so as to be a stand-alone manuscript published in a peer-reviewed scientific journal and, thus, provides the background information required to understand and interpret the findings presented therein. Consequently, there is some necessary overlap between chapters. Each chapter begins with a title page, followed by the text with the corresponding tables and figures. For the reader's convenience, the references for all chapters are combined into a single reference list at the end of the thesis.

Chapter 2

Dynamics of cetacean mixed-species groups: A review and conceptual framework for assessing their functional significance

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Dynamics of cetacean mixed-species groups: A review and conceptual framework for assessing their functional significance

2.1 Abstract

Numerous species of cetaceans have been recorded in mixed-species groups. By forming groups with individuals of different species, cetaceans may reduce predation risk, improve foraging, and gain social benefits. Most accounts of cetacean mixed-species groups, however, are descriptive and little is known about their functions. Furthermore, research has been hindered by inconsistent use of terminology and the lack of a conceptual framework to guide investigations. We reviewed the cetacean literature to compare how mixed-species groups have been termed and defined, to assess their characteristics, to evaluate what is known about their potential functions, and to provide directions for future study. In total, we reviewed 203 studies reporting observations of cetacean mixed-species groups. These mixed-species groups involved 54 different species, predominantly delphinids, that formed 216 different species pairs with varied morphologies and levels of relatedness. Cetacean mixed-species groups occurred across the globe, from tropical to cold temperate seas, from shallow coastal waters to the open ocean, and varied in characteristics such as group size and frequency of occurrence. Only 27 of the reviewed studies proposed and discussed the potential functions of cetacean mixed-species groups, suggesting reduced predation risk (5 species pairs), improved foraging (17 species pairs), and social benefits (12 species pairs) as the main drivers. In most cases, however, the factors that drive the formation of cetacean mixed-species groups remain unknown. Amongst the reviewed studies, mixed-species groups were referred to by various terms, often with no explicit definitions. To reduce this inconsistency, we recommend that future studies use only the term *mixed-species group* which we define as individuals of two or more species found in close spatial proximity due to mutual or unreciprocated attraction derived from evolutionary grouping benefits. There were also few structured investigations to confirm mixed-species group occurrence and to analyse their potential causes and consequences. To facilitate the study of cetacean mixed-species groups, we developed a conceptual framework that establishes diverse approaches to, firstly, distinguish mixed-species groups from chance encounters and aggregations and to, secondly, investigate their potential functions. This is necessary if we are to advance this field of study and improve our understanding of the role that mixed-species groups play in species and community ecology.

2.2 Introduction

Group living is fundamental to numerous species of animals as it conveys various benefits and costs (Alexander 1974, Krause & Ruxton 2002, Majolo & Huang 2018). By forming groups, individuals may decrease the risk of predation, improve foraging, increase their reproductive chances, and decrease the energetic cost of movement (Krause & Ruxton 2002, Majolo & Huang 2018). Individuals may also incur costs including increased competition for resources, increased probability of detection by predators, inbreeding, and increased risk of disease transmission among group members (Alexander 1974, Krause & Ruxton 2002, Majolo & Huang 2018). Studies on the costs and benefits of group living have provided a comprehensive understanding of the principles underlying group formation, particularly for groups composed of individuals of the same species. Much less is known, however, about the dynamics of groups composed of multiple species (Morse 1977, Stensland et al. 2003, Goodale et al. 2017). Mixed-species groups, also termed interspecific, polyspecific, or heterospecific groups or associations (Whitesides 1989, Heymann & Buchanan-Smith 2000, Stensland et al. 2003), are broadly defined as sets of individuals of two or more species that are seen in such close association that they can be regarded as members of the same group (Stensland et al. 2003). As such, mixed-species groups occur when there is an attraction between heterospecific individuals (Stensland et al. 2003, Cords & Würsig 2014). This attraction can be either mutual or unreciprocated, as long as the presence of the attracted species is tolerated by the other (Stensland et al. 2003). Mixed-species groups should be distinguished from aggregations of animals that are attracted to a common resource or that respond in a similar way to environmental stimuli and from chance encounters that result from the coincidental meeting of co-occurring species (Table 2.1) (Waser 1982, 1984, Cords & Würsig 2014). Mixed-species groups are thought to occur because they provide evolutionary benefits over individuals, populations, or species that do not mix (Stensland et al. 2003, Whitehead 2008, Ward & Webster 2016, Goodale et al. 2017). These benefits form the basis of the three principal functional explanations for the formation of mixed-species groups: reduced predation risk, improved foraging, and social advantages (Whitesides 1989, Stensland et al. 2003, Cords & Würsig 2014, Sridhar & Guttal 2018). Participation in mixed-species groups can lead to changes in behaviour and habitat use of one or more of the species involved as individuals alter their ecology in response to the presence of heterospecifics (Peres 1992b, Wolters & Zuberbühler 2003, Porter & Garber 2007, Sridhar et al. 2009). Thus, assessing the underlying causes and functions of mixed-species groups is important to better understand the dynamics of ecological communities (Veit & Harrison 2017, Zou et al. 2018).

Mixed-species groups have been recorded amongst closely and distantly related species including fishes (Lukoschek & McCormick 2000), birds (Sridhar et al. 2009), and mammals

(Stensland et al. 2003). Amongst mammals, mixed-species groups have been most commonly documented in ungulates, primates, and cetaceans (Morse 1977, Heymann & Buchanan-Smith 2000, Stensland et al. 2003, Cords & Würsig 2014, Heymann & Hsia 2015). Cetaceans, particularly delphinids, are known to form mixed-species groups with other cetaceans relatively frequently (Frantzis & Herzing 2002, Stensland et al. 2003, Bearzi 2005, Cords & Würsig 2014), as well as with other marine mammal species including pinnipeds (Bearzi 2006, Bacon et al. 2017) and sirenians (Kiszka 2007). Despite the apparent widespread occurrence of cetacean mixed-species groups (reviewed in: Stensland et al. 2003, Cords & Würsig 2014), large gaps remain in our understanding of their function and the mechanisms underlying their formation. This is largely due to the lack of dedicated studies on the potential drivers and associated costs and benefits of cetacean mixed-species groups (Stensland et al. 2003). The development of such studies is, in turn, hindered by inconsistent terminology and the absence of a conceptual framework to guide the development of cetacean mixed-species group studies. In the literature, several terms, including *association*, *aggregation*, and *mixed-species group*, are used interchangeably with varying definitions (Stensland et al. 2003). Moreover, there is no clear outline of how to distinguish cetacean mixed-species groups from chance encounters and aggregations and how to subsequently investigate their function. Consistent terminology and clear conceptual frameworks are essential when studying ecological phenomena to enable clear communication and to allow comparisons across taxa and regions (Fauth et al. 1996, Hall et al. 1997). Thus, the development and utilisation of such terminology and frameworks is key to the advancement and understanding of ecological topics.

Here, we review the literature on cetacean mixed-species groups to: 1) address any inconsistencies in terminology and definitions; 2) assess their characteristics (i.e., the species involved, occurrence, and distribution); 3) evaluate what is known about their potential functions; and 4) use the results to propose standardised terminology and a conceptual framework to assist future studies with characterising their dynamics and functions.

Table 2.1 Glossary of terms.

Term	Definition	References
mixed-species group	A set of individuals of two or more species that are seen in such close association that they can be regarded as members of the same group.	Stensland et al. 2003
chance encounter	A set of individuals of two or more species that are found in spatial proximity due to chance alone.	Waser 1982, Whitesides 1989
aggregation	A set of individuals of two or more species that are found in spatial proximity because they are attracted towards a common resource or respond to the same environmental stimuli.	Waser 1982, Powell 1985, Goodale et al. 2017

2.3 Methods

2.3.1 Literature review

We used the databases Scopus, ScienceDirect, and Web of Science and the search engine Google Scholar to search for relevant journal articles, book chapters, reports, and theses that contained records of cetacean mixed-species groups. As various terms, including *association* and *aggregation*, are often used interchangeably to refer to mixed-species groups, we included these terms in our literature search. More specifically, we combined each of several adjectives, including *mixed-species*, *interspecific*, *heterospecific*, and *polyspecific* with each of the key terms, including, but not limited to, *group*, *aggregation*, *association*, and *interaction* to form 40 phrases that refer to mixed-species groups (see Table S1.1 for a full list of the search terms). These phrases were combined with the English names of relevant taxa (i.e., cetacean, whale, dolphin, and porpoise) to create the full search queries. Each of the search queries was entered into the databases and search engine and the citation information of all the results (e.g., titles, abstracts, authors) was downloaded. The titles and abstracts of the results were then read and analysed. Studies on captive animals were removed as they do not represent natural grouping patterns. Studies that were based entirely on data that was obtained remotely (e.g., passive acoustics) or from isotopic or genetic analyses were also removed as they do not contain the observations required to analyse grouping dynamics. The remaining studies were reviewed and those that described multiple species of cetaceans as forming *aggregations*, *associations*, *groups*, or a term that is often considered synonymous (e.g., *school*, *herd*, and *pod*) were included for further analysis. Studies that used any term with an explicit definition that clearly distinguished it from a mixed-species group, however, were not included, as were studies that simply recorded species in the same area with no clear indication of mixed-species group formation. Finally, the reference lists of the included studies were searched to find any additional publications that were missed by the initial searches.

2.3.2 Analysis

The studies that met the criteria for inclusion were then reviewed to produce a comprehensive compilation of records of cetacean mixed-species groups. The taxonomic classification of all cetaceans involved in mixed-species groups was recorded to the lowest taxonomic level following the 2020 Society for Marine Mammalogy Committee on Taxonomy (Committee on Taxonomy 2020). Subsequent analyses of species composition were conducted on a species and family level. Where possible, we noted any additional information regarding group size, behaviour, and frequency of mixed-species groups to provide a more detailed understanding of the dynamics of cetacean mixed-species groups. All the terms used to describe mixed-species groups, as well as any explicit definitions of those terms, were also recorded.

To gain insights into the distribution and frequency of cetacean mixed-species groups across the major ocean basins we mapped their geographical distribution using QGIS (QGIS Development Team 2019) and Plotly (Plotly Technologies Inc. 2015). As the precise geographical locations of the mixed-species groups were often unavailable, we assigned a location value (i.e., ocean basin) to each study based on the study area. Additionally, to understand and visualise the spatial distribution of and the relationships between the cetacean species that most often form mixed-species groups, we constructed a social network diagram where each node represents a species and each edge the occurrences of a species pair in mixed-species groups. The edges were weighted according to the total number of studies reporting each species pair while the sizes of the nodes were made proportional to the total number of partner species that each species had. The average values of each species' distribution in terms of water depth and latitude were obtained from the Encyclopedia of Marine Mammals (Würsig et al. 2018) and used to position each species' node along the x and y axes, respectively, in the network diagram.

Finally, to determine the level to which cetacean mixed-species groups have been researched, the studies were separated into those that simply reported the occurrence of cetacean mixed-species groups and those that used observations or investigations to propose functional explanations for them. Details of these investigations and their conclusions were then compiled. Analysis of the data was conducted using Python (Python Software Foundation 2016) and all figures were created using Plotly (Plotly Technologies Inc. 2015) in Python.

2.4 Results

The literature search returned 2154 results, of which 98 were studies that met our criteria for inclusion. Additionally, 94 studies were added by tracing cited studies and a further 11 studies were obtained from a bibliography of publications on cetacean mixed-species groups (Rowley 2020), amounting to a total of 203 studies. Cetacean mixed-species groups appear to have been first reported in the literature in 1961, with the majority of reports having been published since 1990 (Figure 2.1).

2.4.1 Definitions and terminology

Out of the 203 studies obtained from the literature review, 116 studies (57.1%) referred to situations where multiple species of cetaceans were observed in close spatial proximity as *groups*, 95 (46.8%) as *associations*, 42 (20.7%) as *schools*, 26 (12.8%) as *aggregations*, while 11 studies (5.4%) used other terms such as *assemblage*, *encounter*, and *herd* (Figure 2.2). Over a third of the studies (36.0%) used multiple terms synonymously. Of those studies that used the term *group*, only 39 (33.6%) provided either a specific definition of a mixed-species group or a definition of group that was applied to both single-species groups and mixed-species groups. This trend was similar for the terms *association* (18 definitions, 19.0% of studies) and *aggregation* (8 definitions, 30.8% of studies), while only 3 (7.1%) studies that used the term *school* provided an explicit definition of this term (Figure 2.2). Furthermore, only five studies utilised some technique (e.g., analysis of interspecies association patterns or a minimum time limit) to confirm that potential mixed-species groups were indeed mixed-species groups and not simply chance encounters or aggregations.

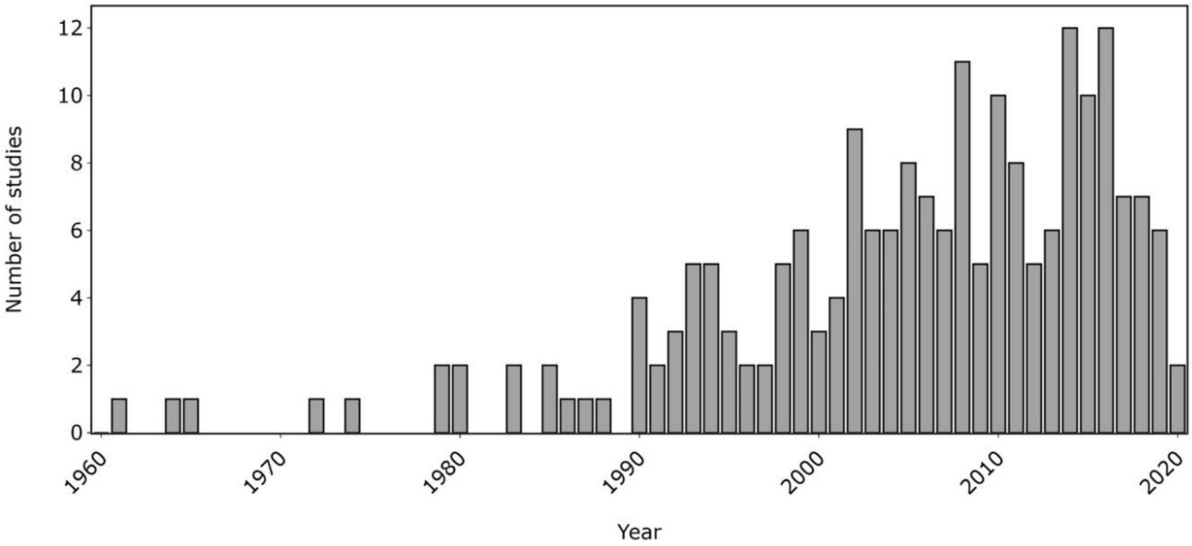

Figure 2.1 Number of reviewed studies reporting cetacean mixed-species groups from 1961 to 2020.

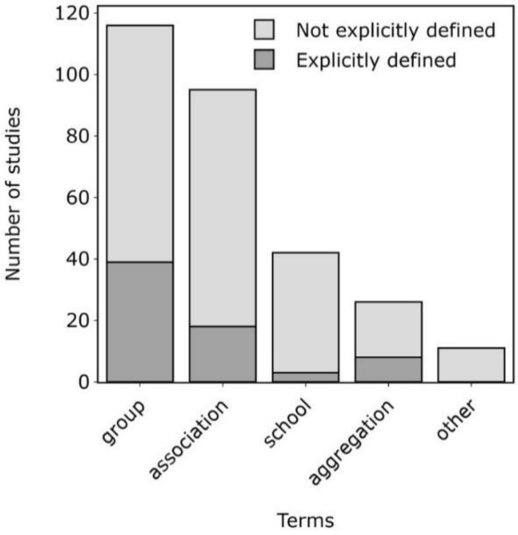

Figure 2.2 Number of reviewed studies published between 1961 and 2020 that used several terms (i.e., *group*, *association*, *school* and *aggregation*), with or without an explicit definition, to refer to situations where multiple species of cetaceans were observed in close spatial proximity. Other terms, including *assemblage*, *encounter*, and *herd*, are combined in the final bar. These terms were typically preceded by a variety of adjectives including *mixed-species*, *interspecific*, and *heterospecific*. The sum of the bars is greater than the total number of studies found by the review as over a third of the studies employed multiple terms.

2.4.2 Species composition and diversity

The reviewed studies revealed that 54 species of cetaceans belonging to five families of Odontocetes (Delphinidae, Kogiidae, Phocoenidae, Physeteridae, and Ziphiidae) and three families of Mysticetes (Balaenidae, Balaenopteridae, and Eschrichtiidae) were reported to form groups with other cetacean species. Of these species, 43 were Odontocetes and 11 were Mysticetes. The Odontocetes most commonly reported in mixed-species groups belonged to the family Delphinidae, with 197 studies reporting participation in mixed-species groups for almost all known species. The only species of the family Physeteridae, the sperm whale (*Physeter macrocephalus*), was also well represented with 25 studies reporting its occurrence in mixed-species groups. In contrast, species of the remaining Odontocete families (i.e., Phocoenidae, Ziphiidae, and Kogiidae) were rarely reported in mixed-species groups. Amongst the Mysticetes, the family Balaenopteridae accounted for most of the records (48 studies and 7 species), followed by the single Eschrichtiidae species – the gray whale (*Eschrichtius robustus*) (9 studies), and the family Balaenidae (6 studies and 3 species).

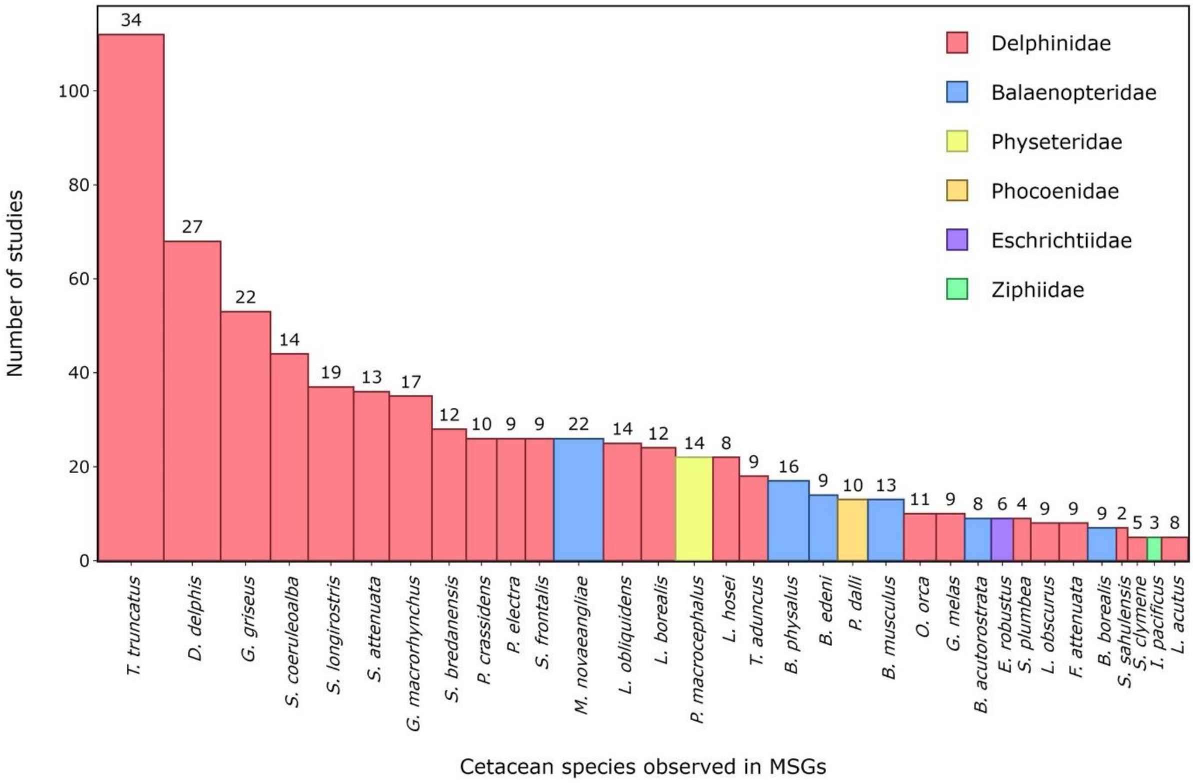

Figure 2.3 The 33 species of cetaceans that were reported in mixed-species groups by five or more studies published between 1961 and 2020 that were obtained from a literature review on cetacean mixed-species groups. The bar heights represent the number of studies reporting each species' participation in mixed-species groups as displayed on the y axis. The bar widths are proportional to the total number of species that each species has been observed with in mixed-species groups, i.e., the number of partner species, which is written above each bar. The bars are coloured according to the species' family.

At the species level, the common bottlenose dolphin (*Tursiops truncatus*), the common dolphin (*Delphinus delphis*), and Risso's dolphin (*Grampus griseus*) were the three most commonly reported cetacean species in mixed-species groups (Figure 2.3). These same three species also had the greatest diversity of partner species in mixed-species groups, with the common bottlenose dolphin associating with a total of 34 different species, the common dolphin with 27, and Risso's dolphin with 22 (Figure 2.3 and Figure 2.4). Among Mysticetes, the humpback whale (*Megaptera novaeangliae*) was the most often reported species in mixed-species groups and also the one with the highest diversity of partner species (Figure 2.3). Other delphinid species, along with several species of Balaenopteridae, made up the majority of the 33 cetacean species that were reported in mixed-species groups by more than five studies, with only four species representing the remaining cetacean families: the sperm whale, Dall's porpoise (*Phocoenoides dalli*), the gray whale, and Longman's beaked whale (*Indopacetus pacificus*) (Figure 2.3).

The reported cetacean mixed-species groups typically contained only two species, yet groups composed of up to four species were also observed (e.g., Ballance & Pitman 1998, Kinzey et al. 2000, Anderson 2005, Anderson et al. 2006, Weir 2011, Bacon et al. 2017, Alves et al. 2018). We found records for 216 different species pairs observed within mixed-species groups, 47 of which were recorded by 5 or more studies (Figure 2.4). Almost all species pairs (91.7%) were from different genera yet the majority belonged to the same family (56.9%) and suborder (i.e., Odontoceti or Mysticeti) (73.2%). In particular, the majority of species pairs in cetacean mixed-species groups consisted of two delphinid species (50.9% of reported species pairs). Furthermore, of the 47 species pairs with five or more records, 35 (74.5%) comprised two delphinid species and all but two involved at least one delphinid (45 species pairs, 95.7%) (Figure 2.4). The most commonly reported species pairs in mixed-species groups were: common dolphin – striped dolphin (*Stenella coeruleoalba*) (34 studies), Risso's dolphin – common bottlenose dolphin (32 studies), and spinner dolphin (*Stenella longirostris*) – pantropical spotted dolphin (*Stenella attenuata*) (27 studies) (Figure 2.4). Many species pairs were found together much less frequently, with the majority (169 pairs) being reported by fewer than 5 studies. Marine mammal surveys across a variety of habitats and spatial scales typically gauged the proportion of cetacean groups that were mixed to be under 10% (Table 2.2). Dedicated studies of certain cetacean species that are known to form mixed-species groups, on the other hand, reported higher frequencies, with mixed-species groups accounting for up to a third of all groups sighted in some populations (Table 2.3) (Frantzis & Herzing 2002, Acevedo-Gutiérrez et al. 2005, Thompson 2010, Kiszka et al. 2011a).

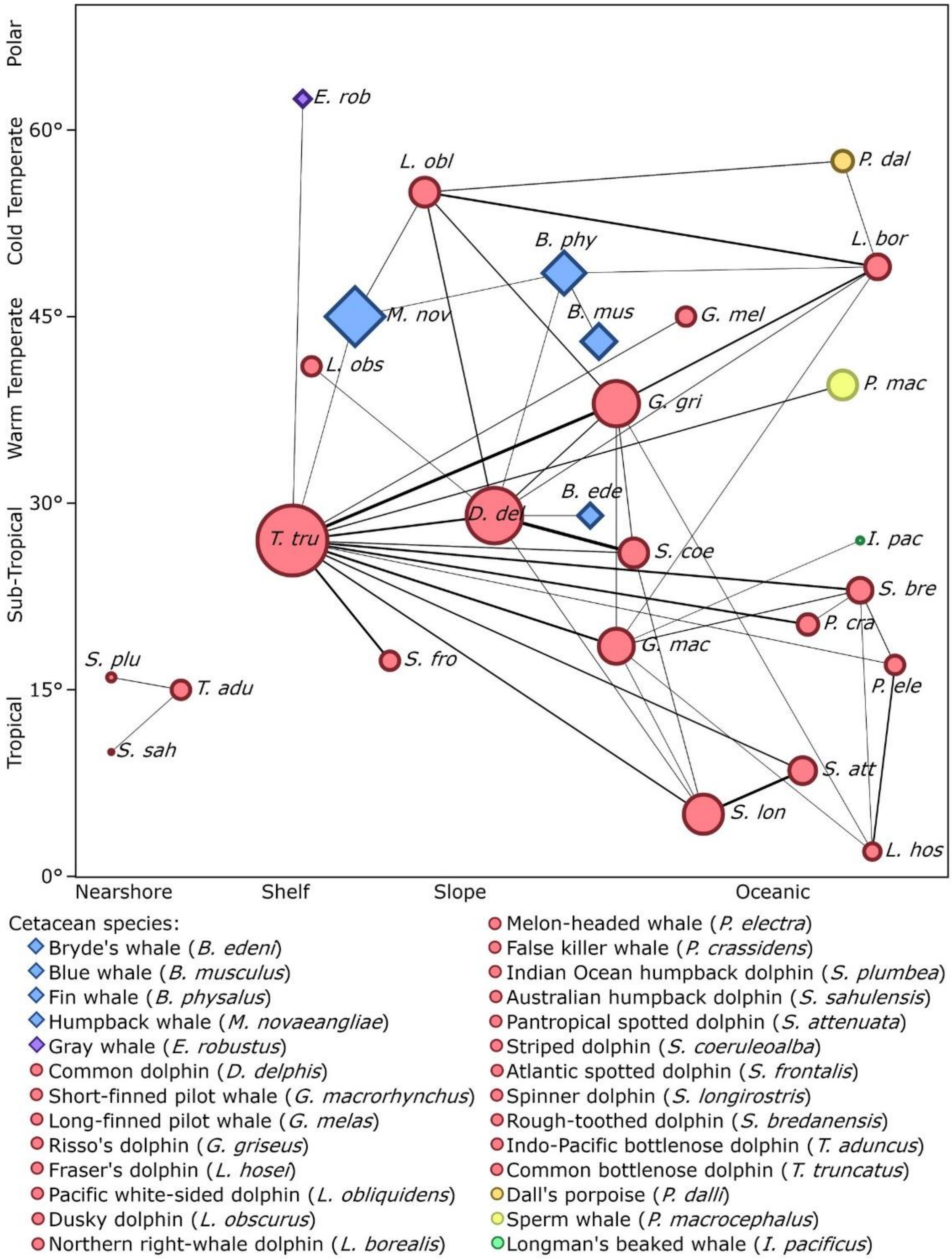

Figure 2.4 Social network diagram showing the 47 species pairs (edges) that were reported together in mixed-species groups by five or more of the studies reviewed. The width of each edge is proportional to the total number of studies that reported that pair of species. The shape of each node indicates if the species is a Mysticete (diamond) or an Odontocete (circle) while the colours represent the species' family. The size of each node is proportional to the total number of partner species that each species has. Each species' node is placed approximately according to its average distribution with the x axis representing water depth and the y axis representing latitude.

Table 2.2 Cetacean mixed-species groups as a percentage of all groups (i.e., single- and mixed-species groups) that were observed during surveys for species belonging to the target taxa. All surveys were boat-based except those of Bacon et al. (2017) which was aerial-based and Koper & Plön (2016) which was land- and boat-based.

Target taxon	Location	Mixed %	Reference
Odontocetes	Tropical Eastern Pacific	28.0	Oswald et al. 2008
Marine mammals	Eastern Tropical Pacific	12.0	Kinzey et al. 2000
Odontocetes	Temperate Eastern Pacific	11.0	Oswald et al. 2008
Marine mammals	Eastern Tropical Pacific	11.0	Kinzey et al. 2000
Cetaceans	Madeira	7.8	Alves et al. 2018
Cetaceans	La Réunion	6.3	Dulau-Drouot et al. 2008
Cetaceans	Santa Monica Bay, California	5.3	Bearzi & Saylan 2011
Cetaceans	Subtropical south-western Atlantic	5.2	Di Tullio et al. 2016
Cetaceans	Maldives	4.5	Anderson 2005
Cetaceans	Western Tropical Indian Ocean	4.4	Ballance & Pitman 1998
Marine mammals	Southern California Bight	2.0	Bacon et al. 2017
Cetaceans	Algoa Bay, South Africa	1.9	Koper & Plön 2016
Cetaceans	Northern Gulf of Mexico	1.4	Maze-Foley & Mullin 2006

Table 2.3 Mixed-species groups involving delphinids recorded as a percentage of all groups (i.e., single- and mixed-species groups) of particular populations of the listed species as obtained through dedicated studies of mixed-species groups.

Species	Location	Mixed %	Reference
Stenella coeruleoalba – Delphinus delphis – Grampus griseus	Gulf of Corinth, Greece	35.0	Frantzis & Herzing 2002
Sotalia guianensis – Tursiops truncatus	Gandoca-Manzanillo, Costa Rica	32.4	Acevedo-Gutiérrez et al. 2005
Sotalia guianensis – Tursiops truncatus	Gandoca-Manzanillo, Costa Rica	23.6	Thompson 2010
Stenella attenuata – Stenella longirostris	Mayotte	21.0	Kiszka et al. 2011
Stenella frontalis – Tursiops truncatus	Bahamas	15.2	Herzing & Johnson 1997
Stenella frontalis – Tursiops truncatus	Bahamas	8.9	Melillo et al. 2009

2.4.3 Distribution and habitat

Cetacean mixed-species groups were observed from tropical to cold temperate waters in all the major ocean basins, except for the Southern Ocean (Figure 2.5). Furthermore, they were observed across a range of depths and at varying distances to shore, including: shallow coastal waters (<20 m; e.g., Acevedo-Gutiérrez et al. 2005, Hunt 2018), over the continental shelf (20-200 m; e.g., Gowans & Whitehead 1995, Mullin et al. 2004), around oceanic islands (e.g., Anderson 2005, Quérouil et al. 2008, Gannier 2009, Kiszka et al. 2011), and in the open ocean (<2,000 m; e.g., Scott & Cattanach 1998, Jackson et al. 2008).

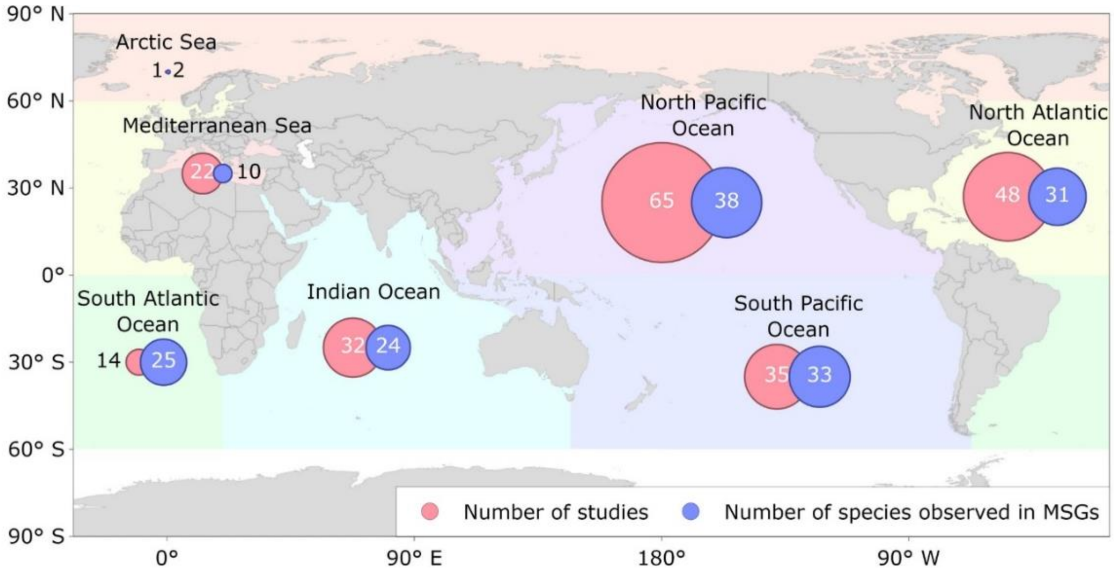

Figure 2.5 Geographical distribution of the location of the studies reviewed that reported cetacean mixed-species groups across the major ocean basins from 1961 to 2020. Numbers inside circles represent the number of reviewed studies reporting the occurrence of cetacean mixed-species groups in each ocean basin and the number of cetacean species observed in those mixed-species groups.

2.4.4 Functional explanations for cetacean mixed-species group formation

Of the 203 studies reviewed, 27 discussed potential functional explanations based on specific observations or investigations of cetacean mixed-species groups (Table 2.4). These studies covered 25 species pairs of cetaceans, 7 of which had multiple proposed functional explanations. In total, 5 species pairs were hypothesised to form mixed-species groups to reduce predation risk, 17 to improve foraging, and 12 to gain social benefits (Table 2.4). These hypotheses, rather than conclusions, rely on inferences drawn from behavioural observations and spatial variations in the distribution of single-species groups and mixed-species groups. Few studies (n=5) determined that observed groupings were mixed-species groups rather than mere chance encounters or aggregations and no study, to our knowledge, has directly tested whether participation in cetacean mixed-species groups provides antipredator, foraging, or social benefits to group members. Nevertheless, the results provide an indication of the factors that may potentially drive cetacean mixed-species group formation.

Table 2.4 Pairs of cetacean species observed in mixed-species groups for which the potential functional explanations have been proposed. A question mark indicates that the benefit has been hypothesised based on observations but not investigated.

Species	Functional Explanation(s)	References
Balaenoptera edeni – Delphinus delphis	foraging	Burgess 2006, Stockin et al. 2009
Megaptera novaeangliae – Orcinus orca	foraging	Jourdain & Vongraven 2017
Megaptera novaeangliae – Tursiops aduncus	foraging?	Koper & Plön 2016
Eschrichtius robustus – Tursiops truncatus	social	Shane 1994
Delphinus delphis – Grampus griseus	social?	Frantzis & Herzing 2002
Delphinus delphis – Stenella coeruleoalba	social	García et al. 2000, Frantzis & Herzing 2002
	foraging	Quérouil et al. 2008
Delphinus delphis – Stenella frontalis	foraging	Quérouil et al. 2008
Delphinus delphis – Tursiops aduncus	antipredator?	Koper & Plön 2016
Delphinus delphis – Tursiops truncatus	foraging	Quérouil et al. 2008
Globicephala macrorhynchus – Tursiops truncatus	foraging	Shane 1994
Grampus griseus – Lagenorhynchus obliquidens	foraging	Black 1994, Bacon et al. 2017
Grampus griseus – Lissodelphis borealis	foraging	Smultea et al. 2014, Bacon et al. 2017
Grampus griseus – Stenella coeruleoalba	social?	Frantzis & Herzing 2002
Grampus griseus – Tursiops truncatus	foraging; social?	Shane 1994, Hodgins et al. 2014, Bacon et al. 2017
Lagenorhynchus obliquidens – Lissodelphis borealis	foraging?; antipredator?	Black 1994
Lissodelphis borealis – Physeter macrocephalus	foraging	Smultea et al. 2014
Orcaella heinsohni – Sousa sahulensis	social	Parra 2005
Pseudorca crassidens – Tursiops truncatus	foraging; antipredator?; social?	Zaeschmar et al. 2013, 2014
Sotalia guianensis – Tursiops truncatus	social	Acevedo-Gutiérrez et al. 2005, Thompson 2010
Sousa plumbea – Tursiops aduncus	antipredator?; foraging?; social?	Koper & Plön 2016

Sousa sahulensis – Tursiops aduncus	foraging?	Corkeron 1990
Stenella attenuata – Stenella longirostris	antipredator; social?	Scott & Cattanach 1998, Psarakos et al. 2003, Kiszka et al. 2011
Stenella coeruleoalba – Stenella frontalis	foraging	Quérouil et al. 2008
Stenella frontalis – Tursiops truncatus	social	Herzing & Johnson 1997, Herzing et al. 2003, Melillo et al. 2009, Elliser & Herzing 2016a, b
	foraging	Quérouil et al. 2008
Tursiops truncatus – Physeter macrocephalus	social	Shane 1994, Wilson & Krause 2013s

2.4.4.1 Antipredator advantage hypothesis

One of the most common functional explanations for the formation of mixed-species groups is that participating individuals benefit from a reduced risk of predation (Whitesides 1989, Stensland et al. 2003). The presence of heterospecifics with a greater ability to detect predators or better defensive capabilities can lead to the formation of mixed-species groups (Whitesides 1989, Heymann & Buchanan-Smith 2000, Stensland et al. 2003, Kiszka et al. 2011a, Cords & Würsig 2014). In addition, an increase in group size as a result of forming a mixed-species group can have similar effects and can also dilute the risk of predation on individual group members (Gygax 2002b, Cords & Würsig 2014, Goodale et al. 2017).

In the oceanic eastern tropical Pacific, pantropical spotted and spinner dolphins often form mixed-species groups (e.g., Au & Perryman 1985, Reilly 1990, Scott & Cattanach 1998, Oswald et al. 2008). Long-term observations show no evidence of foraging when in mixed-species groups, likely due to interspecific differences in foraging behaviour, thus making foraging benefits an unlikely driver of these mixed-species groups (Norris & Dohl 1980, Scott & Cattanach 1998). Instead, given the potential high risk of predation faced by these oceanic dolphins from pelagic sharks, killer whales (*Orcinus orca*) and other large delphinids (e.g., false killer whales, *Pseudorca crassidens*), it has been suggested that these species form mixed-species groups to reduce predation risk (Scott & Cattanach 1998). More specifically, spinner dolphins, which feed on the deep scattering layer at night and rest during the day (Norris & Dohl 1980), may seek refuge amongst groups of pantropical spotted dolphins, which are active and more alert during the day, and thus benefit from their vigilance (Scott & Cattanach 1998). These species also form mixed-species groups around the island of Mayotte in the Indian Ocean (Gross et al. 2009, Kiszka et al. 2011a). Here, the absence of feeding and social interactions between the two species does not support the foraging and social benefits hypotheses, respectively. Instead, these mixed-species groups form when spinner dolphins shift habitat to deeper waters where pantropical spotted dolphins preferentially occur, suggesting that spinner dolphins initiate these mixed-species groups, possibly to reduce predation risk while transiting between resting areas (Kiszka et al. 2011a).

2.4.4.2 Foraging advantage hypothesis

Foraging benefits gained from mixed-species groups may take the form of an improved ability to detect, herd, and/or utilise food resources (Stensland et al. 2003) and may be obtained by mutual or non-mutual information exchange and coordinated foraging (Whitesides 1989, Sridhar et al. 2009). Gatherings of different cetacean species at prey aggregations are fairly common and may also include seabirds, sharks, and large predatory fishes (Würsig & Würsig 1979, Evans 1982, Scott & Cattanach 1998, Markowitz 2004, Kiszka et al. 2015, Veit & Harrison 2017). Although these gatherings involve the presence of different species in close spatial proximity, and so may be considered mixed-species groups, it is not always clear if their formation is due to a mutual attraction to common prey or an attraction between species (Quérouil et al. 2008).

Mixed-species groups of common bottlenose dolphins and false killer whales have been observed in numerous locations (e.g., (Scott & Chivers 1990, Anderson 2005, Maze-Foley & Mullin 2006, Baird et al. 2008), including off the coast of New Zealand where they seem to engage in cooperative foraging (Zaeschmar et al. 2013). During foraging, both species feed on the same species of fishes after herding and driving them towards the surface (Zaeschmar et al. 2013). The apparent cooperative nature of the foraging suggests that these mixed-species groups may provide mutualistic benefits. Nonetheless, the degree of cooperation is unknown and the possibility of social parasitism cannot be disregarded (Zaeschmar et al. 2014).

Common bottlenose dolphins, particularly the offshore ecotype, in tropical and warm temperate waters of the Pacific and Atlantic Oceans also regularly form mixed-species groups with short-finned pilot whales (*Globicephala macrorhynchus*) (e.g., (Scott & Chivers 1990, Mangels & Gerrodette 1994, Gannier 2000, Weir 2006) and with Risso's dolphins (*Grampus griseus*) (e.g., Scott & Chivers 1990, Bearzi 2005, Maze-Foley & Mullin 2006, Weir 2011, Bacon et al. 2017, Viana 2019), particularly when the latter species are foraging (Norris & Prescott 1961, Shane 1994). The benefit here, however, may not be mutual. Common bottlenose dolphins tend to initiate the formation of mixed-species groups and short-finned pilot whales sometimes display avoidance behaviour when common bottlenose dolphins approach. This suggests that the common bottlenose dolphins seek out the short-finned pilot whales and Risso's dolphins to improve foraging success, although it is unknown if the other species benefit from these mixed-species groups (Shane 1994, Bacon et al. 2017). Common bottlenose dolphins have also been frequently observed with long-finned pilot whales (*Globicephala melas*) around New Zealand (Markowitz 2004, Zaeschmar 2014), in the North

Atlantic (Gowans & Whitehead 1995, Weir et al. 2001), and in the Mediterranean (Cañadas et al. 2002), possibly for similar reasons, although these mixed-species groups have not been investigated in detail.

Off the coast of New Zealand, Bryde's whales (*Balaenoptera edeni*) often follow feeding common dolphin groups and it has been hypothesised that the Bryde's whales benefit from the common dolphins' ability to herd and concentrate epipelagic fish schools (O'Callaghan & Baker 2002, Burgess 2006, Stockin et al. 2009). Similarly, in Norway, humpback whales (*Megaptera novaeangliae*) lunge feed on herring schools that are herded by killer whales (Jourdain & Vongraven 2017). It is hypothesised that in this case, humpback whales benefit from the foraging effort of killer whales who may, in turn, be negatively affected by the interspecific competition for prey (Burgess 2006, Jourdain & Vongraven 2017).

2.4.4.3 Social advantage hypothesis

Cetaceans, particularly delphinids, are highly social animals with often complex social structures (Mann et al. 2000, Gowans et al. 2007). Accordingly, there are multiple contrasting social motives that have been hypothesised to lead to both agonistic and affiliative social mixed-species groups involving aggressive, sexual, playful, and caring behaviours (e.g., Herzing & Johnson 1997, Stensland et al. 2003, Parra 2005, Acevedo-Gutiérrez et al. 2005, Herzing & Elliser 2013).

Common bottlenose and Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas are often observed in mixed-species groups, with members engaging in socio-sexual behaviours (Herzing & Johnson 1997, Melillo et al. 2009, Herzing & Elliser 2013). These sexual interactions are typically initiated by common bottlenose dolphins, mostly subadults, who may seek copulations with Atlantic spotted dolphins as they are unable to copulate with conspecifics due to their lower intraspecific social status (Melillo et al. 2009). Alternatively, these dolphins may use sexual behaviour to reduce levels of aggression by replacing aggressive interactions with sexual ones (Melillo et al. 2009). Furthermore, male Atlantic spotted and male common bottlenose dolphins have also been observed forming interspecific coalitions (defined as "*the joining of forces by two or more parties during a conflict of interest with other parties*": de Waal & Harcourt 1992, Herzing & Johnson 1997), to both chase away other males and pursue females of both species, although subsequent copulation is only intraspecific (Herzing & Johnson 1997). Additionally, males of these species often engage in sexual interactions with each other (Herzing & Johnson 1997, Herzing & Elliser 2013). In these cases, sexual-aggressive behaviours between males and shared pursuits of females may form bonds that later provide a benefit when they form interspecific coalitions during aggressive encounters (Herzing & Johnson 1997).

Aggressive and sexual behaviours are also typical of mixed-species groups that involve common bottlenose dolphins and Guiana dolphins (*Sotalia guianensis*) along Costa Rica’s Caribbean coast (Acevedo-Gutiérrez et al. 2005, May-Collado 2010). Male common bottlenose dolphins exhibit aggressive behaviours towards Guiana dolphins, such as biting, body slamming, and chasing, seemingly in order to separate female Guiana dolphins from their conspecifics to mate with them (May-Collado 2010). These observations are supported by photographic evidence and sightings of putative hybrids, although genetic confirmation of hybridisation is required (Acevedo-Gutiérrez et al. 2005). Common and Indo-Pacific (*Tursiops aduncus*) bottlenose dolphins have been observed exhibiting aggressive-sexual behaviours towards Australian (*Sousa sahulensis*) and Indian Ocean humpback dolphins (*Sousa plumbea*) (Saayman et al. 1972, Baldwin et al. 2004, Minton et al. 2010, Ansmann 2011, Cerchio et al. 2015). Off the coast of Zanzibar, young male Indo-Pacific bottlenose dolphins harass female Indian Ocean humpback dolphins, possibly as a means of practising and developing skills involved in social behaviours in order to increase their social status (Stensland et al. 2003).

Similar interactions occur in northern Australia between Australian humpback dolphins and Australian snubfin dolphins (*Orcaella heinsohni*). In Cleveland Bay, North Queensland, Australian humpback and Australian snubfin dolphins live in sympatry, have overlapping ranges and exhibit interspecies affiliative and aggressive interactions (Parra 2005, 2006). Aggressive interactions are more frequently observed and are mainly initiated by adult male Australian humpback dolphins, who pursue and seek physical contact with adult female Australian snubfin dolphins. The female Australian snubfin dolphins, often accompanied by calves, attempt to avoid these interactions and flee (Parra 2005). It is hypothesised that male Australian humpback dolphins may use these interactions as opportunities for physical training or skill development, a function that would have beneficial effects for interactions with female conspecifics (Parra 2005). This is similar to what has been suggested for incidences of male common bottlenose dolphins attacking and killing harbour porpoises (*Phocoena phocoena*) in Scotland and California (Patterson et al. 1998, Cotter et al. 2012).

Affiliative behaviours, including interspecific alloparenting are also occasionally recorded. Herzing & Johnson (1997), for example, reported two cases from the Bahamas of adult female Atlantic spotted dolphins swimming with common bottlenose dolphin calves. In New Zealand, Markowitz (2004) observed a short-term association of a calf common dolphin and an adult dusky dolphin (*Lagenorhynchus obscurus*) while Stensland et al. (2003) refer to an observation of an Indian Ocean humpback dolphin calf that travelled for several hours with a large group of Indo-Pacific bottlenose dolphin mothers and calves in Zanzibar. It is not known, however, whether these social behaviours are isolated events or if they represent broader patterns of interspecific behaviour.

Mixed-species social behaviours may also be driven by a lack of conspecifics. In the Mediterranean Sea, common dolphins regularly form mixed-species groups with striped dolphins (e.g., Forcada et al. 1994, Cañadas & Hammond 2008, Bearzi et al. 2011, Santoro et al. 2015, Santostasi et al. 2016) and, on occasion, Risso's dolphins (e.g., Cañadas et al. 2002, Frantzis & Herzing 2002, Bearzi et al. 2016) and common bottlenose dolphins (e.g., Ryan et al. 2014, Pace et al. 2015, Espada et al. 2019). Common dolphin populations in the Mediterranean Sea have declined dramatically since the 1980s (Bearzi et al. 2003) and, in areas where they are now uncommon, the frequency of mixed-species groups is higher (Frantzis & Herzing 2002). It has, therefore, been suggested that the lack of interactions with conspecifics might be an important driver of the formation of mixed-species groups in this region. Interactions between common dolphins and other species appear to be mainly socially driven (García et al. 2000, Frantzis & Herzing 2002) and there are numerous records of hybrid individuals between common and striped dolphins (Bearzi et al. 2011, Santostasi et al. 2016, Antoniou et al. 2018, Bonizzoni et al. 2019) and between common and common bottlenose dolphins (Espada et al. 2019).

2.5 Discussion

Many species of cetaceans in a variety of habitats have been reported to form mixed-species groups, potentially due to the evolutionary benefits (antipredator, foraging and social) they may gain. The studies on cetacean mixed-species groups reviewed here often used terminology inconsistently and most did not confirm that observed sets of individuals did indeed form mixed-species groups, rather than mere chance encounters or aggregations. Thus, we cannot be certain that all the records in this review truly represent mixed-species groups, however, because they are potentially mixed-species groups, they were included and treated as such. Furthermore, many studies lacked the thorough testing of hypotheses that is required to determine the potential functional explanations of the observed mixed-species groups.

To better understand the incidence and ecological role of cetacean mixed-species groups, we need to go beyond descriptive accounts and investigate the behavioural and ecological drivers of their formation (Stensland et al. 2003). We reviewed the literature on cetacean mixed-species groups to: address inconsistencies in terminology; assess their characteristics (e.g., species involved, location, frequency); and evaluate what is known about their functional role. Finally, we discuss the results of this review and propose a standardised terminology and a conceptual framework to assist future research (Figure 2.6).

2.5.1 Current knowledge on cetacean mixed-species groups

Amongst the cetacean species that have been reported in mixed-species groups, delphinids are the most frequently involved and the ones with the most diversity of partner species. The dynamic and fluid social structure of many delphinid species could potentially facilitate the formation of mixed-species groups (Stensland et al. 2003) as could a higher risk of predation when compared to the larger cetaceans, such as the baleen whales. Cetacean species with broad distributions centred on the sub-tropics and the warm temperate zone, such as the common bottlenose dolphin, also appear to be disproportionately represented, with more records of participation in mixed-species groups and more partner species. This is possibly a result of their abundance and widespread distribution bringing them often into contact with a range of other cetacean species. These species are also, however, amongst the most studied (Wells & Scott 2018), while many of those that are rarely, or never, reported in mixed-species groups, such as the beaked whales, are poorly studied (MacLeod 2018). Consequently, these results may not reflect the true composition and diversity of cetacean mixed-species groups and may be influenced by the greater research effort dedicated to certain species.

Most of the 216 species pairs that were reported in mixed-species groups were composed of two delphinids, however there was considerable variation in the relatedness, morphology, and behaviour of partner species. Some mixed-species groups were composed of pairs of closely related and morphologically similar species, such as pantropical spotted and spinner dolphins (e.g., Scott & Cattanach 1998, Kiszka et al. 2011), while others consisted of distant and dissimilar species, such as common dolphins and Bryde’s whales (e.g., Burgess 2006, Stockin et al. 2009, Penry et al. 2011). Furthermore, some species pairs were frequently reported together (e.g., common dolphin – striped dolphin and spinner dolphin – pantropical spotted dolphin) (Table 2.3), while others (e.g., common bottlenose dolphin – dusky dolphin) have been rarely, if ever, observed together in mixed-species groups (Würsig & Würsig 1979, Markowitz 2004). Most cetacean species pairs belonged to different genera but the same family and suborder, suggesting that a moderate level of dissimilarity between cetacean species is favourable to mixed-species group formation. This is in accordance with research on other taxa, including primates and birds, where it has been shown that optimum levels of dissimilarity in characteristics such as diet, habitat use, and body size increase the frequency of mixed-species group occurrence (Heymann & Buchanan-Smith 2000, Sridhar et al. 2009, Heymann & Hsia 2015, Sridhar & Guttal 2018). Currently, however, it is not well understood which are the biological factors that determine if and how often cetacean species form mixed-species groups, but future analysis of the similarities and dissimilarities in corresponding characteristics between pairs of cetacean species could provide insight into this question.

It is apparent that mixed-species groups are formed by both inshore and offshore species of cetaceans in a variety of habitats, however, the lack of available information regarding the distribution and grouping dynamics of cetacean mixed-species groups makes it challenging to establish any detailed patterns. We can, nonetheless, observe several potential trends pertaining to the influence of environmental factors. Water depth and distance to shore appear to affect mixed-species groups in the same way they do single-species groups (Wells et al. 1980), with coastal species often forming small groups of 5 – 20 individuals (e.g., Herzing & Johnson 1997, Acevedo-Gutiérrez et al. 2005, Thompson 2010) and oceanic species forming large groups of hundreds and even thousands (e.g., Hill & Barlow 1992, Wade & Gerrodette 1993, Scott & Cattanach 1998, Appler et al. 2004, Dulau-Drouot et al. 2008). For some species, such as the common bottlenose dolphin, mixed-species groups have been shown to be more common in oceanic waters (Scott & Chivers 1990). Potentially higher predation risk offshore may drive certain species to form larger groups (Gygax 2002a) including mixed-species groups when faced with a low abundance of conspecifics. However, some species that inhabit shallow coastal waters also frequently form mixed-species groups (e.g., Herzing & Johnson 1997, Acevedo-Gutiérrez et al. 2005, Thompson 2010), so the drivers of mixed-species group formation likely vary across taxa and habitats. Cetacean mixed-species groups were most commonly reported in the North Pacific and North Atlantic, potentially due to the higher species diversity within those areas (Kaschner et al. 2011, Pompa et al. 2011), although this result may also be influenced by uneven research effort (Kaschner et al. 2012).

2.5.2 A conceptual framework for investigating the functional significance of cetacean mixed-species groups

To facilitate future studies, we use the results of this review to propose a standardised terminology and a conceptual framework that 1) defines and characterises cetacean mixed-species groups (Figure 2.6, Boxes 1a-1i) and that 2) details how to investigate their functions by testing relevant hypotheses (Figure 2.6, Boxes 2a-2g).

2.5.2.1 Defining and characterising cetacean mixed-species groups

After evaluating the terms and definitions used in the reviewed studies and the underlying processes involved in the formation of mixed-species groups, we propose to expand on the definition provided by Stensland et al. (2003) (Table 2.1). This definition considered a mixed-species group to be a set of individuals of two or more species that are seen in such close association that they can be regarded as members of the same group.

Firstly, the application of this definition to mixed-species groups requires an explicit definition of *group* that contains rules that can be applied in field research settings (Figure 2.6, Box 1d). Definitions of *group* should be biologically meaningful and consistent across species and studies (Krause & Ruxton 2002, Whitehead 2008). However, what defines a cetacean group remains a contentious and unresolved issue (Connor et al. 1998, 2000, Gibson & Mann 2009). The spatial proximity of individuals is the most often used criterion for determining group membership along with behaviour and directionality, although there is considerable variation in how each of these criteria is applied (Whitehead 2008, Gibson & Mann 2009). In the studies obtained by this literature review the threshold distances for delimiting group membership ranged from 10 m to 1000 m. In the broader cetacean literature, commonly used definitions are equally varied and include: a 10 m chain rule (Smolker et al. 1992); a 100 m fixed point rule (Irvine et al. 1981); and individuals "*in apparent association, moving in the same direction and often, but not always, engaged in the same activity*" (Shane 1990). The inconsistency in definitions of group causes confusion and weakens comparisons between studies, yet, as it stands, there is no clear solution to this problem. Dedicated work on this subject is needed to, firstly, determine how groups are defined in the cetacean literature and to, secondly, formulate biologically meaningful definitions via quantitative analyses of parameters such as inter-individual distances or the coordination between individuals (Krause & Ruxton 2002, Whitehead 2008, Croft et al. 2008). Until such work is done, we recommend that studies of cetacean mixed-species groups explicitly state the definition used and any justification for their choice.

Secondly, we emphasise that, as a type of group, mixed-species groups provide evolutionary benefits to at least some participants and are consequently formed and maintained by a mutual or unreciprocated attraction between individuals. Therefore, they should be distinguished from chance encounters that occur at random and aggregations of individuals that are attracted towards a common resource or that respond to the same environmental stimuli (Waser 1982, Powell 1985, Whitesides 1989, Goodale et al. 2017) (Figure 2.6, Box 1f). Null models can be used to assess whether sightings of multiple species in close proximity correspond to non-random patterns. For example, gas models and computer simulations recreate the movement of individuals in their environment and can be used to test whether encounter rates and durations occur at random or not (Figure 2.6, Box 1f) (Waser 1982, Whitesides 1989, Hutchinson & Waser 2007). Such approaches are all but absent from studies of cetaceans, likely because they require input data regarding the travel speed and diameter of groups that may be difficult to acquire (Cords & Würsig 2014). Nevertheless, these data could be obtained through dedicated studies that incorporate group focal follows and technologies that facilitate their acquisition such as unmanned aerial vehicles (UAVs), satellite tracking, and theodolite observations.

Analyses of individual association patterns can be conducted on multiple species, provided that individuals of each species can be feasibly identified (Farine et al. 2012, Zaeschmar et al. 2014, Elliser & Herzing 2016a). Null models can be used to analyse these networks in order to determine if individuals display non-random patterns of association and, therefore, are not found together by chance (Whitehead 2008, Farine 2017). Additionally, by accounting for alternate factors that may bring individuals together, such as spatial overlap or shared resource use, it is possible to determine the influence that social preference (i.e., attraction and avoidance) has on observed patterns of association (Whitehead 2008, Farine 2017). This has been done for single-species social networks and could be done on a mixed-species basis (Frère et al. 2010, Farine et al. 2012, Strickland et al. 2017, Zanardo et al. 2018, Hunt et al. 2019, Diaz-Aguirre et al. 2020). In this case, evidence of strong and/or preferential associations between individuals of different species after alternate factors are taken into account would be indicative of attraction between individuals, suggesting that the species form groups and not aggregations (Figure 2.6, Box 1f).

Alternative modelling approaches include occupancy modelling based on presence/absence data, which can be used to analyse species co-occurrence patterns to determine if there is avoidance or attraction between co-occurring species (Richmond et al. 2010, MacKenzie et al. 2018). Where such modelling is not practical, alternative criteria can be used. For example, situations where species are observed together for less than a minimum time limit can be considered to have occurred by chance (Kiszka et al. 2011a, Jourdain & Vongraven 2017). Such time limits may be arbitrary, but, alternatively, could be based on a comparison of the duration of single-species groups and mixed-species groups.

Thirdly, although the overall attraction amongst participants in a mixed-species group may be mutual or unreciprocated, the presence of each species must be tolerated by the other (Stensland et al. 2003). Consequently, there are several interspecific relationships that we do not consider to fall within the scope of mixed-species groups because they exclusively involve agonistic interactions where species do not congregate for the purpose of group formation (Figure 2.6, Box 1e). More specifically, we exclude predator-prey relationships, competition-based relationships (e.g., Shane 1995), and incidences where heterospecifics are used as "objects" in object-oriented play (e.g., Baird 1998, Patterson et al. 1998, Cotter et al. 2012). Mixed-species groups that, on occasion, involve agonistic behaviours, but that also involve affiliative and neutral behaviours (e.g., Herzing & Johnson 1997, Acevedo-Gutiérrez et al. 2005) are not excluded. Finally, we recommend the use of the term *mixed-species group* rather than other terms such as *interspecific*, *polyspecific*, or *heterospecific group* or *association*, as it was the most commonly employed in the studies that we reviewed and is also widely applied in the study of other taxa (Stensland et al. 2003, Goodale et al. 2017).

In summary, we define a mixed-species group as individuals of two or more species found in close spatial proximity due to a mutual or unreciprocated attraction derived from evolutionary grouping benefits. Mixed-species groups may involve affiliative, neutral, and agonistic behaviours excluding instances of predation, competition, and heterospecific "object" play.

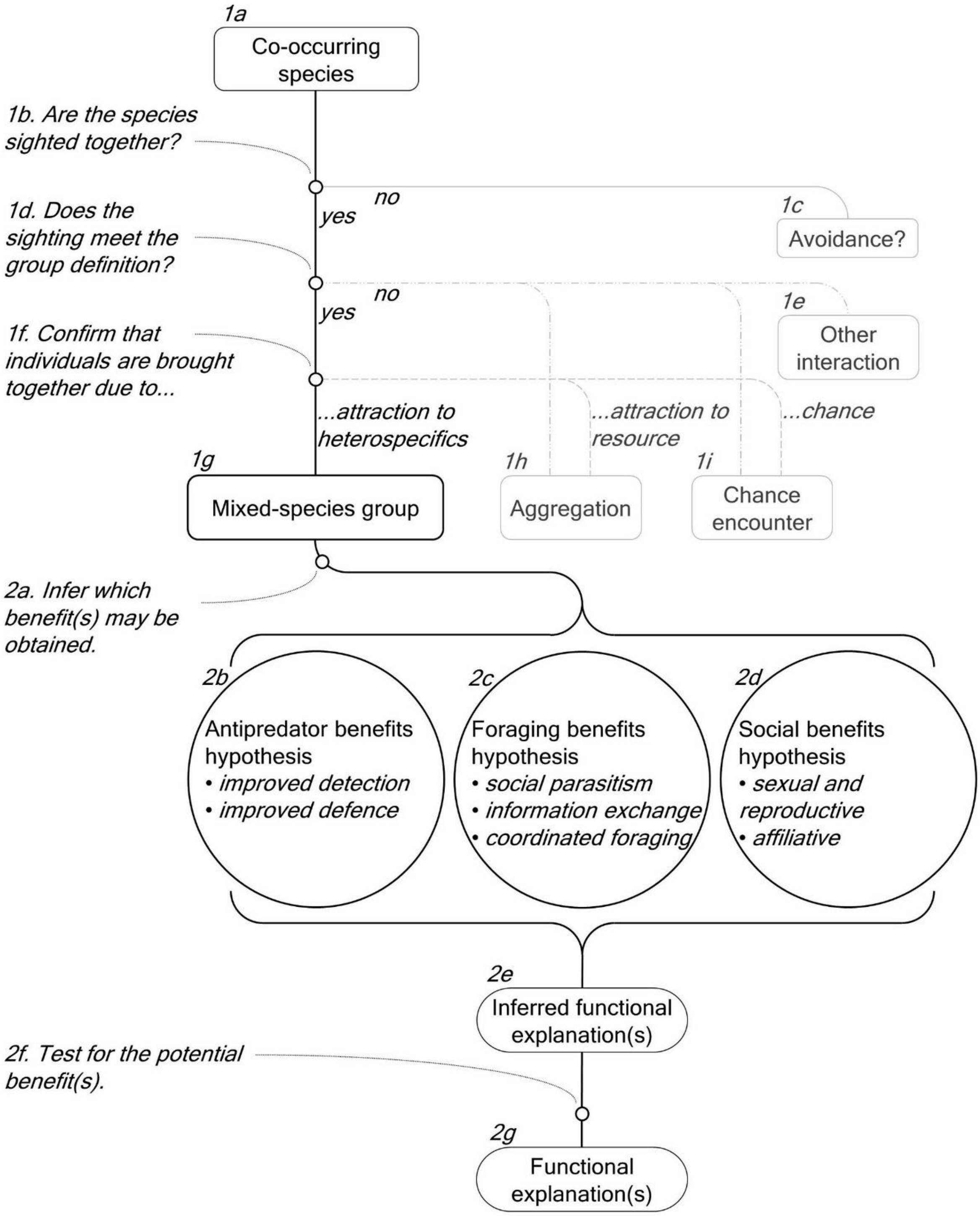

Figure 2.6. A conceptual framework for studying cetacean mixed-species groups. The framework details the steps required to determine that the species form a mixed-species group (Boxes 1b, 1d, and 1f) and to establish the potential function(s) of the mixed-species group (Boxes 2a and f).

2.5.2.2 Investigating the functional explanations for cetacean mixed-species group formation

Once it has been established that the occurrence of different species of cetaceans in close proximity does represent a mixed-species group, and not a chance encounter nor an aggregation, the next step should be to investigate what drives species to group (Figure 2.6, Box 2a). Throughout any investigation, all three functional explanations (Figure 2.6, Box 2b-d) should ideally be considered for each species involved as the functional explanations are not mutually exclusive and each species will not necessarily obtain the same benefits and costs (Stensland et al. 2003, Goodale et al. 2017). Furthermore, it is best to independently consider and compare mixed-species groups to single-species groups of each species because the differences between them will demonstrate how participation in mixed-species groups affects each species' biology, in turn revealing what drives them to form mixed-species groups (Sridhar & Guttal 2018).

To investigate the function of cetacean mixed-species groups, one needs to identify which benefits each species may obtain by analysing ecological, behavioural, and group characteristic data that are relevant to each hypothesis being tested. This should begin with reviewing the existing knowledge of each species' ecology and grouping dynamics through the perspective of the theory on mixed-species group formation to evaluate which functional explanations are more probable. Data should then be obtained directly from the study populations, including species distributions and abundance, group characteristics (e.g., size, composition, and cohesiveness), encounter rates, and behaviour (e.g., behavioural states, events, and transitions) of both single-species groups and mixed-species groups. These data should be combined with relevant environmental (e.g., depth, habitat, and distance to shore) (Scott & Chivers 1990, Kiszka et al. 2011a), food availability (e.g., distribution, abundance, and prey biomass), predation risk (e.g., predator distribution and abundance), and temporal data (e.g., time of day, season, and group duration). This will enable the identification of important factors for mixed-species group formation and can be indicative of the functional explanations for mixed-species groups formation, as detailed in the following sections.

Data on cetacean distribution, abundance, grouping dynamics, and behaviour may be obtained by dedicated boat- and land-based surveys with appropriate sampling protocols and, potentially, the integration of new technologies such as UAVs, acoustic recording, and biologging (Nowacek et al. 2016, Andrews et al. 2019). These technologies provide great potential to acquire data that are relevant to investigations of potential functional explanations but remain underutilised in the study of cetacean mixed-species groups. For example, radio-tags have been used to record the location and diving patterns of dolphins and the tuna that associate with them to track and compare the movements and behaviours of the different species (Scott et al. 2012). Innovative approaches and new technologies, such as those listed above (Nowacek et al. 2016), may also allow the direct measurement of parameters that are indicative of any benefits (e.g., predation attempts and successes, prey capture success rate, food intake rate, reproductive success, and social standing). This would make it possible to confirm that a benefit is gained by determining if these parameters are affected by mixed-species group participation. Here, we discuss several analytical approaches and present potential results which lend support to each of the three principal hypotheses for mixed-species group formation. Each of these approaches presents its own unique challenges that may make them practically and financially unfeasible in certain situations. Therefore, we provide a range of suggestions and entrust to researchers the decision of which approaches are most suitable to be implemented in their studies.

2.5.2.2.1 Antipredator advantage hypothesis

Individuals are more likely to form mixed-species groups for antipredator benefits (Figure 2.6, Box 2b) when the perceived risk of predation is high and when other avoidance tactics cannot be used (e.g., use of safer habitats, formation of large single-species groups). Increased mixed-species group size can be indicative of increased group vigilance and, therefore, decreased predation risk for individuals involved in mixed-species groups (Herzing & Johnson 1997, Scott & Cattanach 1998, Gygax 2002b, Majolo et al. 2008, Melillo et al. 2009, Kiszka et al. 2011a). A shift to habitat with a higher perceived predation risk when in mixed-species groups compared to single-species groups also supports the antipredator benefits hypothesis, as does increased travelling and resting behaviours (Kiszka et al. 2011a). Additionally, a predation risk landscape, based on the distribution of predators or bite scars on each species, could be employed to determine how predation risk, potentially combined with environmental factors, influences the prevalence and characteristics of mixed-species groups. Playback experiments and biologging have been employed to record the reactions of single-species groups of cetaceans to the simulated presence of potential predators (Curé et al. 2012, Bowers et al. 2018, Curé et al. 2019) and similar experiments could be undertaken to determine if simulated predator presence increases the propensity of species to form mixed-species groups, as has been done for primates (Noë & Bshary 1997). Finally, and although it is undoubtedly a logistical challenge, the level of predation risk would ideally be compared between single-species groups and mixed-species groups by recording failed and successful predation attempts or by analysing individual vigilance rates as a measure of perceived predation risk (Wolters & Zuberbühler 2003, Sridhar et al. 2009, Stojan-Dolar & Heymann 2010).

2.5.2.2.2 Foraging advantage hypothesis

Co-occurring species may form mixed-species groups in order to gain potential foraging benefits (Figure 2.6, Box 2c) (Smultea et al. 2014, Sridhar & Guttal 2018). A high or increased prevalence of feeding when in mixed-species groups argues in favour of this hypothesis (Quérouil et al. 2008, Zaeschmar et al. 2014, Bacon et al. 2017), as do observations of species foraging together or following foraging heterospecifics (Shane 1994, Burgess 2006, Zaeschmar et al. 2013, Smultea et al. 2014, Bacon et al. 2017, Jourdain & Vongraven 2017). Evidence, from playback experiments incorporating biologging or UAVs, that a species is attracted to vocalisations of foraging heterospecifics could also be indicative of a foraging benefit (Suzuki & Kutsukake 2017). Rates of prey capture success and energy intake have been used in studies of primates and birds to determine whether the presence of heterospecifics increases feeding success (Peres 1992b, Sridhar et al. 2009). The use of underwater video of feeding events, potentially recorded with a camera integrated into a biologger (Pearson et al. 2019, Linsky et al. 2020), could allow this, although the difficulties and costs would be considerable. For species that are assumed to improve foraging when in mixed-species groups, one could record and compare the time that individuals spend searching for food when in single-species groups and mixed-species groups to see if search time is reduced when heterospecifics are present.

2.5.2.2.3 Social advantage hypothesis

Species that may gain social benefits (Figure 2.6, Box 2d) typically exhibit high or increased levels of social activity when in mixed-species groups compared to when they are in single-species groups (Herzing & Johnson 1997, García et al. 2000, Acevedo-Gutiérrez et al. 2005, Melillo et al. 2009), while a lack of social interactions argues against this hypothesis (Quérouil et al. 2008, Kiszka et al. 2011a). Additionally, the presence of aggressive (e.g., tail slaps and open-mouth postures), sexual (e.g., erections, mating, and presence of hybrids), and affiliative behaviours (e.g., alloparental care, play, and non-aggressive body contact) provides evidence of social benefits and may also assist in unravelling the complexity of social interactions by providing insight into their nature (Herzing & Johnson 1997, Parra 2005, Acevedo-Gutiérrez et al. 2005, Melillo et al. 2009). Increased group size of mixed-species groups can also be related to social behaviour (Acevedo-Gutiérrez et al. 2005) while a preferential attraction to the vocalisations of socialising heterospecifics (demonstrated with playback experiments) would be expected from species that form mixed-species groups to obtain social benefits. Social advantages are more difficult to quantify and measure (Stensland et al. 2003), however, from a long-term study, it may be possible to record and compare the mating and reproductive success or the social status of individuals with regard to how often they are observed interacting with heterospecifics.

2.5.3 Conclusions and directions for future research

Our findings show that cetacean mixed-species groups are potentially diverse and complex in various aspects: the species involved, the habitats where they occur, their frequency, and their ecological functions. There are, however, two main impediments to the advancement of our understanding of cetacean mixed-species groups: 1) inconsistent terminology and the lack of approaches to distinguish them from mere aggregations and chance encounters and 2) the lack of studies designed to investigate their dynamics and function. We believe that our proposed terminology and conceptual framework can aid in overcoming these impediments by serving as a guide for future studies of cetacean mixed-species groups. Thus, we strongly encourage our colleagues to employ this framework and to improve upon it as new information and technological developments become available. Research on mixed-species groups of terrestrial species has, so far, led the way by developing the theoretical basis for mixed-species group formation, by detailing ideal approaches for their investigation, and by revealing the broader influence that mixed-species groups can have on the behaviour and ecology of the species involved (Stensland et al. 2003, Sridhar et al. 2009, Goodale et al. 2020). By conducting detailed and structured investigations of cetacean mixed-species groups, we will likewise be able to further unravel their ecological functions and improve our understanding of the role that they play in community ecology.

Chapter 3

How to define a dolphin "group"? Need for consistency and justification based on objective criteria

How to define a dolphin “group”? Need for consistency and justification based on objective criteria.

3.1 Abstract

Group living is a critical component of the ecology of social animals such as delphinids. In many studies on these animals, groups represent sampling units that form the basis of the collection and analysis of data on their abundance, behaviour, and social structure. Nevertheless, defining what constitutes a group has proven problematic. There is inconsistency in the terms and criteria used and many definitions lack biological justification. We conducted a literature review and an online expert survey to assess various terms (*group*, *school*, *party*, and *pod*) and their definitions as applied to delphinids to identify issues to ultimately make recommendations. Of 707 studies analysed, 325 explicitly defined one or more terms, providing 344 definitions. Additionally, 192 definitions were obtained from the survey. Amongst these definitions, *group* was the most common term used (review: 286 definitions, 83.1%; survey: 69 definitions, 35.9%) and the most familiar to the survey respondents (73 respondents, 100.0%). In definitions of *group*, spatial proximity was the most used criterion (review: 200 definitions, 71.2%; survey: 53 definitions, 81.5%) followed by behaviour (review: 176 definitions, 62.6%; survey: 38 definitions, 58.5%). The terms and criteria used to define delphinid groups vary considerably. Rather than proposing a single formal definition, we instead recommend that the term *group* and spatial proximity criteria be used to define sampling units of individuals observed in the field. Furthermore, we propose a process for formulating definitions that involves analysing inter-individual distances to determine naturally occurring patterns that are indicative of group membership. Although this process is based principally on the spatial proximity of individuals, it could also incorporate the behaviour of group members by evaluating the influence of behaviour on inter-individual distances. Such a process produces definitions that are biologically meaningful and compatible across studies and populations, thus increasing our ability to draw strong conclusions about group living in delphinids.

3.2 Introduction

Animal groups consist of interacting individuals that actively achieve and maintain spatial proximity due to attraction between them (Connor 2000, Krause & Ruxton 2002, Whitehead 2008, Majolo & Huang 2018). As such, groups differ from aggregations of individuals that form due to an external factor (e.g., a food resource) (Krause & Ruxton 2002, Whitehead 2008, Croft et al. 2008). The attraction between grouped individuals stems from the evolutionary basis for group living – the benefits gained from grouping (e.g., reduced predation risk, improved foraging, and enhanced reproductive opportunities) outweigh the costs (e.g., increased inter-individual competition and disease transmission) (Krause & Ruxton 2002, Ward & Webster 2016, Majolo & Huang 2018). Consequently, grouping behaviour influences individual and population level processes including fitness, genetic structure, and the transmission of information and disease (Silk 2007, Archie et al. 2008, Rushmore et al. 2013).

In practice, groups represent the sampling unit of interest in many studies, such as those that investigate the underlying drivers of social behaviour (Krause & Ruxton 2002). Consequently, groups are often central to the study of animal behaviour and behavioural ecology and, thus, their investigation necessitates a clear consensus on what represents a group. Yet, the concept of group suffers from inconsistent definitions and confusing use of terms which hinder effective scientific communication, evaluation of foundational ideas, and comparisons between studies (Jax 2006, Viscido & Shrestha 2015, Nakazawa 2020). Theoretical definitions provide broad interpretations of what constitutes a group. For example, Whitehead (2008) defined groups as “*sets of animals that actively achieve or maintain spatiotemporal proximity over any time scale and within which most interactions occur*” and Wilson (1975) defined them as “*any set of organisms, belonging to the same species, that remain together for a period of time while interacting with one another to a distinctly greater degree than with other conspecific organisms*”. While such definitions are generally congruent and effectively encapsulate theoretical concepts of group, they are qualitative and have limited utility in the field as they provide no objective and reproducible means of assigning observed animals into groups (Viscido & Shrestha 2015).

Consequently, researchers have developed operational definitions that are based on diverse empirical criteria, including spatial proximity, behaviour, and directionality, with the resulting sets of individuals referred to by a surfeit of terms (e.g., *group*, *party*, *flock*, and *school*) (Whitehead 2008, Gibson & Mann 2009, Kasozi & Montgomery 2020). For example, a 50 m threshold distance has been used to define *groups* of roe deer (*Capreolus capreolus*) (Pays et al. 2007), a 500 m radius from an estimated centre has been used to define *aggregations* of African savanna elephants (*Loxodonta africana*) (Wittemyer et al. 2005), while *shoals* of guppies (*Poecilia reticulata*) have been defined as individuals within four body lengths of one another (Croft et al. 2006). It should be noted that, although such definitions can effectively delimit spatial clusters of individuals, they do not necessarily identify the underlying driver (i.e., attraction between members of a group versus an external factor that gives rise to an aggregation) (Krause & Ruxton 2002, Croft et al. 2008). Furthermore, a single group defined in such a way does not attest the presence of long-term social bonds between group members (Gowans et al. 2007), instead, it represents an instantaneous observation of animals that is typically treated as a sampling unit (Table 3.1) (Wells et al. 1987, Connor et al. 1998, Farine & Whitehead 2015).

Confusingly, several of the terms used to refer to such sampling units, including *group*, are also used to refer to social units – a related, but distinct, concept (Table 3.1). Social units vary considerably between species and populations, however, in general, they are sets of individuals that display strong and stable associations over periods of days to years (Wells et al. 1987, Connor et al. 1998, Whitehead 2008). The distinction between these sampling and social units has been emphasised by some authors (e.g., Wells et al. 1987, Connor et al. 1998, Whitehead 2008) and is evident in studies that use different terms to refer to each, for example, *groups* – *pods* of killer whales (*Orcinus orca*) (Baird & Dill 1996, Esteban et al. 2016), *parties* – *communities* of chimpanzees (*Pan troglodytes*) (Rushmore et al. 2013), or *parties* – *core social groups* of African savanna elephants (Archie et al. 2006). Sampling and social units are often connected via the “gambit of the group” assumption, where membership in sampling units is used to assess the stability of individual associations in space and time, from which social units are then derived (Whitehead & Dufault 1999, Whitehead 2008). Importantly, social units can also be derived independently of such sampling units by analysing, for example, nearest neighbours, time-lags of photographic identifications, or behavioural interactions (e.g., grooming) (Whitehead 2008, Croft et al. 2008, Tavares et al. 2022). In this study, for clarity, we follow the broad definitions outlined in Table 3.1 to distinguish groups that represent sampling units and social units. Moreover, unless otherwise stated, we use the term *group* to refer to a sampling unit of individuals observed in the field (Table 3.1).

Table 3.1 Broad definitions of groups that represent sampling units and social units and common criteria and analyses used to demarcate them.

	Sampling Unit	Social Unit
Broad definition	An instantaneous observation in the field of a set of individuals that maintain spatial proximity over a period of minutes to hours[a]	A set of individuals that display strong associations over a period of months to years[a]
Criteria to determine membership	Spatial proximity, behaviour, direction of movement, level of coordination and interaction[b]	Social network analysis, association indices (e.g., half weight index)[c]

[a] The definitions are based on the definitions of *school* and *group* from Wells et al. (1987) and Connor et al. (1998), however we chose to not use these terms to avoid confusion caused by inconsistency in how they are used in the literature

[b] Connor et al. (2000) and Gibson & Mann (2009)

[c] Whitehead (2008)

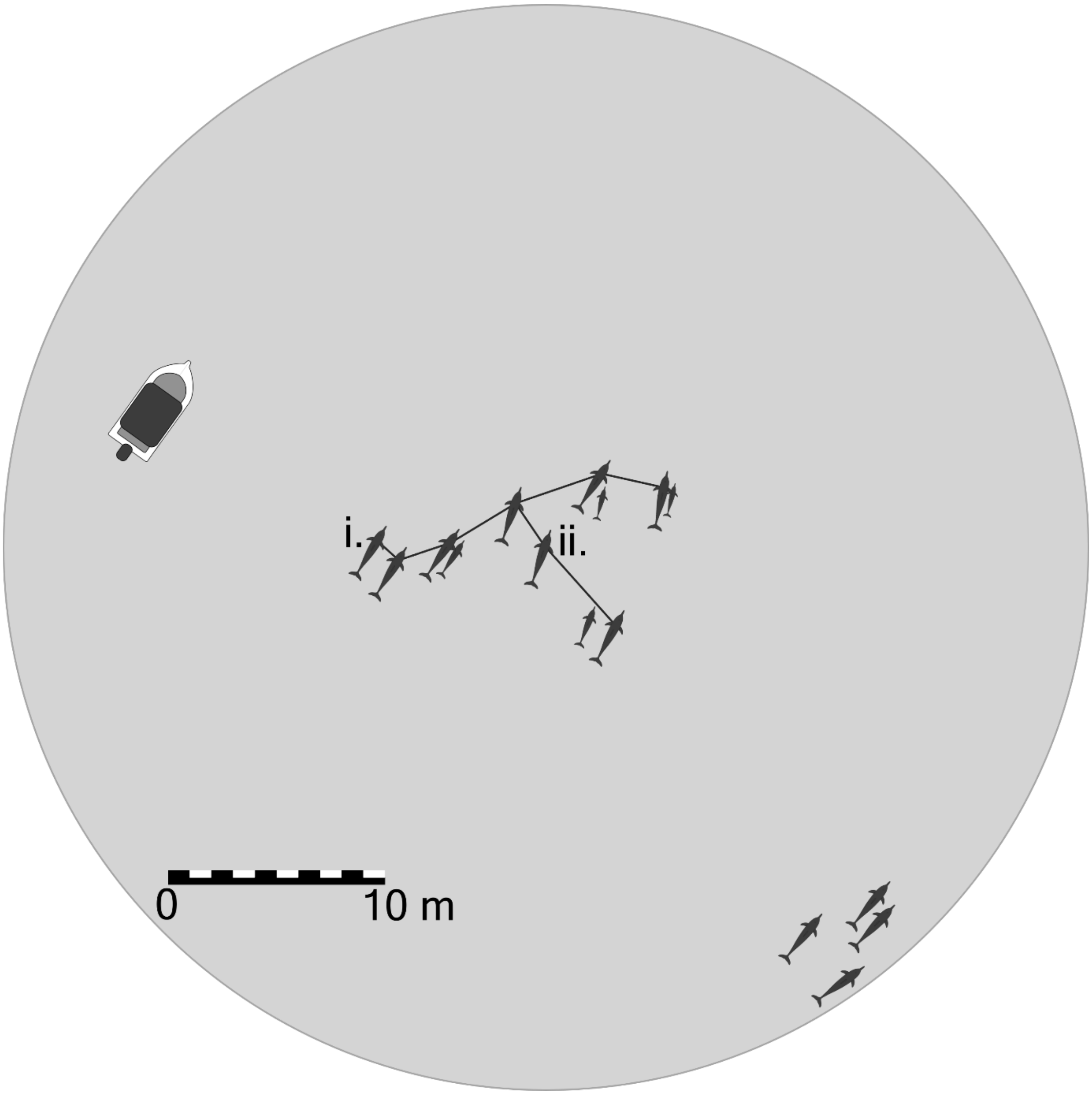

Figure 3.1 Two ways that spatial proximity rules are applied in group definitions: a 10 m chain rule, represented by the lines beginning from the individual closest to the research vessel (i) and extending to all those within 10 m of another group member; and a 25 m focal individual rule, represented by the shaded circle, where all individuals within 25 m of a focal individual (ii) are considered members of the same group. Note that the two definitions result in distinct delimitations of group with different data on measures of sociality. For example, the 10 m chain rule results in a group of 12 individuals, while the 25 m focal individual rule results in a group of 16.

Groups often form the basis for the collection and analysis of data and, thus, they are a fundamental part of the study methods and should be explicitly and appropriately defined (Mann 1999, Martin & Bateson 2007, Gibson & Mann 2009, Franks et al. 2010). Nevertheless, the issue of how exactly to operationally define groups has proven problematic (Aureli et al. 2012, Viscido & Shrestha 2015, Kasozi & Montgomery 2020). This is, in part, due to the contrasting requirements of two opposing, yet valid, arguments. On the one hand, it has been argued that group definitions should be standardised, thus enhancing our potential to draw broad conclusions from comparative studies (Dudzinski et al. 1993, Viscido & Shrestha 2015, Kasozi & Montgomery 2020). Disparate definitions may produce contrasting results whose differences are attributable to methodological inconsistencies, rather than variation in behaviour (Connor 2000, Viscido & Shrestha 2015). For example, in the situation illustrated in Figure 3.1, the 10 m chain rule and the 25 m focal individual rule result in two different delimitations of group with divergent data on measures of sociality (e.g., group size, number of associates, and sex/age composition). Thus, the definition of a *group* influences the nature of the data obtained, potentially reducing comparability between studies whose definitions are incompatible (Connor 2000, Gygax 2002b, Gibson & Mann 2009, Viscido & Shrestha 2015). On the other, it has been argued that group definitions should be tailored to study populations and questions in order to account for differences in the biology of the population (e.g., grouping dynamics, size, and communication range) and the study methods (Krause & Ruxton 2002, Kasozi & Montgomery 2020). For studies of similar species, a reasonable compromise between these two arguments should be possible, allowing for increased comparability between studies without detracting from the relevance of the definitions (Dudzinski et al. 1993, Viscido & Shrestha 2015, Kasozi & Montgomery 2020).

In addition to balancing the aforementioned arguments, group definitions should be biologically meaningful to the animals to which they are applied (Krause & Ruxton 2002, Croft et al. 2008). Approaching study questions from the perspective of the individuals involved can provide insight into grouping behaviour and resulting social organisation (Aureli & Schino 2019). To achieve this, definitions should, ideally, be derived from empirical analyses of relevant parameters, such as inter-individual distances, coordination, or communication range, which may vary between taxa (Krause & Ruxton 2002, Whitehead 2008, Croft et al. 2008). Finally, as groups represent sampling units, they should be defined in such a way that they are practical, objective, and reproducible in field research settings. By appropriately defining group, researchers improve their ability to collect meaningful and standardised data and, thus, strengthen the conclusions of their studies.

Delphinids are highly social animals and grouping behaviour is an integral part of their life history, behaviour, and ecology (Connor 2000, Gygax 2002b, Gowans et al. 2007). Nevertheless, in published studies, group definitions are often absent, subjective, or arbitrary – a problem that is compounded by overlapping use of terms (Dudzinski et al. 1993, Connor et al. 1998, Connor 2000, Gygax 2002b, Gibson & Mann 2009). The issues surrounding delphinid group definitions have been raised by various authors: Connor et al. (2000) briefly reviewed group definitions applied to bottlenose dolphins (*Tursiops* sp.) and the ramifications of their differences on measures of group size; Mann (1999) emphasised the importance of defining group as part of sampling protocols; Syme et al. (2021) highlighted the need for explicit group definitions when studying mixed-species groups; and Gibson & Mann (2009) discussed the different criteria that have been used to define groups in research on dolphins and primates, emphasising that differences in group definitions hinder comparisons between studies. Nevertheless, there is still no consensus on which terms and criteria to use when defining delphinid groups and many definitions lack biological justification and are inadequate in certain situations. Moreover, possible solutions to these issues, such as the use of common terms and criteria or a standardised process to formulate definitions, are lacking.

We conducted a literature review of published studies and an online survey of the delphinid research community to: 1) determine which terms (i.e., *group*, *school*, *party*, and *pod*) are most commonly used, compare how they are defined, and propose recommendations for their future use; 2) assess the criteria in group definitions in terms of their use, relevance, and applicability; 3) identify issues associated with current group definitions as well as their potential solutions; and 4) propose a process for formulating group definitions. Due to the diversity of grouping behaviours that delphinids exhibit, a single definition that encapsulates all delphinid groups is unreasonable and unachievable. Accordingly, we do not aim for such a definition, but rather for the use of explicit group definitions that are appropriate for the study species and questions at hand, yet based on a set of common objective criteria and, preferably, derived via a standardised process. Such improved practices in defining delphinid groups will facilitate future socio-ecological research on these group-living species.

3.3 Methods

3.3.1 Literature review

We searched the citation database Scopus for studies on delphinids by using a search query composed of three parts: the 17 genera of the family Delphinidae (Society for Marine Mammalogy Committee on Taxonomy 2020); the four key terms (i.e., *group*, *school*, *party*, and *pod*); and terms describing core research areas including *association*, *behavioural ecology*, *social network*, and *social organisation* (see Table S2.1 for the complete search query). Additionally, the results were restricted to peer-reviewed journal articles and book chapters published in English. The citation information of all results, including the abstracts, was downloaded using the Python package `pybliometrics` (Python Software Foundation 2016, Rose & Kitchin 2019).

We filtered the results by reading the abstracts to keep only those studies that either included visual observations of delphinid groups, used delphinid groups or a derived value (e.g., group size or membership) as a factor in analysis, or reviewed and discussed delphinid social groups. Studies that were exclusively based on data obtained remotely (e.g., passive acoustic monitoring) or from dead animals (e.g., necropsies) were removed, as were studies of captive delphinids because they do not represent natural grouping behaviour. By this process, we limited the review to studies where a definition of one or more of the key terms was likely to be necessary and present.

The full texts of the retained results were then downloaded and automatically searched for definitions of the key terms using custom-written scripts in Python (Python Software Foundation 2016). Where the automatic search encountered no definitions, the text was manually searched to verify if any definitions were present and had been overlooked. All definitions were then extracted and compiled along with information concerning the publication, including the year of publication and the study species. Finally, any studies that were cited in the extracted definitions but missed by the initial search were downloaded, filtered, and examined for definitions by the same procedure as described above. This tracing process was repeated as many times as necessary to ensure that citations were traced back to the original study.

3.3.2 Online survey

To further understand how delphinid researchers define the key terms and to provide an opportunity for direct comment, we conducted an online survey using Qualtrics Software (Qualtrics 2020). The respondents were asked whether they were familiar with each term and, if they were, whether they considered it a synonym of any of the others. The respondents then defined the term, listed any scientific publications as a reference for their definition, and provided details of any difficulties that they had experienced with applying the definition. Additionally, the respondents were asked to state their main study species (see Table S2.2 for the full survey). The survey was circulated via the MARMAM mailing list (https://lists.uvic.ca/mailman/listinfo/marmam), an email list for marine mammal researchers (about 15000 members in January 2020). Additionally, the same survey was sent to attendees of a workshop held at the 2019 World Marine Mammal Science Conference entitled *Sociality in riverine, lagoon-living, and coastal cetaceans: A descriptive analysis*, where this topic was discussed. The survey was open for voluntary completion during a period of three months, at which point all responses were recorded. Responses that were incomplete or that did not contain at least one explicit definition were removed from further analysis. The online survey was conducted under approval from the Human Research Ethics Committee of Flinders University, South Australia.

3.3.3 Analysis

In order to gain an understanding of the use and acceptance of the key terms, we recorded the number of times that they were defined in the reviewed studies and in the survey responses as well as how familiar they were to the survey respondents. Additionally, to quantify the overlap in the use of the key terms, we calculated the percentage of survey respondents that considered each term to be a synonym of each of the others. Where a survey respondent considered a term to be synonymous with a previously defined term, we transcribed the definition of the previously defined term to the synonym.

All the definitions from the literature review and the online survey were classified as either sampling or social units based on the broad definitions and criteria listed in Table 3.1. In other words, definitions that were based on criteria such as spatial proximity and behaviour and that were applied to individuals observed in the field were classified as sampling units, whereas definitions based on analyses conducted post-sampling to establish patterns of association between individuals were classified as social units. This was necessary because sampling and social units are distinct concepts and, consequently, they are not comparable. Making this distinction also served to compare how the key terms are employed.

As they are not the focus of this review, definitions that were classified as social units were excluded from the following analysis of criteria. Due to low sample size (n≤40) and the high rate of synonymy with *group*, the definitions of *school*, *party*, and *pod* as sampling units were also excluded from the following analysis of criteria.

The definitions of *group* as a sampling unit, however, were evaluated in terms of the criteria that they included to determine which criteria were considered most important. To achieve this, we followed an evaluation process (Table S2.3) to determine which of eight non-mutually exclusive criteria each definition contained (i.e., spatial proximity, behaviour, movement and directionality, number of individuals, visual range of the observers, interactions, temporal proximity, and species present). This involved assessing whether the definitions contained any parts that met the requirements for each criterion. Finally, to understand the origins of the definitions, we recorded the scientific publications that were cited in support of each definition.

3.4 Results

3.4.1 Literature review and online survey

The initial literature search returned 1662 studies to which a further 63 were added after reviewing the citations within the definitions. This amounted to a total of 1725 studies, nearly half of which (707 studies, 41.0%) were retained after the filtering process. Of the studies that were retained, 325 (46.0%) contained an explicit definition of one or more of the key terms and were kept for further analysis (hereafter, "reviewed studies"). These reviewed studies covered over four decades of research (1978 to 2022) (Figure S2.1) on a diverse range of delphinids, totalling 32 species from 16 genera (Figure S2.2). Most studies (173 studies, 52.2%), however, focussed on the genus *Tursiops*.

From the online survey, we received a total of 214 responses, 73 (34.1%) of which contained one or more explicit definitions of the key terms (hereafter, "survey responses"). The survey responses were primarily completed by NGO researchers (19 respondents, 26.0%), academics (12 respondents, 16.4%), post-doctoral researchers (10 respondents, 13.7%), PhD students (10 respondents, 13.7%), and private consultants (8 respondents, 11.0%) with the remaining categories each accounting for <10% of respondents each (Figure S2.3a). The respondents mostly had more than five years of experience researching delphinids (65 respondents, 89.0%) (Figure S2.3b), chiefly in the fields of ecology, conservation, and behaviour (Figure S2.3c). The principal study species of the survey respondents were also varied, covering 24 species from 13 genera, with the genus *Tursiops* being predominant (52 respondents, 71.2%) (Figure S2.2).

3.4.2 Familiarity and synonyms

The terms *group* and *pod* were the most familiar to the survey respondents, with 73 (100.0%) and 70 (95.9%) respondents familiar with them, respectively (Figure S2.2). The term *school* was familiar to 52 (71.2%) respondents, while *party* was only familiar to 15 (20.6%) (Figure S2.2). The term *party* was considered to be synonymous with *group* by most of the respondents who were familiar with this term (11 respondents, 73.3%), while *school* and *pod* were considered to be synonymous with *group* by approximately half of the respondents who were familiar with them (*school*: 27 respondents, 51.9%; *pod*: 35 respondents, 50.0%).

3.4.3 Definitions

The reviewed studies provided a total of 344 definitions, mostly of the term *group* (286 definitions, 83.1%), with relatively few definitions of *school* (29 definitions, 8.4%), *pod* (24 definitions, 7.0%), and, in particular, *party* (5 definitions, 1.5%). Similarly, the survey responses contained 192 explicit definitions, mainly of the term *group* (69 definitions, 35.9%), followed by *pod* (66 definitions, 34.4%), *school* (43 definitions, 22.4%), and *party* (14 definitions, 7.3%).

In both the reviewed studies and the survey responses, the clear majority of definitions of *group* (reviewed studies: 281 definitions, 98.3%; survey responses: 65 definitions, 94.2%) and *school* (reviewed studies: 29 definitions, 100.0%; survey responses: 39 definitions, 90.7%) represented sampling units (Figure S2.3). In contrast, *pod* was principally defined as a social unit in the definitions from the reviewed studies (19 definitions, 79.2%) and as a sampling unit by just over half of the definitions from the survey responses (37 definitions, 56.1%) (Figure S2.3).

3.4.3.1 Criteria used to define group

When defining *group* as a sampling unit, the spatial proximity of individuals was the most used criterion in the definitions from both datasets (reviewed studies: 200 definitions, 71.2%; survey responses: 53 definitions, 81.5%) (Figure 3.2). Spatial proximity was measured with 32 different rules (e.g., 10 m chain rule) in the reviewed studies and eight in the survey responses. Amongst these rules, distances between individuals were typically estimated using either a chain rule, a fixed-point rule, or a focal individual rule (Figure 3.1) while the threshold distances that were employed varied largely, from five metres to 10 km, and were estimated in both standard units (e.g., metres) and relative units (e.g., body lengths).

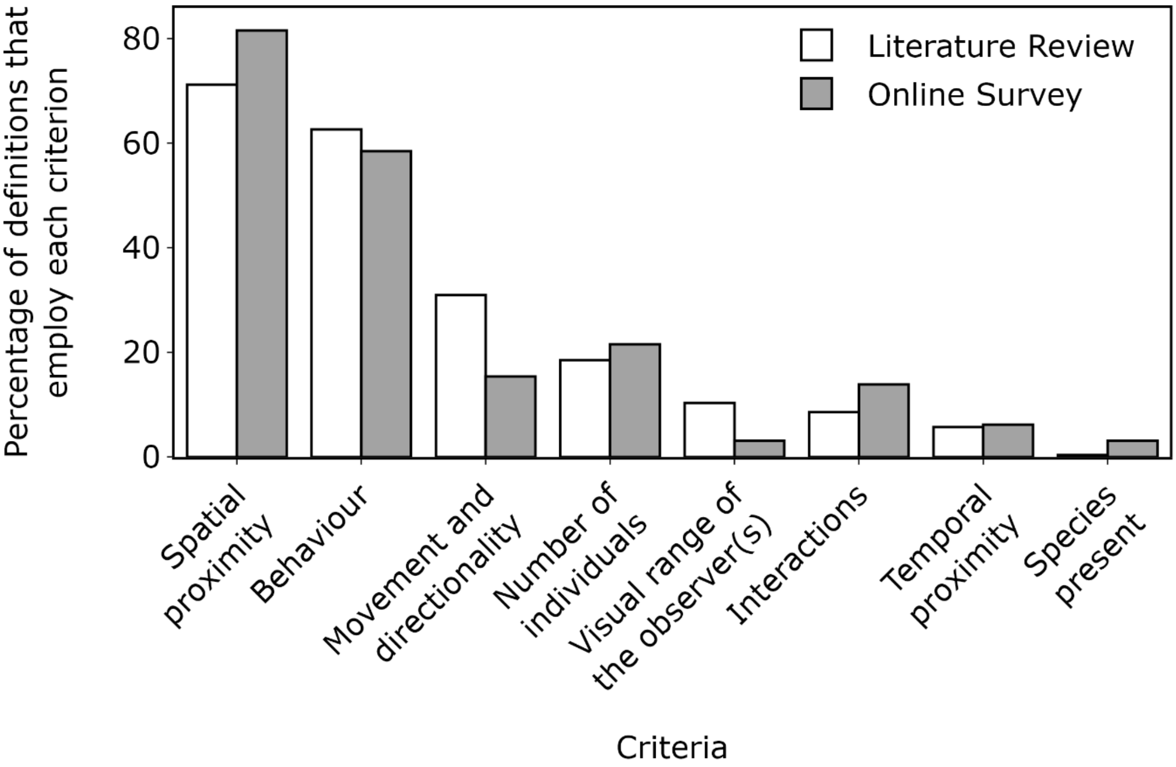

Figure 3.2 Percentage of definitions, obtained from a literature review and an online survey, that employed each of several criteria to determine membership in delphinid groups.

The behaviour of the animals was the second most common criterion in definitions of *group* from both datasets (reviewed studies: 176 definitions, 62.6%; survey responses: 38 definitions, 58.5%) (Figure 3.2). Although the criteria were worded in numerous ways, they typically required the individuals to be engaged in the same or similar behaviour in order to be considered members of the same group. Additionally, from the reviewed studies, 87 definitions

(31.0%) considered that animals in a group must move in the same direction as did 10 (15.4%) from the survey responses (Figure 3.2).

From the reviewed studies, 52 definitions (18.5%) specified the number of individuals as a criterion for the definition of *group* as did 14 (21.6%) from the survey responses. These definitions were principally divided into those that stated that any number of individuals can constitute a group (reviewed studies: 36 definitions, 69.2%; survey responses: 2 definitions, 14.3%) and those that specified that a group must contain two or more individuals (reviewed studies: 16 definitions, 30.8%; survey responses: 9 definitions, 64.3%). The remaining criteria (i.e., the visual range of observers, interactions, temporal proximity, and species present) were employed in only a few definitions (<15%) from both datasets (Figure 3.2).

3.4.3.2 Studies cited to support the definition of group

Of the definitions of *group* from the reviewed studies, 206 (73.3%) contained citations of the peer-reviewed literature. In total, 83 different publications were cited to support the group definitions. We considered four of these – Shane (1990), Smolker et al. (1992), Irvine et al. (1981), and Wells et al. (1987) – to be key references as they were cited in more than 5% of the definitions (Table 3.2). It is worth noting that these four references, and their group definitions, are based on studies of a single delphinid genus: *Tursiops*.

Table 3.2 The key studies cited in definitions of *group* (i.e., cited in >5% of the definitions) and their original definitions

Original definition	Study	Number of citations in the definitions from the reviewed studies
A pod *was defined as any group of dolphins observed in apparent association, moving in the same direction and often, but not always, engaged in the same activity*[a]	Shane (1990)	43 (20.3%)
Operationally, a dolphin was considered to be a member of a party *if it was within 10 meters of any other member (a 10 meter "chain" rule)*[a]	Smolker et al. (1992)	38 (17.9%)
Consequently, all bottlenose dolphins sighted within about 100 m of the boat were defined as a group	Irvine et al. (1981)	18 (8.5%)
Dolphins sighted within an area of approximately 100 m radius were considered to be in a single school *(=group, Irvine et al., 1981)*[a]	Wells et al. (1987)	12 (5.7%)

[a] Note that the original definitions, except that of Irvine et al. (1981), are not for the term *group*, but rather for the terms *pod*, *party*, and *school*

3.5 Discussion

When considering the diversity of grouping behaviours that are exhibited by the numerous delphinid species, it is evident that an all-encompassing definition of group that can be applied to all species, situations, and studies is an unrealistic goal (Krause & Ruxton 2002, Kasozi & Montgomery 2020). Nevertheless, there is potential to consolidate terms and criteria and strengthen the biological basis of delphinid group definitions, thus reducing inconsistency and improving comparability between definitions while increasing their biological relevance and maintaining their utility in the field. Given the wide variety of studies and researchers that rely on groups of dolphins as their sampling units, we acknowledge that our sample of definitions may not be all-inclusive. However, we believe that through our comprehensive literature review and online survey we have obtained a representative sample of how delphinid groups are defined by researchers, allowing us to assess the key terms and criteria to ultimately make recommendations for their future use. Furthermore, we highlight some of the challenges and considerations that researchers are faced with when defining delphinid groups and propose a standardised process, based on objective criteria, to facilitate the formulation of biologically meaningful definitions, thus assisting future studies.

3.5.1 The need for explicit definitions

The first issue encountered was the frequent lack of an explicit definition of the term used to refer to delphinid groups, with over half of the retained studies not providing one. Therefore, we reaffirm previous recommendations that, for each term used, authors explicitly state the definition of the term and any justification for the choice of term and definition (Dudzinski et al. 1993, Mann 1999, Martin & Bateson 2007).

3.5.2 Bias towards *Tursiops* in commonly used definitions

Amongst the definitions that we obtained, from both the review and the survey, there was a notable bias towards studies of the genus *Tursiops*. This is, perhaps, unsurprising given that both *Tursiops* species, particularly the common bottlenose dolphin (*Tursiops truncatus*), have widespread, typically coastal, distributions and are often the focus of research (Jarić et al. 2015, Wang 2018, Wells & Scott 2018). Furthermore, the four most common citations in the *group* definitions – Shane (1990), Smolker et al. (1992), Irvine et al. (1981), and Wells et al. (1987) – were studies of coastal *Tursiops* populations. Nevertheless, these definitions were applied to other species. For example, the 10 m chain rule of Smolker et al. (1992) was applied to 14 species from 12 genera. This may be problematic if the grouping dynamics of *Tursiops* are not representative of the other species. To avoid the risk of projecting inferences taken from a certain species onto incompatible species, research on group formation needs to be more inclusive, particularly given the diversity in delphinid grouping behaviour.

3.5.3 Terms used to refer to delphinid groups

A principal source of confusion when discussing delphinid groups is the inconsistent use of terms. The most familiar and commonly defined term in studies of delphinids is *group*, which has widespread use as a sampling unit. The term *school* has been used alongside *group* as a means of differentiating between sampling and social units (Wells et al. 1987, Connor et al. 1998), however this distinction appears to be somewhat blurred. Additionally, it appears that *school* has fallen into disuse amongst delphinid researchers, potentially due to its connotations of and connections to fisheries studies. The term *party* is not commonly used in studies of delphinids, despite its use in studies of primates and elephants (e.g., Archie et al. 2006, Rushmore et al. 2013, Machanda et al. 2013). Finally, unlike the other terms, *pod* is employed chiefly as a social unit, particularly when referring to stable, long-lasting units of genetically-related individuals, such as pods of killer whales.

These trends lead us to make two recommendations regarding the future use of the terms *group*, *school*, *party*, and *pod* in studies of delphinids. Firstly, we recommend that *group* be used exclusively to refer to sampling units because it was the most familiar and most commonly defined term and was considered as a sampling unit by the majority of definitions. Secondly, we recommend that *pod* be applied solely to stable social units of genetically related individuals and that other types of social unit be defined by different terms (i.e., not *group* nor *pod*), for example, *band*, *clan*, or *alliance*, depending on the species’ social organisation. We believe that this is justified because, although it was not unanimous in the survey responses, there is clearly a strong tendency to use *pod* to describe such social units. Moreover, limiting the terms *group* and *pod* to one use and ceasing to use less frequent terms (i.e., *school* and *party*) will increase consistency and clarity.

3.5.4 Delphinid group definitions

When discussing delphinid group definitions, we focus specifically on the operational definitions that are applied in the field to delimit groups of delphinids that are typically treated as sampling units (Table 3.1). We follow previous work in advocating for definitions that: reconcile the contrasting requirements of the need to standardise definitions and the need to tailor definitions to individual studies; are derived from a relevant biological parameter and are, thus, biologically meaningful to the animals being studied; and are practical, objective, and reproducible, thus allowing for accurate sampling in the field (Croft et al. 2008, Aureli et al. 2012, Viscido & Shrestha 2015, Kasozi & Montgomery 2020). Such definitions increase the capacity of field biologists to make meaningful observations.

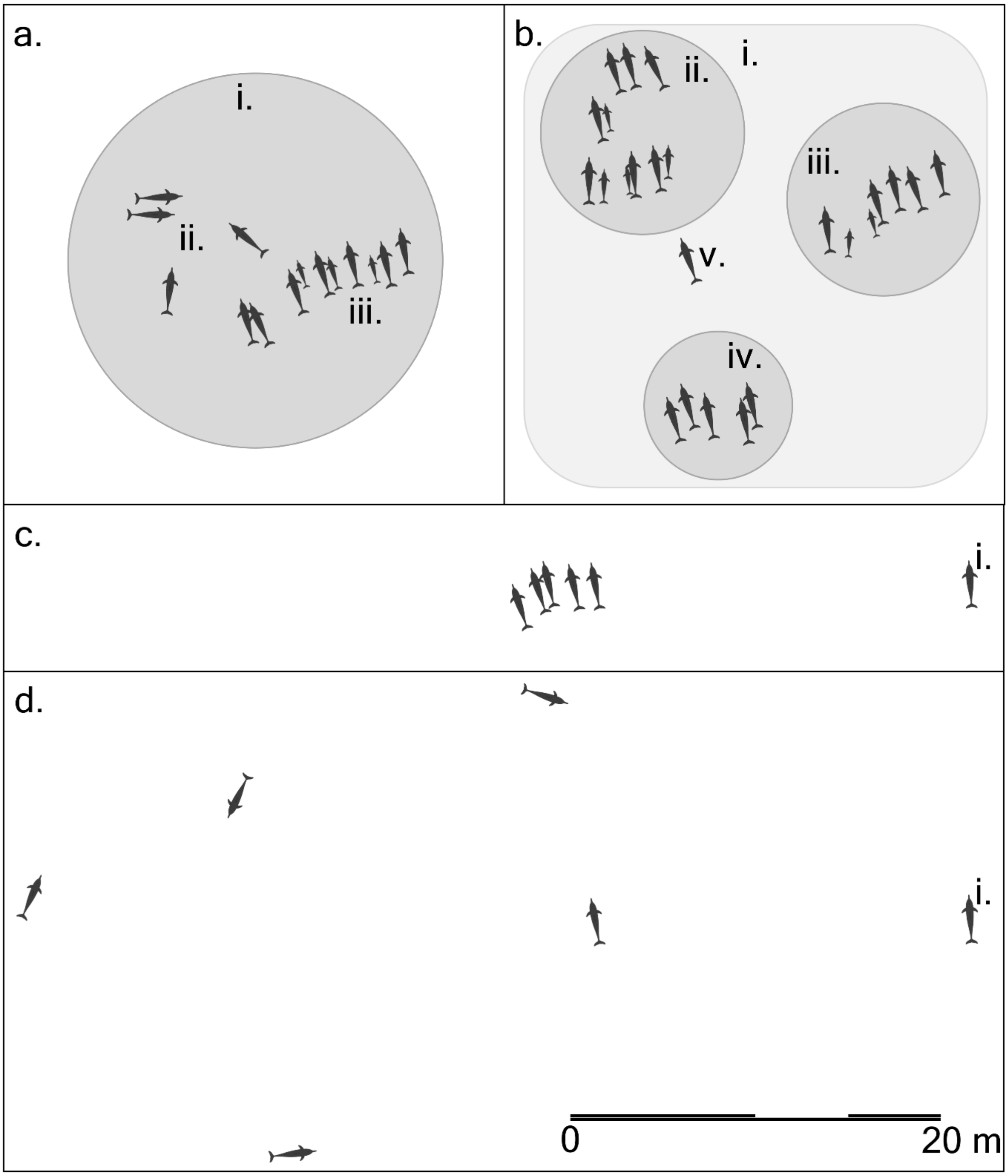

Figure 3.3 Various situations that challenge delphinid group definitions: (a) animals form a distinct spatial cluster (i) but differ in their behaviour (e.g., socialising, ii, and resting, iii); (b) several subgroups (ii, iii, and iv) form a single large group (i) and individuals move between subgroups (v); (c and d) changes in cohesiveness affect the relative importance of fixed threshold distances such that the sixth individual (i) is an outlier when the other five are resting (c), but not when they are foraging (d) despite being separated by the same distance (20 m) from its nearest neighbour in both situations.

3.5.4.1 Criteria used to define delphinid groups

Although no single delphinid group definition can be applied universally, it would be feasible for studies of delphinids to, at least, base their definitions on shared criteria. This would ensure a degree of compatibility between them while allowing for some necessary variation to account for differences between study populations. Accordingly, to determine which criteria are most appropriate, we evaluate the four most commonly used criteria in definitions of delphinid groups (i.e., spatial proximity, behaviour, movement and directionality, and the number of individuals) with regards to: their use amongst delphinid researchers and, more broadly, in studies of animal behaviour and ecology; their relevance to the biological concept of group; and their applicability in the field.

Spatial proximity amongst individuals is regarded as an essential criterion for delimiting group membership (Krause & Ruxton 2002, Whitehead 2008, Croft et al. 2008, Kasozi & Montgomery 2020) and was included in over two thirds of the definitions of *group* from both the reviewed studies and the survey responses. Furthermore, spatial proximity can be quantified with rules that can be readily and objectively reproduced in the field (e.g., 10 m chain rule, 100 m chain rule). These rules are similar in principle and construct to those found in studies of other taxa (e.g., Wittemyer et al. 2005, Archie et al. 2006, Rushmore et al. 2013, Machanda et al. 2013, Castles et al. 2014, Kasozi & Montgomery 2020). Nevertheless, we encountered several issues regarding the use of spatial proximity to define delphinid groups: firstly, there are certain situations where fixed measures of spatial proximity are difficult to apply and may not adequately capture the complexity of spatial organisation (Figure 3.3); secondly, some threshold distances do not consider the practical limitations inherent to visual observations of delphinids; and, thirdly, we found little biological justification for the choice of spatial proximity rules. Nevertheless, we believe that these issues can be overcome by careful formulation of a definition and we dedicate the following sections of this article to discussing them and their potential solutions in more detail.

Behaviour was commonly used in definitions of *group* while the direction and movement of the observed animals was used as a criterion in only a few definitions, almost always alongside a behaviour criterion and often in accordance with the definition given by Shane (1990) (Table 3.2). Behaviour and directionality are not usually mentioned in theoretical group definitions (e.g., Wilson 1975, Whitehead 2008, Ward & Webster 2016) and are only occasionally employed in group definitions of other taxa (Kasozi & Montgomery 2020). Additionally, the vagueness and subjectivity of some behaviour criteria (e.g., “*often, but not always, engaged in the same activity*”) allow for inconsistencies to arise (Mann 1999, Kasozi & Montgomery 2020). The directionality criteria were similarly subjective and no means of quantifying directionality was provided. Furthermore, survey respondents reported difficulties in applying behaviour and directionality criteria when animals in close proximity form a distinct, cohesive spatial unit but differ in their behavioural state and direction of movement (Figure 3.3a) and when animals are spread out so far that their behaviour and movements cannot be reliably noted. Given the subjectivity and the lack of quantification of directionality criteria, we recommend excluding them from group definitions. Behaviour criteria also entail certain complications, however, given the influence of behaviour on inter-individual distances and, thus, spatial proximity, we recommend that behaviour be incorporated into the formulation of group definitions (Denardo et al. 2001, Aureli et al. 2012).

The final issue concerns the number of individuals that constitutes a group (Dudzinski et al. 1993, Krause & Ruxton 2002). A few definitions specified that a group could contain any number of individuals (i.e., including single individuals) while a few stated that a group must contain two or more individuals. Most definitions, however, did not explicitly state a number of individuals required to constitute a group. Common usage of the word *group* implies the presence of multiple individuals and, from a biological perspective, a single individual cannot display the fundamental features of a group (e.g., proximity, attraction, and interaction amongst individuals). Therefore, we do not consider that a single individual constitutes a group. Nevertheless, single individuals are important when considering ecological questions and they should be included in relevant analyses so as to not bias the results (Dudzinski et al. 1993, Krause & Ruxton 2002). A potential solution, as mentioned in the survey responses and employed in some of the reviewed studies (e.g., Karczmarski 1999), is to use multiple terms, for example, *singleton* (single individual), *group* (two or more individuals), and *sighting* (singletons and groups), the latter of which can then be used in analysis.

3.5.4.2 Challenges faced when defining groups and their potential solutions

Although spatial proximity is key when defining delphinid groups, we identified several issues concerning its use. Firstly, certain situations make it difficult to apply spatial proximity rules. Numerous delphinids are known to, at times, display multiple levels of spatial organisation (Figure 3.3b). For example, spinner (*Stenella longirostris*) and pantropical spotted dolphins (*Stenella attenuata*) form supergroups containing multiple groups (or subgroups) that each maintain their respective boundaries (Kiszka et al. 2011a). In these situations, group, which represents a single level of spatial organisation, will not necessarily capture the full complexity of the animals’ grouping dynamics. Consequently, it may be necessary to define multiple levels of grouping with unique terms (e.g., *subgroup*, *group*, and *supergroup*).

Furthermore, the cohesiveness of delphinid groups varies, often according to behaviour. For example, animals may form tight groups to rest and spread out to forage (Gowans et al. 2007). Changes in group spacing can render a single, fixed threshold distance inadequate because the importance of that distance changes according to the spacing amongst individuals (Miller

& Gerlai 2011). If, for example, five individuals are resting with an average nearest neighbour distance of one metre, then, intuitively, a sixth individual 20 m from them is not part of their group (Figure 3.3c). If, on the other hand, five individuals are foraging with an average nearest neighbour distance of 25 m, then, intuitively, a sixth individual 20 m from the closest of them is part of their group (Figure 3.3d). Assuming that our intuition regarding group membership is accurate, a 10 m chain rule would correctly separate the sixth individual in the first situation, but would incorrectly separate it, and many others, in the second. Conversely, a 50 m chain rule would incorrectly include the sixth individual in the first situation but would correctly include all individuals in the second. What is required, then, is a flexible spatial proximity rule that can account for changes in cohesiveness (e.g., one with a different distance threshold for each behavioural state) (Miller & Gerlai 2011).

Although group definitions should be based on relevant biological parameters, we cannot be oblivious to the practical limitations that we, researchers, are subject to. For example, any visual observation of a delphinid group is inherently limited by the visual range of the observers. Particularly when larger threshold distances are employed (e.g., 1000 m), certain individuals that meet the spatial proximity requirements may be beyond the limits of reliable observation or even detection. Moreover, to mitigate potential biases introduced by visual assessment of distances over water, researchers should periodically train field observers by estimating distances over water to objects placed at known intervals, as determined with a line or rangefinder. Thus, the limitations of visual observations should be considered and minimised when developing and applying definitions of group.

Finally, and perhaps most importantly, when defining group, we must consider what is biologically meaningful to the animals (Croft et al. 2008, Viscido & Shrestha 2015, Kasozi & Montgomery 2020). Yet, of the 200 definitions from the reviewed studies that employed a spatial proximity criterion, only four justified their distance on a measured parameter (acoustic communication range: Parsons et al. (2009) and Foster et al. (2012); and nearest neighbour distances: Visser et al. (2014) and Visser et al. (2017)). This raises the question: are the distances used to define groups appropriate for the species to which they are applied?

Two studies – Parsons et al. (2009) and Foster et al. (2012) – based their spatial proximity criterion on the estimated acoustic communication range of the study species, resulting in a distance threshold of 10 km. Such an approach is advantageous because it is based on a variable that is intrinsically linked to group formation. There are, however, certain drawbacks. Active space (i.e., the range at which an acoustic signal can be detected and recognised) is known to vary according to numerous environmental (e.g., substrate type, sea state, salinity, and water depth) and biological variables (e.g., frequency, species, and position of the animal in the water column) (Janik 2000, Quintana-Rizzo et al. 2006). Accordingly, the estimated active space of delphinid whistles ranges from several hundred metres to 25 km (Janik 2000, Miller 2006, Quintana-Rizzo et al. 2006). This poses two issues. Firstly, a threshold distance based on an active space calculated under certain conditions may not be relevant under different conditions. Secondly, the individuals in a group that is delimited by acoustic communication range are likely to be dispersed over an area that is too large to be reliably observed visually.

It seems, then, that a threshold distance that permits reliable visual observation of all group members is likely to fall within the limits of delphinid acoustic communication range and the corresponding group is likely, therefore, to include only a subset of all potentially interacting individuals. This is not an issue per se as the theoretical concept of group does not require the group to contain all interacting animals, but rather those that interact most (Wilson 1975, Whitehead 2008). Equivalent situations are found amongst other taxa. African savanna elephants, for example, recognise contact calls of family members at distances of up to 2.5 km (McComb et al. 2003), well beyond the distances that are used for determining group membership (e.g., 100 m: Archie et al. (2006); 500 m: Wittemyer et al. (2005)). It is necessary, however, to determine a point that marks a meaningful change in the level of interaction.

This can be achieved through empirical analyses of inter-individual distances (Krause & Ruxton 2002, Martin & Bateson 2007, Whitehead 2008). Clutton-Brock et al. (1982), for example, analysed the spacing of red deer (*Cervus elaphus*) and found that inter-individual distances were distributed bimodally with a discontinuity around 50 m. This distance was verified by behavioural analysis and subsequently used to define red deer *parties* (Clutton-Brock et al. 1982). Similar techniques have been conducted on spider monkeys (*Ateles geoffroyi*) with group behaviour incorporated into the analysis to determine how it affects group spacing (Ramos-Fernández 2005, Aureli et al. 2012).

Two of the reviewed studies – Visser et al. (2014) and Visser et al. (2017) – achieved a similar outcome by selecting a threshold distance in situ based on the estimated distance from a focal individual to its nearest neighbour (Visser et al. 2014). This method is beneficial because it is adaptable to changes in cohesiveness, however, it is necessary to track a focal individual which could present challenges.

3.5.5 A proposed process for formulating delphinid group definitions

We believe that an ideal approach to improve delphinid group definitions is via the use of a standardised process by which researchers can formulate definitions for their study populations. Similar ideas have been recommended previously (Krause & Ruxton 2002, Martin & Bateson 2007, Whitehead 2008) and employed in studies of ungulates (Clutton-Brock et al. 1982), primates (Ramos-Fernández 2005), and fishes (Miller & Gerlai 2008), but not, to our knowledge, in studies of delphinids. After studying these previously used techniques, evaluating the identified issues, and considering the unique challenges associated with delphinid research, we propose such a process. It involves analysing inter-individual distances to determine naturally occurring patterns that indicate appropriate distances at which to delimit groups.

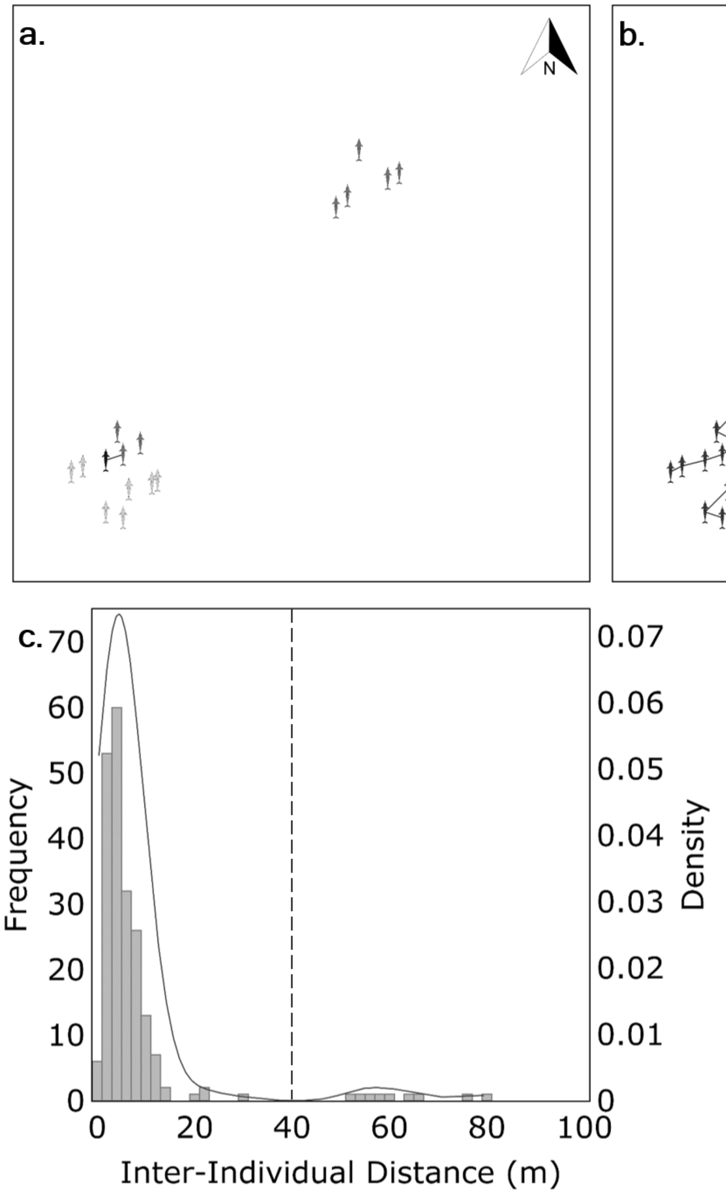

Figure 3.4 Simulated example of the proposed process for determining threshold distances for delphinid group definitions. This involves (a) measuring inter-individual distances from each individual to its nearest neighbour in a constant direction (e.g., north), before (b) plotting the distribution of these distances. This is repeated until sufficient samples have been obtained (c) and a cut-off point (dashed line) can be determined by the presence of any discontinuities as determined by, for example, analysing the gradient of a density curve.

Despite the difficulties associated with observing wild delphinids, photogrammetry using unmanned aerial vehicles (Scott & Perryman 1991, Dawson et al. 2017) or portable stereo photogrammetry systems (Howland et al. 2012, Macfarlane et al. 2015) offers feasible ways of measuring inter-individual distances. It is necessary to consider, however, which inter-individual distances to measure. Possible options include the distances from each individual within a given area to its nearest neighbour in a constant direction (e.g., north) (Clutton-Brock et al. 1982) (Figure 3.4a and b) or the distances from a focal individual to all others within a certain radius (Ramos-Fernández 2005, Aureli et al. 2012). The nearest neighbour in a constant direction option seems the most reasonable to us as nearest neighbours are arguably the most important in terms of interactions and maintenance of group cohesion (Partridge 1981, Ballerini et al. 2008, Miller & Gerlai 2008) while measuring in a constant direction captures any discontinuities in inter-individual distances, rather than simply capturing the minimum distances between individuals (Figure 3.4). Moreover, nearest neighbour distances are typically what is tested by the commonly employed chain rules. The next step is to determine a threshold distance by plotting the distribution of the observed inter-individual distances and finding a naturally occurring cut-off point (e.g.: a discontinuity, Clutton-Brock et al. (1982); or a steep decline, Ramos-Fernández (2005)) by analysing the gradient of a density curve (Figure 3.4c). Finally, it would be beneficial to incorporate behaviour into any such investigation by considering its influence on spatial proximity (Denardo et al. 2001, Aureli et al. 2012). This can be achieved by either comparing the behaviour of individuals allocated to the same or different groups (Clutton-Brock et al. 1982) or by incorporating behaviour as a factor in analysis (Aureli et al. 2012).

The result of this process would be a group definition based on a threshold distance that would be applied in the field as a chain rule. We recognise that the proposed process will not completely solve the issues associated with defining groups and that any definition produced via this process will still be susceptible to the problems that are inherent to observational delphinid research (e.g., observing animals that spend long periods underwater). Nevertheless, by utilising techniques such as the proposed process, the issues associated with defining delphinid groups can be mitigated, thus improving the quality of the associated data. More specifically, group definitions produced via the proposed process would, firstly, be based on a biologically meaningful parameter that is relevant to the study population and would, secondly, be reproducible, objective, and practical, as has been recommended (Krause & Ruxton 2002, Whitehead 2008, Croft et al. 2008, Viscido & Shrestha 2015). Furthermore, in situations where there are multiple levels of spatial organisation, the distribution of inter-individual distances would present multiple cut-off points, allowing for the determination of multiple threshold distances (e.g., one for subgroup and one for group). If behaviour were incorporated as a factor, it would be possible to determine a threshold distance for each behavioural state. Thus, the resulting chain rule would be adaptable to the behaviour and cohesiveness of the animals. If such a technique were standardised and applied to different species in diverse locations, then, although the resulting threshold distances would presumably vary, they would still be compatible because they would be formulated via the same process and would, therefore, represent the same aspect of grouping dynamics. Thus, we strike a compromise between the need to standardise definitions and the need to tailor definitions to the biology of each study population (Krause & Ruxton 2002, Martin & Bateson 2007, Aureli et al. 2012, Viscido & Shrestha 2015, Kasozi & Montgomery 2020). We recognise that, due to the cost, training, and time required to implement this process, it will not always be feasible. If that is the case, we recommend that researchers use the term *sighting* as a sampling unit to refer to both *singletons* (i.e., single animals) and *groups* (i.e., two or more individuals within close spatial proximity). Moreover, *groups* should be defined by one of the two spatial proximity rules that were most commonly used in the definitions from both the reviewed studies and the survey responses: the 10 m chain-rule or the 100 m chain-rule (Table 3.2). Whether these distances are biologically meaningful is challenging to assess, yet, by using standardised terms and distances we can decrease inconsistency and improve comparability of published studies. Finally, we emphasise that, regardless of the term used, authors must provide an explicit formal definition.

3.6 Conclusion

Our literature review and online survey raise several issues concerning delphinid group definitions. Inconsistent use of terms and criteria hamper comparisons across species and locations. We believe that these difficulties can be overcome by a consensus on the use of terms and criteria. By analysing definitions from a range of publications and by providing the delphinid research community with the opportunity to contribute via an online survey, we believe that we have pursued a democratic path towards such a consensus. Accordingly, the conclusions and recommendations that we provide are drawn from the perspectives of those who wrote the reviewed studies and completed the online survey. These perspectives, combined with broader work on animal grouping behaviour, illustrate how we can address those issues that require further dedicated work to be minimised, such as the lack of justification and the inadequacy of group definitions in certain situations. We believe that our proposed process takes a step in the right direction by providing an empirical way of formulating biologically meaningful definitions that are compatible but that still account for variation in grouping dynamics. We hope that this review provides guidance to researchers and students in our field when confronted with the task of defining delphinid groups.

Chapter 4

Habitat partitioning, co-occurrence patterns, and mixed-species group formation in sympatric delphinids

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Habitat partitioning, co-occurrence patterns, and mixed-species group formation in sympatric delphinids

4.1 Abstract

Numerous species have been reported to form mixed-species groups, however, little is known about the interplay between niche partitioning and mixed-species group formation. Furthermore, it is often unclear whether species come together by chance due to overlapping habitat preferences, by shared attraction to resources, or by attraction between them. We assessed habitat partitioning, co-occurrence patterns, and mixed-species group formation of sympatric Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around the North West Cape, Western Australia with a joint species distribution model and temporal analyses of sighting data. Australian humpback dolphins preferred shallower and more nearshore waters than Indo-Pacific bottlenose dolphins, yet these species co-occurred more often than expected by chance given shared responses to environmental variables. Indo-Pacific bottlenose dolphins were sighted more often than Australian humpback dolphins during the afternoon, however, we did not find any temporal patterns in the occurrence of mixed-species groups. We propose that the positive association in the species' occurrence is partly due to the active formation of mixed-species groups. By evaluating habitat partitioning and co-occurrence patterns, this study provides direction for future work which should proceed to investigate the benefits that these species may gain from grouping with each other.

4.2 Introduction

Ecologically similar species that co-occur and share similar habitats typically display some degree of niche partitioning as natural selection favours traits that reduce competition (Grinnell 1924, Pianka 1974, Roughgarden 1976, Chesson 2000, Tokeshi 2009). By consuming different resources or by utilising resources in different places or at different times, sympatric species manage to coexist (Chesson 2000, Tokeshi 2009). The degree of niche partitioning between species affects species diversity and community composition and, therefore, is a critical aspect of community ecology (Pianka 1974, Chesson 2000). Where species' niches overlap, they may occur within close spatiotemporal proximity and even form mixed-species groups.

Mixed-species groups have been reported amongst diverse species, from rainforest birds and primates to oceanic cetaceans (Stensland et al. 2003, Cords & Würsig 2014, Goodale et al. 2017, Syme et al. 2021). They occur when individuals of multiple species actively achieve and maintain spatiotemporal proximity due to a mutual or unilateral attraction. This attraction stems from the evolutionary benefits that can be gained from grouping with heterospecifics (e.g., reduced predation risk, enhanced foraging, and increased social interactions) (Krause & Ruxton 2002, Stensland et al. 2003, Goodale et al. 2017, Syme et al. 2021). The stability, frequency, and benefits of mixed-species groups can be influenced by the species' habitat use and patterns of co-occurrence (Greenberg 2000, Heymann & Buchanan-Smith 2000, Cords & Würsig 2014, Goodale et al. 2017, Sridhar & Guttal 2018). For example, as a result of utilising different forest strata when in mixed-species groups, primates may exhibit complementary predator vigilance (e.g., those in lower strata are more vigilant to terrestrial threats while those in higher strata are more vigilant to arboreal and aerial threats) resulting in decreased predation risk for the group (Heymann & Buchanan-Smith 2000, Cords & Würsig 2014), while differences in dietary niche mean that birds that form mixed-species groups can gain the antipredator benefits of grouping while experiencing less severe competition for food than they would in single-species groups (Greenberg 2000, Sridhar & Guttal 2018).

Within a given ecosystem, species from the same trophic guild can co-occur at high densities and share similar habitats. Therefore, individuals of different species may periodically encounter each other by chance (Waser 1984, Whitesides 1989, Cords & Würsig 2014, Goodale et al. 2017). Such chance encounters, however, are unlikely to have any evolutionary significance (Waser 1982, Whitesides 1989). Where species utilise the same localised resources (e.g., food pulses or resting areas), encounters between individuals of multiple species may occur more frequently. In this case, their co-occurrence is best described as an aggregation as it results from a shared, but independent, attraction to a given resource (Goodale et al. 2017, Syme et al. 2021).

Although they may appear outwardly similar, chance encounters and aggregations should be clearly distinguished from mixed-species groups for which functional benefits have been hypothesised for a range of species (Krause & Ruxton 2002, Goodale et al. 2017, Syme et al. 2021). More specifically, this involves determining whether there is attraction amongst individuals (i.e., they truly form a group) or if their occurrence in spatiotemporal proximity is simply a chance encounter due to overlapping habitat preferences or an aggregation due to shared attraction to resources (Waser 1984, Whitesides 1989, Syme et al. 2021). During chance encounters and aggregations, individuals of multiple species occur in close proximity and may exhibit similar behaviours. As a result, they may appear to form a cohesive group and they may even meet the various criteria that are used by researchers to define groups in the field (e.g., spatial proximity and behaviour) (Krause & Ruxton 2002, Kasozi & Montgomery 2020). Consequently, various analytical methods have been proposed to confirm that species observed together in apparent mixed-species groups are indeed brought together by attraction.

The ideal gas model, for example, has been used to study mixed-species groups of primates (Waser 1982, 1984, Hutchinson & Waser 2007). This method estimates expected encounter rates by simulating the movements of groups through space. However, it requires detailed information on group travel speed, diameter, and density that are not always readily obtainable, particularly for fast-moving marine species (Cords & Würsig 2014). Alternatively, presence-absence data of sympatric species can be analysed with null model randomisation tests to determine if species co-occurrence rates are significantly above or below what would be expected by chance (Gotelli 2000). Although null models have been used to analyse the co-occurrence rates of terrestrial and marine species (Astaras et al. 2011, Mammides et al. 2018, Haak et al. 2020), they do not consider the possibility that non-random patterns of co-occurrence result from shared responses to environmental features (Pollock et al. 2014, Ovaskainen et al. 2016).

More recently, joint species distribution models (JSDMs) have been developed to address this issue (Warton et al. 2015). By simultaneously modelling multiple species' responses to both environmental factors and to heterospecific presence, JSDMs can separate correlations in species occurrence into that which is due to environmental factors (i.e., environmental correlation) and that which is unexplained (i.e., residual correlation) (Pollock et al. 2014, Ovaskainen et al. 2017, Ovaskainen & Abrego 2020). The residual correlation can be the result of either non-measured environmental or biotic factors or interactions between the species (e.g., avoidance or attraction). However, as environmental factors and species interactions can, in theory, generate identical presence-absence data, these two possibilities are statistically indistinguishable (Ovaskainen et al. 2016, Blanchet et al. 2020). Despite this limitation, JSDMs can effectively identify non-random relationships between species while accounting for the influence of measured environmental factors (Ovaskainen et al. 2017, Haak et al. 2020). Thus, JSDMs can determine whether species are found together in close spatiotemporal proximity by chance, provide inferences about potential biotic interactions, including attraction, and provide evidence for niche partitioning (Ovaskainen et al. 2017, Ovaskainen & Abrego 2020).

Many delphinid species co-occur in the same habitat and even form mixed-species groups, however the mechanisms promoting their coexistence and the drivers of mixed-species group formation are poorly understood (Stensland et al. 2003, Bearzi 2005, Parra 2006, Kiszka et al. 2011b, Cords & Würsig 2014, Syme et al. 2021, Parra et al. 2022). Previous studies have hypothesised that delphinids form mixed-species groups for a variety of reasons, which, broadly speaking, correspond to three proposed functional explanations: to improve foraging, to reduce predation risk, and to gain social benefits (Stensland et al. 2003, Cords & Würsig 2014, Syme et al. 2021). Few studies, however, have considered that delphinids could come together, not by attraction between species, but rather by chance due to shared use of space or by shared attraction to resources.

Australian humpback (*Sousa sahulensis*, hereafter "humpback dolphins") and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, hereafter "bottlenose dolphin"') overlap in range across the coastal waters of northern Australia (Allen et al. 2012, Brown et al. 2012, Palmer et al. 2014) with humpback dolphins tending to occupy shallower and more nearshore waters than bottlenose dolphins (Corkeron 1990, Hunt et al. 2020, Haughey et al. 2021, Hanf et al. 2022). Around the North West Cape, Western Australia, these two species occur in sympatry, and have been reported in mixed-species groups (Brown et al. 2012, Hunt 2018). Here, we investigated spatial and temporal occurrence patterns of humpback and bottlenose dolphins around the North West Cape to assess habitat partitioning and determine whether the species occur together more or less often than expected by chance given their responses to environmental factors. We evaluated the extent and nature of habitat partitioning and co-occurrence between the species both spatially, with a JSDM, and temporally, by analysing their occurrence to detect any diel, seasonal, or yearly patterns in their co-occurrence. We hypothesised that they would display spatial habitat partitioning, with humpback dolphins in shallower water nearer to the coast, but not temporal partitioning. Furthermore, we hypothesised that, after accounting for shared responses to environmental factors, the co-occurrence of humpback and bottlenose dolphins would be higher than that expected by chance. This study represents an important step in understanding habitat partitioning and coexistence in sympatric species as well as the drivers of the formation of mixed-species groups.

4.3 Methods

4.3.1 Study site

The North West Cape, Western Australia, is bordered to the west and north by Ningaloo Reef, whose sandy coral lagoons are protected by a shallow reef crest that falls away steeply towards open water, and to the east by Exmouth Gulf, whose shallow, turbid waters contain scattered coral reefs, seagrass meadows, and mangroves (CALM MPRA 2005, Cassata & Collins 2008). The waters of the North West Cape provide important habitat for a diverse array of species, including both humpback and bottlenose dolphins (Hunt et al. 2017, Haughey et al. 2021).

4.3.2 Data collection

The study area covered approximately 175 km^2 of shallow (<40 m deep), inshore (<5 km from shore) waters from Exmouth, north around the Cape, to the southern end of South Lagoon

(Figure 4.1). This area was surveyed repeatedly from a 5.6 m research vessel by following two predetermined, opposing, zigzag transect routes at a constant speed averaging 7 knots (Figure 4.1). Surveys were conducted across six austral winter (April to October) field seasons (2013-2015, 2018-2019, and 2021) during daylight hours and optimal survey conditions (i.e., Beaufort scale ≤3 and no rain or fog) (Hunt et al. 2017). Following the recommendations of Syme et al. (2022), *sightings* consisted of both single individuals and *groups*, which were operationally defined as two or more individuals within 100 m of one another and engaged in similar behaviour. Upon each dolphin sighting, relevant data were recorded, including the GPS location, the time, and the species present.

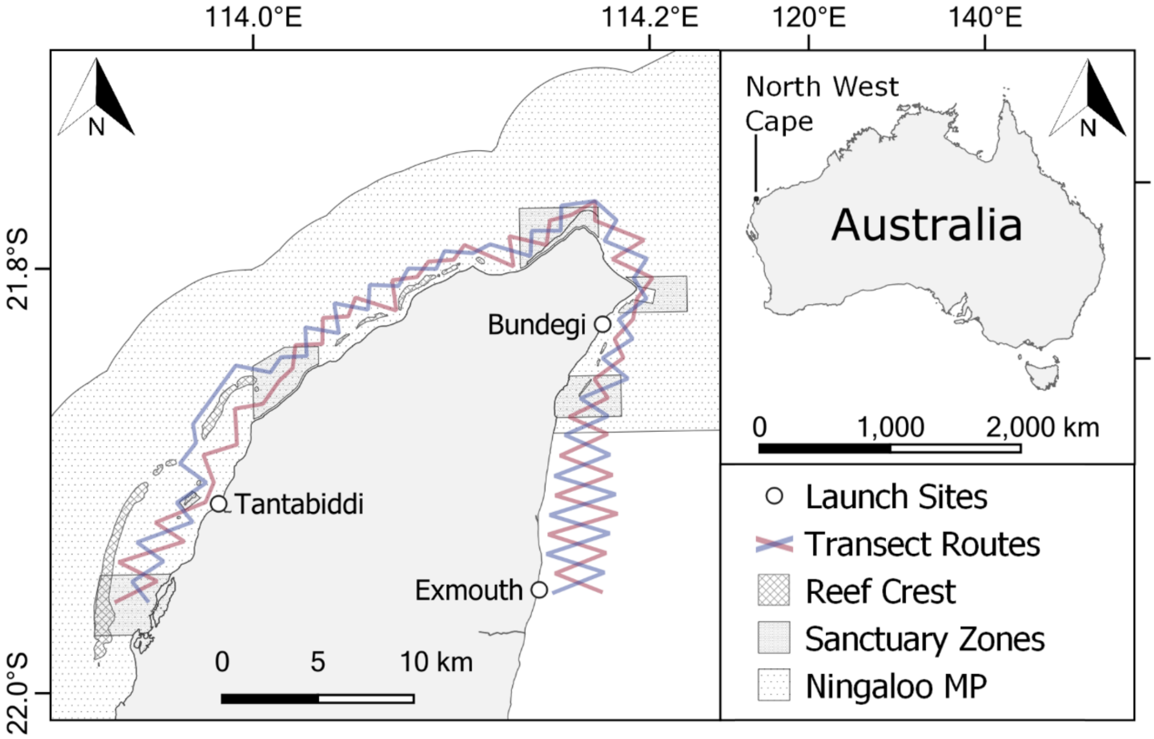

Figure 4.1 The North West Cape, Western Australia, showing vessel launch sites and two opposing, zigzag transect routes used to survey for Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*).

4.3.3 Ethics approvals and permits

Data collection was conducted under permit from the Western Australian Government Department of Biodiversity, Conservation and Attractions (formerly Department of Parks and Wildlife) (permit numbers: SF009240, SF009768, SF010289, and FO25000012) and the Australian Government Department of Defence (Naval Communication Station Harold E Holt) with ethics approval from the Flinders University Animal Welfare Committee (project numbers: E383 and E462/17).

4.3.4 Data preparation

The preparation of all input data for the JSDM (i.e., sites, sighting data, survey effort data, and environmental data) was conducted within the PyQGIS API using Python 3.8.0 (Python Software Foundation 2016) and QGIS 3.8.3 Zanzibar (QGIS Development Team 2019). The study area was divided into 540 grid squares (i.e., sites) of 500 x 500 m. These sites formed the basis for the layers of the response variables (i.e., presence-absence of each species) as well as the environmental predictor variables (i.e., water depth and distance to shore) and survey effort (Table 4.1). This grid size resolution is in line with previous studies on the distribution of inshore dolphins (Zanardo et al. 2017, Hunt et al. 2020, Haughey et al. 2021) and is a balance between coarser resolutions (e.g., 1000 m), which lead to decreased model performance, and finer resolutions (e.g., 100 m), which are more heavily affected by background absences (Gottschalk et al. 2011, Hanberry 2013). Furthermore, this size is sufficiently small to capture the variation in the habitat characteristics of the study site and corresponds to the spatial criterion used in the group definition which, being a chain-rule, allows for the group members to be spread over a larger area than the distance threshold.

Binary presence-absence data were generated for each species by plotting the dolphin sightings from each survey day and determining if each species was either present (1) or absent (0) in each site. Survey effort was calculated for each survey day by adding a 250 m buffer to the recorded GPS track of the research vessel and then calculating the survey effort area within each site (Table 4.1). This buffer distance approximates the reliable visual survey coverage for inshore dolphins from the research vessel. Due to low sighting rates, the daily presence-absence and survey effort data were pooled into three austral seasons: autumn (March–May), winter (June–August), and spring (September–November) (Figure S3.1 and Figure S3.2). This was necessary to avoid issues with model convergence caused by zero-inflation (Zuur et al. 2010, Ovaskainen et al. 2017).

Water depth and distance to shore were included as environmental covariates because both influence the distribution of and demarcate niche partitioning between various dolphin species, including humpback and bottlenose dolphins (Parra et al. 2006b, Zanardo et al. 2017, Passadore et al. 2018, Hunt et al. 2020, Haughey et al. 2021). Most notably, recent research has shown that water depth and distance to shore are the two key factors influencing the distribution of the humpback and bottlenose dolphin populations of the North West Cape (Hunt et al. 2020, Haughey et al. 2021). Other environmental and anthropogenic factors (e.g., habitat type, sea surface temperature, or distance to boat ramps), on the contrary, were found to have little to no effect (Hunt et al. 2020, Haughey et al. 2021) and, consequently, were not included in our analysis.

Environmental factors were sampled across the same sites (i.e., 500 x 500 m grid squares) that were used for determining species presence-absence. Distance to shore was measured as the Euclidean distance from the centre of each site to the nearest land and water depth for each site was calculated with the Ordinary Kriging Tool (SAGA Toolbox: Conrad et al. 2015) from in situ measurements ($n = 5024$) taken with the research vessel's depth sounder (Table 4.1 and Figure S3.3). Before conducting the analysis, we tested for collinearity between the environmental variables in RStudio 1.2.5 (RStudio Team 2019) with Pearson's correlation coefficient and a threshold of $|r| < 0.7$ (Zuur et al. 2010, Dormann et al. 2013).

Table 4.1 The predictor variables included in the joint species distribution model of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around the North West Cape, Western Australia, and their data sources. Values for predictor variables were calculated within the PyQGIS API using Python 3.8.0 (Python Software Foundation 2016) and QGIS 3.8.3 Zanzibar (QGIS Development Team 2019).

Predictor variable	Units	Data source
Water depth	m	Water depth for each site was calculated with the Ordinary Kriging Tool (SAGA Toolbox: Conrad et al. 2015) from in situ measurements (n=5024) taken with the research vessel's depth sounder.
Distance to shore	m	Distance to shore was measured as the Euclidean distance from the centre of each site to the nearest land.
Cumulative survey effort	m^2	Daily survey effort was calculated by adding a 250 m buffer to the recorded GPS track of the research vessel and then calculating the survey effort area within each site. Cumulative survey effort was calculated by summing the daily survey effort for each austral season (i.e., autumn, winter, and spring).

4.3.5 Joint species distribution model

We analysed the co-occurrence of humpback and bottlenose dolphins around the North West Cape with the Hierarchical Modelling of Species Communities (HMSC) framework (Ovaskainen et al. 2017) implemented in RStudio 1.2.5 (RStudio Team 2019) with the package `Hmsc 3.0` (Tikhonov et al. 2020). The HMSC framework employs hierarchical Bayesian JSDMs and Markov chain Monte Carlo (MCMC) sampling to model the occurrence of species while accounting for environmental filtering, resulting in a residual species association matrix (i.e., the **Ω** matrix) (Ovaskainen et al. 2017, Tikhonov et al. 2020).

The response variable of our JSDM consisted of the presence-absence data of humpback and bottlenose dolphins in each season across all 540 sites (the **Y** matrix). Accordingly, a probit regression model was employed with the environmental factors (i.e., water depth and distance to shore) and survey effort included as fixed effects (the **X** matrix). In accordance with the hierarchical nature of the sampling regime, random effects were included for both site and season. Moreover, to account for the spatial arrangement of the sites, the site-level random effect was included as a spatially explicit random effect based on geographic location, defined as the coordinates of the centre of each site.

The posterior distribution was sampled using four MCMC chains of 375000 iterations each. For each chain, the first 125000 iterations were discarded as the transient while the remaining 250000 iterations were thinned by 1000 to produce 250 posterior samples – 1000 posterior samples in total. Model convergence was evaluated by assessing the effective sample sizes and by examining the potential scale reduction factors of the model parameters (Gelman & Rubin 1992). Model fit was assessed with the area under the curve (AUC) (Pearce & Ferrier 2000) and Tjur's R^2 statistics (Tjur 2009) for both explanatory and predictive power, calculated with two-fold cross-validation of the model (Tikhonov et al. 2020, Ovaskainen & Abrego 2020). The relative influence of the fixed (i.e., environmental variables and survey effort) and random effects (i.e., site and season) was evaluated with variance partitioning (Tikhonov et al. 2020) while habitat partitioning between humpback and bottlenose dolphins was assessed by predicting occurrence probabilities for each species across environmental gradients of water depth and distance to shore while normalising the remaining variables to their mean values (Tikhonov et al. 2020, Ovaskainen & Abrego 2020). The residual association between humpback and bottlenose dolphins (i.e., the omega parameter) was used as the basis to investigate the possibility and nature of interactions between these species (Ovaskainen et al. 2017, Tikhonov et al. 2020, Ovaskainen & Abrego 2020). Parameter estimates were deemed significant if the posterior probability was ≥0.95 (Ovaskainen & Abrego 2020).

4.3.6 Temporal analysis

We analysed temporal partitioning between the species and temporal variation in the observed frequency of mixed-species sightings across three temporal scales: diel, seasonal, and yearly. For the diel analysis, time of day was separated into morning (0600 to 1000 hours), midday (1000 to 1400 hours), and afternoon (1400 to 1900 hours) while for the seasonal and yearly analyses, each surveyed season (i.e.: autumn, winter, and spring) and year (i.e.: 2013, 2014, 2015, 2018, 2019, and 2021) constituted a time period, respectively. To assess temporal partitioning, we used a chi-square test to compare the number of sightings of humpback dolphins (single- and mixed-species) to the number of sightings of bottlenose dolphins (single- and mixed-species) across the time periods for each temporal scale. We also determined whether the proportion of sightings that were mixed varied over time. Specifically, we used a Fisher's exact test, due to the low sample size, to compare the number of single- and mixed-species sightings across the time periods for each species at each temporal scale. All temporal analyses were conducted in RStudio 1.2.5 (RStudio Team 2019) at a significance level of $\alpha = 0.05$.

4.4 Results

4.4.1 Sightings summary

In total, 564 on-effort sightings were recorded – 221 of humpback dolphins, 299 of bottlenose dolphins, and 44 of both species (Figure 4.2). Thus, mixed-species sightings accounted for 16.6% of all humpback dolphin sightings (single- and mixed-species), 12.8% of all bottlenose dolphin sightings (single- and mixed-species), and 7.8% of all dolphin sightings.

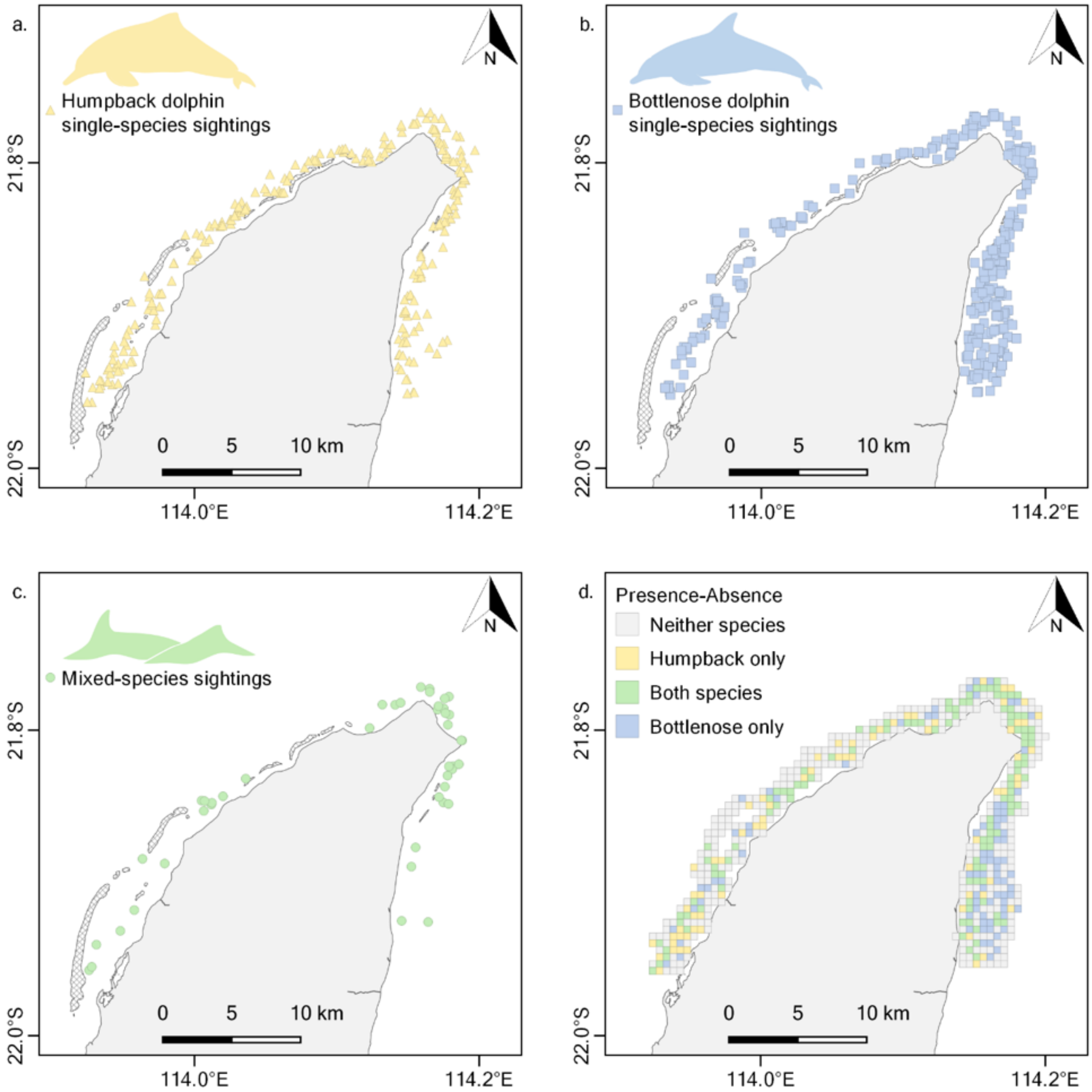

Figure 4.2 On-effort single-species sightings of (a) Australian humpback dolphins (*Sousa sahulensis*) and (b) Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), and (c) mixed-species sightings of both species, as well as (d) overall presence-absence of the species in 540 grids of 500 x 500 m distributed around the North West Cape, Western Australia, from six years of surveys (2013-2015, 2018-2019, and 2021).

4.4.2 Joint species distribution model

Water depth and distance to shore showed a positive collinearity (Pearson's correlation coefficient, $r = 0.56,\ p < 0.001$), but, as it was below the threshold ($|r| > 0.7$) (Zuur et al. 2010, Dormann et al. 2013), both environmental covariates were included in the JSDM. The HMSC diagnostics indicated good MCMC convergence. For both the beta parameters (i.e., species responses to environmental variables) and the omega parameters (i.e., species associations at the site level), the effective sample sizes were close to 1000, and the potential scale reduction factors were mostly below 1.1 (Figure S3.4). The model fit was also satisfactory with mean explanatory and predictive power of 0.86 and 0.77, respectively, as measured by AUC, and 0.20 and 0.14, respectively, as measured by Tjur's R^2 (Table 4.2).

Table 4.2 The explanatory and predictive power of the joint species distribution model of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around the North West Cape, Western Australia, as measured by the area under the curve (AUC) and Tjur's R^2 statistics.

Species	Measure	Explanatory	Predictive
Humpback dolphin	AUC	0.83	0.75
	Tjur's R^2	0.15	0.10
Bottlenose dolphin	AUC	0.90	0.79
	Tjur's R^2	0.27	0.17

The different amounts of influence of the fixed and random effects on the occurrence of humpback and bottlenose dolphins were illustrated by variance partitioning (Figure 4.3). Survey effort accounted for a substantial amount of explained variance for both species (humpback dolphin, 41.5%; bottlenose dolphin, 43.1%), highlighting that detection rates and, thus, observed occurrence rates are heavily dependent on the amount of survey effort conducted in each site. Distance to shore was highly relevant to humpback dolphins (15.9%), but not bottlenose dolphins (1.4%) whereas water depth was important for both (humpback dolphin, 13.7%; bottlenose dolphin, 9.9%).

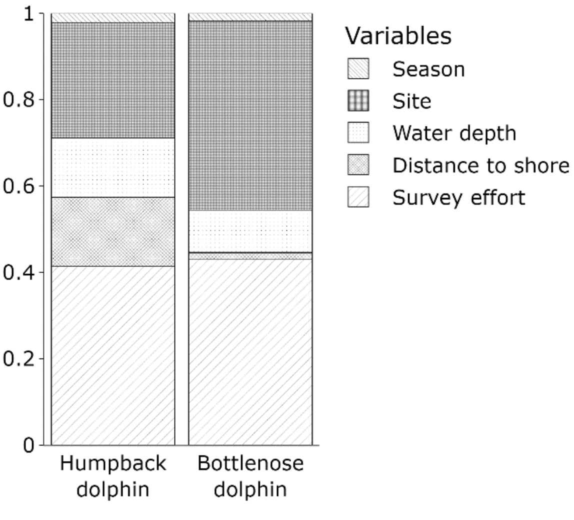

Figure 4.3 The proportion of variance in the occurrence of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around the North West Cape, Western Australia, explained by the random effects (i.e., season and site) and the fixed effects (i.e., water depth, distance to shore, and survey effort) included in the joint species distribution model.

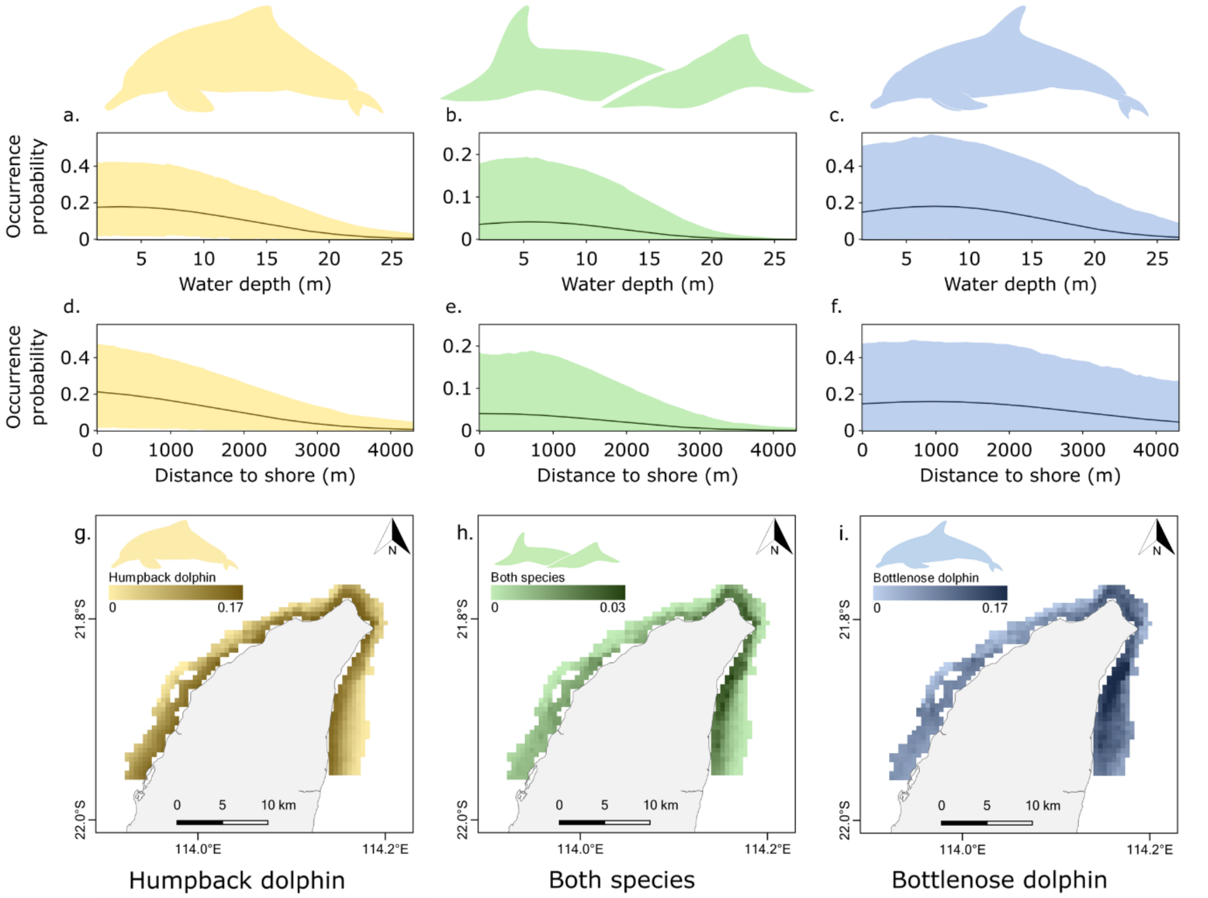

Figure 4.4 Results of a joint species distribution model of the occurrence of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), around the North West Cape, Western Australia. The three columns illustrate the predicted occurrence probability of humpback dolphins, the predicted co-occurrence probability of the two species, and the predicted occurrence probability of bottlenose dolphins relative to water depth (a., b., and c.) and distance to shore (d., e., and f.), as well as across 540 grids of 500 x 500 m (g., h., and i.). In the first (a., b., and c.) and second rows (d., e., and f.), the line represents the mean and the shaded area the 95% credibility interval. Occurrence probabilities for humpback and bottlenose dolphins were calculated while normalising the remaining variables to their mean values. Co-occurrence probabilities were calculated by multiplying the corresponding single-species occurrence probabilities.

The predicted occurrence probability of humpback dolphins was highest at depths of one to five metres and decreased with distance to shore (Figure 4.4a, d, and g) while that of bottlenose dolphins was highest at depths of seven to ten metres and peaked at approximately 1000 m from shore before decreasing (Figure 4.4c, f, and i). The predicted co-occurrence probability of the species showed intermediate trends, peaking at approximately five metres deep and decreasing with distance to shore (Figure 4.4b, e, and h). The spatial random effect (i.e., site) strongly impacted both species (humpback dolphin, 26.7%; bottlenose dolphin, 43.8%), indicating that they display strong preferences for certain sites, while the temporal random effect (i.e., season) had only a minor impact (humpback dolphin, 2.2%; bottlenose dolphin, 1.8%), suggesting that their occurrence is not affected by seasonal changes. Humpback and bottlenose dolphins displayed a strong, positive association in their occurrence with a residual correlation of 0.8 (posterior probability >95%), indicating that, after accounting for their shared responses to environmental factors, they co-occur more often than expected by chance.

4.4.3 Temporal analysis

Single and mixed-species sightings were observed throughout diel, seasonal, and yearly temporal scales (Figure 4.5). We found some evidence for diel temporal partitioning between humpback and bottlenose dolphins ($\chi^2_2 = 11.53, p < 0.001$), with bottlenose dolphins sighted more often than humpback dolphins during the afternoon. There was, however, no significant differences in the number of humpback and bottlenose dolphins sighted across seasons and years (seasons: $\chi^2_2 = 5.31, p = 0.07$; years: $\chi^2_5 = 8.68, p = 0.12$). Finally, no temporal variation in the proportion of single- and mixed-species sightings was detected for either species at a diel (humpback: $p = 0.69$; bottlenose: $p = 0.22$; Fisher's exact test), seasonal (humpback: $p = 0.15$; bottlenose: $p = 0.52$; Fisher's exact test), or yearly scale (humpback: $p = 0.88$; bottlenose: $p = 0.28$; Fisher's exact test).

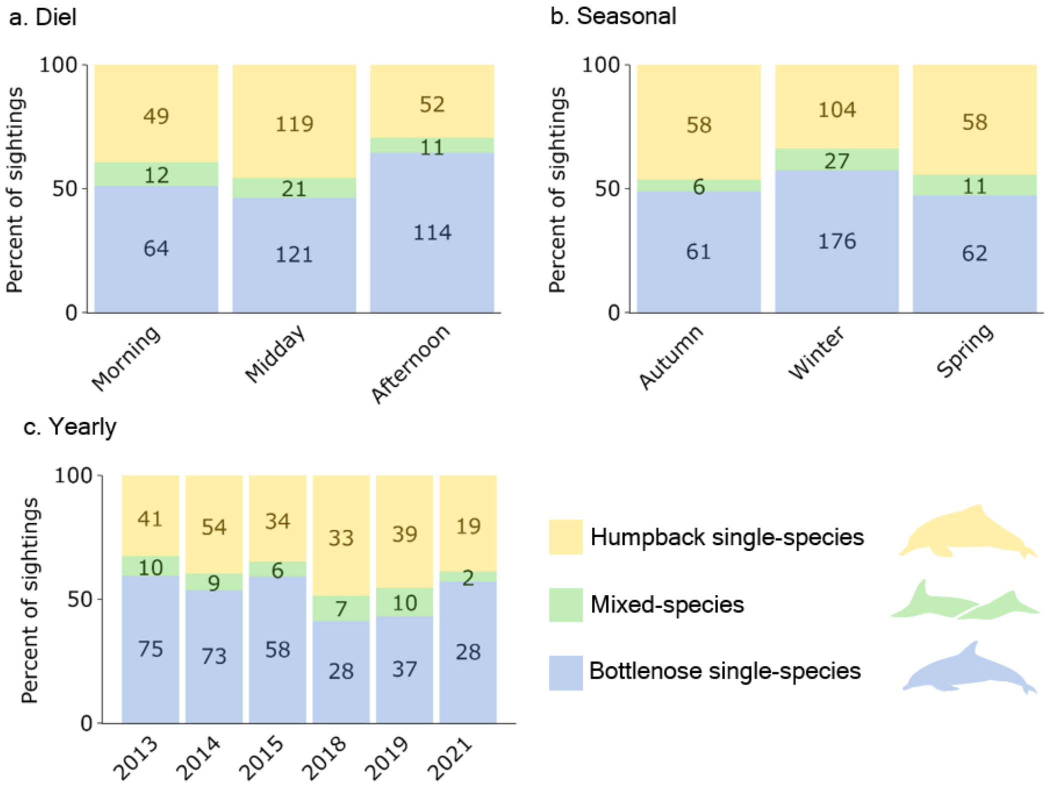

Figure 4.5 The percentage of on-effort sightings that were of only Australian humpback dolphins (*Sousa sahulensis*), only Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), and mixed-species sightings containing both species across three temporal scales – (a) diel: morning (0600 to 1000 hours), midday (1000 to 1400 hours), and afternoon (1400 to 1900 hours); (b) seasonal: autumn (March–May), winter (June–August), and spring (September–November); and (c) yearly. Numbers in the bars are the total number of sightings for each sighting category in that temporal period.

4.5 Discussion

Numerous delphinid species occur in sympatry including many that appear to form mixed-species groups (Stensland et al. 2003, Bearzi 2005, Cords & Würsig 2014, Syme et al. 2021). Few studies have, however, quantitatively assessed the mechanisms that allow sympatric dolphins to coexist and determined whether apparent mixed-species groups are indeed the result of attraction between heterospecific individuals and not simply chance encounters or aggregations around resources (Stensland et al. 2003, Bearzi 2005, Cords & Würsig 2014, Syme et al. 2021). Using sympatric humpback and bottlenose dolphins around the North West Cape, Western Australia, as a model system, we found that the study species display some level of habitat partitioning with regards to water depth and distance to shore. Furthermore, some diel patterns in habitat preferences were also identified. Despite this spatial and temporal partitioning in their habitat use, humpback and bottlenose dolphins displayed a high and positive association after accounting for their shared responses to environmental variables. This suggests that their co-occurrence is not due to chance and that they may actively form mixed-species groups.

Before considering the implications of these findings, however, it is necessary to consider some potential limitations of the data collection and analyses. Given that dolphins spend most of their time underwater and are highly mobile, false negatives (i.e., not detecting a species when it is there) may have occurred, possibly affecting the observed rates of occurrence. Additionally, mixed-species sightings, which were, on average, larger in size (number of individuals) than single-species sightings of either species (unpublished data), may have been easier to detect, possibly inflating the observed rate of co-occurrence (Astaras et al. 2011). Nevertheless, these potential sources of bias were minimised by having the data recorded by trained observers under optimal survey conditions (i.e., Beaufort scale ≤3, no rain or fog) following a predetermined protocol implemented repeatedly across numerous surveys.

4.5.1 Habitat partitioning

Humpback and bottlenose dolphins are ecologically similar – both occur in inshore waters and forage on coastal prey (Parra & Jefferson 2018, Wang 2018). To be able to coexist, they presumably partition available resources and habitats, particularly if resources are limiting (Chesson 2000, Bearzi 2005, Parra 2006, Kiszka et al. 2011b). Both species were observed in the study area throughout the day and during all three seasons and all six years surveyed, with limited evidence for only diel partitioning in habitat use. This suggests that temporal partitioning of habitat use between humpback and bottlenose dolphins around the North West Cape has a minor role in allowing coexistence.

We detected stronger patterns of spatial partitioning, however, with humpback dolphins found in shallower water and closer to shore than bottlenose dolphins. This concurs with previous studies of niche partitioning between these species (Corkeron 1990, Hanf et al. 2022). Elsewhere, it has been shown that, although habitat partitioning may occur, niche partitioning is mediated by differences in trophic niches (Kiszka et al. 2011b, Browning et al. 2014, Parra et al. 2022). Around the North West Cape, the trophic interactions of humpback and bottlenose dolphins are poorly understood, however, opportunistic observations of both species foraging suggest that the species may target different prey. For example, as at other locations (Kiszka et al. 2014), bottlenose dolphins were observed foraging at the surface on epipelagic fish (e.g., *Hemiramphus* sp.), a behaviour that humpback dolphins, which seem to forage mostly on demersal resources, were not observed to perform (JS and GJP personal observations).

In summary, temporal and habitat partitioning, perhaps combined with the use of different resources, may allow humpback and bottlenose dolphins to coexist around the North West Cape. Yet, humpback and bottlenose dolphins were regularly observed in close spatiotemporal proximity and exhibited a high, positive correlation in occurrence. Similarly, in numerous locations, dolphin species that exhibit niche partitioning have also been observed in apparent mixed-species groups (Saayman & Tayler 1979, Corkeron 1990, Gowans & Whitehead 1995, Parra 2006, Browning et al. 2014).

4.5.2 Chance encounters?

By analysing presence-absence data with a JSDM, we quantitatively confirmed that, after accounting for shared environmental responses, the co-occurrence of humpback and bottlenose dolphins around the North West Cape is not the result of chance. Previous studies of dolphin mixed-species groups have established that species do not encounter each other by chance by employing either a minimum time limit (Kiszka et al. 2011a, Jourdain & Vongraven 2017) or by analysing patterns of association between heterospecific individuals (Zaeschmar et al. 2014, Elliser & Herzing 2016a). In many studies of mixed-species groups of mammals, particularly cetaceans, however, it is unclear whether instances of sympatric species occurring in close spatiotemporal proximity are chance encounters due to habitat and temporal overlap, aggregations around prey due to dietary overlap, or the result of attraction between the species (Syme et al. 2021).

Our results also highlight the importance of incorporating environmental factors into analyses of species co-occurrence rates (Ovaskainen et al. 2017, Ovaskainen & Abrego 2020, Blanchet et al. 2020). Humpback and bottlenose dolphins displayed different, yet overlapping, responses to water depth and distance to shore, indicating that shared habitat preferences may be partially responsible for their co-occurrence. These responses to environmental factors would not have been detected with certain previously used methods to assess species co-occurrence, such as null models or ideal gas models, that do not incorporate environmental factors (Pollock et al. 2014, Ovaskainen et al. 2017). Yet, by using a JSDM we identified and accounted for the influence of key environmental factors, revealing a highly positive residual correlation in the occurrence of humpback and bottlenose dolphins.

4.5.3 Potential drivers for species associations

Residual correlation in the co-occurrence of two species does not equate to evidence for ecological interactions between them (Pollock et al. 2014, Ovaskainen et al. 2016, Blanchet et al. 2020). Instead, interspecific interactions are one possible explanation for observed non-random patterns of co-occurrence, alongside missing environmental or anthropogenic variables and biotic interactions with other species, such as predators and prey (Pollock et al. 2014, Ovaskainen et al. 2016, Ovaskainen & Abrego 2020, Blanchet et al. 2020).

It is possible that unmeasured environmental factors are responsible for some of the observed residual correlation. However, previous research on the study species has shown that a range of environmental (e.g., benthic habitat type, slope, seabed complexity, sea surface temperature, distance to reef passage, and distance to reef) and anthropogenic (e.g., distance to sanctuary zones and distance to boat ramp) variables have little to no effect on their distribution (Hunt et al. 2020, Haughey et al. 2021). Therefore, the effect of these covariates on the co-occurrence patterns of humpback and bottlenose dolphins around the North West Cape would presumably be minimal.

The co-occurrence of humpback and bottlenose dolphins could also be explained by biotic interactions. These biotic interactions could take the form of independent interactions between both species and another (Blanchet et al. 2020), for example, mutual avoidance of large sharks could lead to shared use of safer habitats while shared attraction to food pulses could lead to aggregations around schools of fishes (Clua 2001). Alternatively, there could be a direct biotic interaction between the two species, such as an attraction between them stemming from evolutionary benefits that they gain by co-occurring (Stensland et al. 2003, Syme et al. 2021). Disentangling direct interactions between humpback and bottlenose dolphins, from interactions between these species and their predators or their prey is difficult, particularly if both types of interaction influence patterns of co-occurrence (Cords & Würsig 2014, Blanchet et al. 2020). For example, both species may respond similarly to a food pulse because they are independently attracted to the same prey, because they gain some foraging benefit from the other dolphin species, or a combination of both (Clua 2001, Quérouil et al. 2008). Including the distribution and abundance of predators and prey in JSDMs would help to identify the role that predator-prey dynamics play in determining species distributions and co-occurrence patterns (Astarloa et al. 2019). Where data on predators and prey are unavailable, environmental factors can represent proxies for underlying ecological and spatiotemporal processes such as the distribution, availability, and movement of predators and prey. Yet, the included environmental factors could not fully explain the co-occurrence of humpback and bottlenose dolphins. Moreover, if co-occurrence resulted from shared use of safe habitats then the species should co-occur primarily within those habitats (e.g., deep areas with sandy substrate (Heithaus & Dill 2002)), while if co-occurrence resulted from shared attraction to food resources then the species would, presumably, co-occur at times and locations where prey is concentrated, as is the case in the Azores where feeding aggregations of dolphins and tunas occur primarily at dawn and dusk (Clua 2001). Yet, mixed-species sightings were distributed both throughout the study area and across time. Thus, interactions with predators and prey do not seem to fully explain the co-occurrence patterns of humpback and bottlenose dolphins around the North West Cape.

We propose that the positive association in humpback and bottlenose dolphin occurrence is partly the result of attraction between the two species, and, thus, the active formation of mixed-species groups. Three main functional explanations have been proposed as to why mammals, including dolphins, form mixed-species groups: the antipredator, foraging, and social advantage hypotheses (Stensland et al. 2003, Cords & Würsig 2014, Syme et al. 2021). Interestingly, as the temporal analysis did not indicate any diel or seasonal patterns in the occurrence of mixed-species groups, any drivers of their formation are presumably active throughout the day and across seasons. Evidently, further analyses of the characteristics of mixed-species groups (e.g., group size, relative numbers of each species, and sex and age composition) and the behaviours exhibited by the participating individuals are required to determine more precisely what drives sympatric humpback and bottlenose dolphins around the North West Cape to form mixed-species groups. Ultimately, future research should focus on assessing the evolutionary benefits that these species may gain by grouping with heterospecifics.

Chapter 5

Multiple social benefits drive the formation of mixed-species groups of Australian humpback and Indo-Pacific bottlenose dolphins

Multiple social benefits drive the formation of mixed-species groups of Australian humpback and Indo-Pacific bottlenose dolphins

5.1 Abstract

Mixed-species groups are common amongst diverse taxa including fishes, birds, and mammals. Antipredator, foraging, and social benefits have been proposed as functional explanations for mixed-species group formation. Amongst delphinids, mixed-species groups are widespread, but little is known about their function. To investigate the potential benefits of delphinid mixed-species groups, we compared the number of individuals, the age composition, and the behaviour of single- and mixed-species sightings of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) observed around the North West Cape, Western Australia. We found no difference in the number of individuals or the age composition of humpback dolphins present in single- and mixed-species sightings, whereas bottlenose dolphins were present in larger numbers in single-species sightings than in mixed-species sightings due to a higher number of adults. Socialising was the initial observed behavioural state of 36.1% of mixed-species sightings, compared to only 5.1% and 10.3% of humpback and bottlenose dolphin single-species sightings, respectively. Furthermore, both species travelled and foraged less frequently when in mixed-species groups. Of 93 mixed-species groups observed during a focal follow of ≥10 minutes, 32 (34.4%) involved aggressive and/or sexual behaviours typically initiated by bottlenose dolphins towards humpback dolphins while the remaining 61 (65.6%) involved only neutral and affiliative behaviours. The results of this study suggest that the observed mixed-species groups provide multiple social benefits, particularly those pertaining to socio-sexual behaviours and the development and care of young.

5.2 Introduction

Mixed-species groups have been observed amongst diverse taxa, most notably fishes, birds, and mammals (Stensland et al. 2003, Sridhar et al. 2009, Cords & Würsig 2014, Heymann & Hsia 2015, Goodale et al. 2017, Syme et al. 2021). Mixed-species groups form when an attraction between heterospecific individuals causes them to actively achieve and maintain spatiotemporal proximity (Stensland et al. 2003, Goodale et al. 2017, Syme et al. 2021). Accordingly, mixed-species groups should not be confused with chance encounters or with aggregations of animals that display shared responses to environmental stimuli because, unlike these situations, the formation of mixed-species groups is driven by evolutionary benefits (Waser 1984, Whitesides 1989, Stensland et al. 2003). These benefits typically fall within three main hypotheses – the antipredator, foraging, and social advantage hypotheses (Whitesides 1989, Stensland et al. 2003, Syme et al. 2021). These hypotheses are not mutually exclusive and, in some situations, a combination of drivers may affect the occurrence of mixed-species groups (Stensland et al. 2003, Zaeschmar et al. 2014, Syme et al. 2021).

There are diverse mechanisms by which individuals in mixed-species groups may gain evolutionary benefits. For example, antipredator benefits may be derived from the dilution effect, improved defence against predators, or increased group vigilance (Whitesides 1989, Stensland et al. 2003, Goodale et al. 2017) while foraging benefits may be obtained by mutual or non-mutual exchange of information to increase feeding opportunities or cooperative foraging (Whitesides 1989, Stensland et al. 2003, Goodale et al. 2017). Social benefits may be gained when interactions with heterospecifics increase the ability to defend territory or potential mates, increase the number of socio-sexual opportunities, or provide opportunities for individuals to practice a range of social behaviours, from play and alloparental care, to courtship and sexual behaviours, to infanticide (Spinka et al. 2001, Stensland et al. 2003, Syme et al. 2021).

These different benefits, and their corresponding mechanisms, result in patterns in certain group and individual characteristics (e.g., group size, behaviour, and habitat use) according to how and why a given mixed-species groups was formed (Syme et al. 2021). Mixed-species groups that are larger in size than single-species groups are suggestive of antipredator benefits (Heymann & Buchanan-Smith 2000, Sridhar et al. 2009). Furthermore, species that gain antipredator benefits from mixed-species groups often increase their association rate in places and at times of higher predation risk, such as where predators are abundant or when the group contains more vulnerable young individuals (Noë & Bshary 1997, Chapman & Chapman 2000, Wolters & Zuberbühler 2003, Kiszka et al. 2011a). Foraging benefits are indicated by increased foraging behaviour and increased feeding rates in mixed-species groups compared to single-species groups (Heymann & Buchanan-Smith 2000, Sridhar et al. 2009). Also suggestive of foraging benefits are observations of cooperative foraging and a widening of foraging niche as the result of using novel microhabitats or food resources made available by heterospecifics (e.g., primates flushing insects from where they are hiding) when in mixed-species groups (Wolters & Zuberbühler 2003, Zaeschmar et al. 2013, Heymann & Hsia 2015). Where species form mixed-species groups to gain social benefits, interspecific social behaviour is frequent and involves recurring, and often diverse and complex, behavioural interactions from affiliative (e.g., play, grooming, and alloparental care), to aggressive (e.g., chases, forceful physical contact, and biting), and sexual behaviours (van Lawick-Goodall 1968, Herzing & Johnson 1997, Acevedo-Gutiérrez et al. 2005, Struhsaker 2010, Syme et al. 2021). Investigating such behavioural interactions and their relationship to the ratio between species and the sex and age of the individuals involved can provide further insights into the nature and directionality of any social benefits (Herzing & Johnson 1997, Elliser & Herzing 2016a).

Numerous species of delphinids have been observed in mixed-species groups, however most published reports are brief accounts and, consequently, whether they represent true mixed-species groups rather than chance encounters or aggregations is often unknown (Cords & Würsig 2014, Syme et al. 2021). Furthermore, the underlying causes of these interactions remain poorly understood, with several studies proposing the antipredator, foraging, and social advantage hypotheses as potential explanations (Stensland et al. 2003, Cords & Würsig 2014, Syme et al. 2021). These conclusions have typically been reached by analysing and comparing characteristics, such as the number of individuals, the sex and age composition, and the behaviour, of single- and mixed-species groups of the species involved. For example, Kiszka et al. (2011) suggested that spinner dolphins (*Stenella longirostris*) form mixed-species groups with pantropical spotted dolphins (*Stenella attenuata*) around the western Indian Ocean island of Mayotte to reduce predation risk when travelling in deep water on the basis that mixed-species groups were larger than single-species groups, frequently exhibited travelling and resting behaviour, and occurred in areas associated with heightened predation risk. Observations off the California coast of common bottlenose dolphins (*Tursiops truncatus*) joining groups of foraging short-finned pilot whales (*Globicephala macrorhynchus*) led Shane (1994) to conclude that common bottlenose dolphins gain foraging benefits. Social benefits are harder to unravel but the prominence of socialising behaviour and the variety of direct interspecific interactions suggests that they may be the drivers behind several delphinid mixed-species groups including, for example, those of common bottlenose and Guiana dolphins (*Sotalia guianensis*) in Costa Rica (Acevedo-Gutiérrez et al. 2005, May-Collado 2010) and common bottlenose and Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas (Herzing & Johnson 1997, Melillo et al. 2009, Elliser & Herzing 2016a).

Australian humpback (*Sousa sahulensis*) (hereafter “humpback dolphin”) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (hereafter “bottlenose dolphin”) occur in sympatry across northern Australia (Corkeron 1990, Allen et al. 2012, Brown et al. 2012, Palmer et al. 2014) and have been observed to regularly form mixed-species groups (Corkeron 1990, Brown et al. 2012, Hunt 2018). Humpback and bottlenose dolphins around the North West Cape, Western Australia, co-occur more often than would be expected by chance given their shared responses to key environmental variables (Chapter 4). Furthermore, their patterns of co-occurrence do not resemble those of species aggregated around shared resources, suggesting that observed mixed-species groups are indeed the result of an attraction between the species (Chapter 4). Nevertheless, the group size, age composition, and behaviour of mixed-species groups of humpback and bottlenose dolphins are yet to be described in detail and their functional significance remains unknown.

Here, we analysed the characteristics of single- and mixed-species groups of humpback and bottlenose dolphins around the North West Cape in order to assess the possible function of these mixed-species groups. If these species form mixed-species groups to reduce predation risk, we would expect mixed-species groups to be larger, contain more calves, and to travel and rest more frequently than single-species groups. Alternatively, if they form mixed-species groups to improve foraging, then we would expect mixed-species groups to forage more often than single-species groups and, depending on how the foraging benefit is obtained, observations of one species following another during foraging and/or cooperative foraging between the species. Finally, if humpback and bottlenose dolphins gain social benefits from forming mixed-species groups, then we would expect an increase in the frequency of socialising combined with numerous, and potentially diverse, direct interspecific behavioural interactions. Our research contributes to the limited, but increasing, knowledge of the complexity of delphinid mixed-species groups and provides direction for future research to investigate how these potentially diverse benefits apply to and impact the individuals and the species involved.

5.3 Methods

5.3.1 Study site and populations

The North West Cape is found in the Pilbara of Western Australia and is notable for its high biodiversity. To the east, lies Exmouth Gulf, a shallow, turbid embayment with sand and mud seabeds that are home to seagrass meadows, scattered coral reefs, and mangrove forests (Cassata & Collins 2008, Wilson 2013a). To the north and west, lies the World Heritage Listed Ningaloo Reef which separates sandy coral lagoons from the open waters of the Indian Ocean (Cassata & Collins 2008, Wilson 2013a).

The diverse habitat types around the North West Cape are important for both humpback and bottlenose dolphins. Hunt et al. (2017) estimated that the humpback dolphin population consists of 65-102 animals and has, at approximately one dolphin per km^2, the highest recorded density for this species. Consistent with other humpback dolphin (*Sousa* sp.) populations, humpback dolphins around the North West Cape were found to form small groups of up to 19 individuals with an average of 4.6 ± 3.2 (Hunt et al. 2017). The bottlenose dolphin population is larger, with Haughey et al. (2020) estimating the resident population at 141 and the super-population at 370 (including resident and transient individuals) animals across a three year study period (2013-2015). Bottlenose dolphins are also found at a higher density, between 2.4 and 2.8 dolphins per km^2, and form slightly larger groups of up to 30 individuals with an average of 6.4 ± 5.2 (Haughey et al. 2020).

5.3.2 Data collection

Dolphin sightings were recorded during boat-based surveys conducted during the austral winter period of April to October over six years (2013-2015, 2018-2019, and 2021). Surveys followed two pre-determined, opposing, zigzag transect lines and one additional straight transect line, ensuring even coverage over the principal study area, which encompassed approximately 175 km^2 of shallow waters, to 30 m deep, on both sides of the Cape, from Exmouth to South Lagoon (Figure 5.1). Surveys were restricted to daylight hours and good conditions (Beaufort scale ≤3, no rain or fog) to ensure a consistent sighting rate. Additional sightings were recorded during travel to and from the transect lines and during non-transect surveys both inside and outside the principal study area.

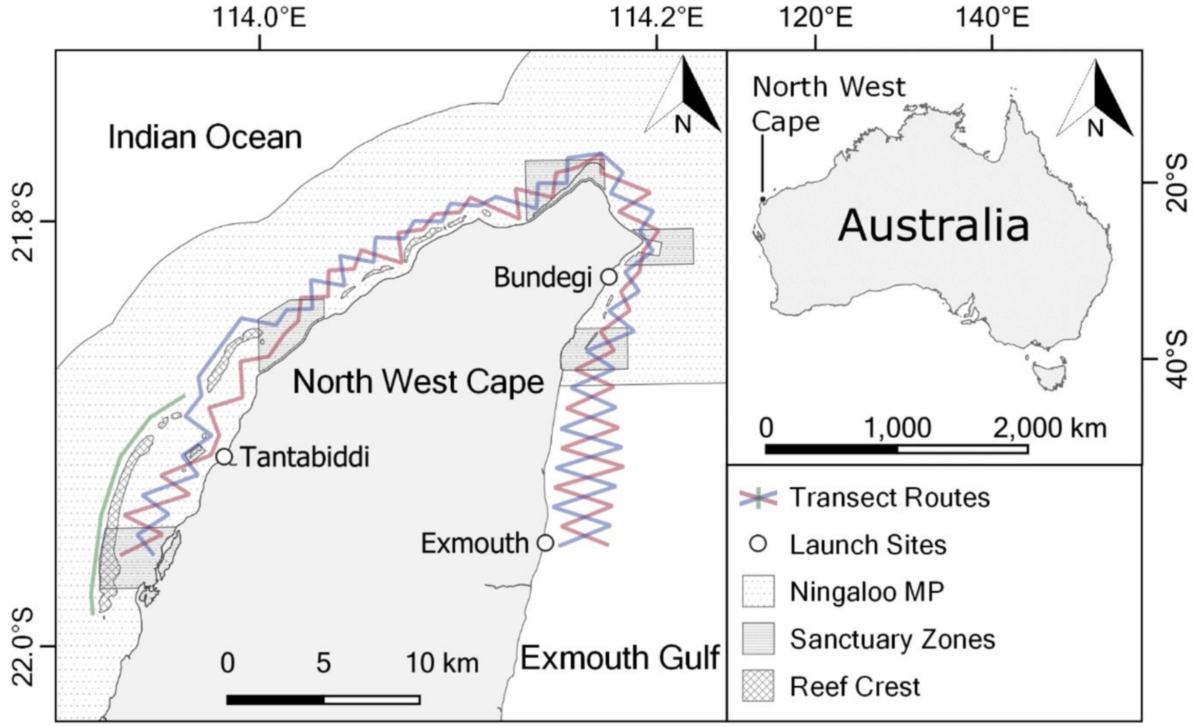

Figure 5.1 The North West Cape, Western Australia, showing the two opposing, zigzag transect routes (blue and red) and the additional straight transect route (green) that were used to survey for Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) as well as the vessel launch sites, Ningaloo Marine Park (dotted area), sanctuary zones (grey shaded areas), and reef crests (crosshatched area).

Following the recommendations of Syme et al. (2022), we use the term *sighting* to refer to both *singletons* (i.e., single animals) and *groups*, which were operationally defined as two or more individuals within 100 m of one another and engaged in similar behaviour (Hunt et al. 2017). The same definition was applied to both single- and mixed-species groups (Stensland et al. 2003, Syme et al. 2021). Additionally, following Weir et al. (2008) and Deutsch et al. (2014), we defined nursery groups as those groups with two or more calves and where calves constituted at least 25% of group members.

Table 5.1 Definitions of behavioural states used during observations of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around the North West Cape, Western Australia.

Behavioural state	Definition
Foraging	Fast, non-directional, sometimes erratic movements with rapid acceleration Frequent, long dives at steep angle Observations of prey
Milling	Slow, non-directional movements with short dives at shallow angle, but most time spent at surface Close proximity, but few interactions
Resting	Very slow, non-directional movements at surface with low activity level Tight group formation
Socialising	Non-directional movements with dives of varying length Frequent aerial behaviours (e.g., leaping) and heads and flukes often above the water surface Close proximity, high levels of interaction including physical contact (e.g., touching, rubbing)
Travelling	Constant, directional movement with regular surfacing, shallow dive angles Group spacing varies

Table 5.2 Definitions used to define the age classes of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around the North West Cape, Western Australia (modified from Parra et al. 2006).

Age Class	Definition
Adult	>2 m long
Juveniles	½ to ⅔ the length of an adult Usually swimming alongside an adult, but sometimes swimming independently
Calf	≤½ the length of an adult Regularly swimming beside or slightly behind an adult

Upon each sighting, key characteristics were recorded including: the species present; the initial behavioural state of the majority of animals sighted (see Table 5.1 for behavioural state definitions); an estimate of the number of individuals; and the age composition, defined as the number of adults, juveniles, and calves (see Table 5.2 for age class definitions). For mixed-species sightings, the number of individuals and the age composition were recorded separately for each species. Where possible, the presumed sex of individuals was determined by either regular close association with a calf or juvenile, observation of the genital area or, for humpback dolphins, sexually dimorphic differences in the location and extent of patches of pigmentation loss and spotting (Brown et al. 2016a, Hunt et al. 2019). When conditions permitted, focal follows were conducted with behavioural events recorded *ad libitum* (Altmann 1974, Mann 1999) until either the dolphins were lost from sight, weather conditions deteriorated, or a limit of one hour was reached.

5.3.3 Data analysis

Sightings of unknown species as well as sightings where the number of individuals, the age composition, or the initial behavioural state were unable to be determined were deemed incomplete and were not included in the analyses. For all the following comparisons of the number of individuals and the age composition, non-parametric randomisation tests were used as the observed data did not meet the assumptions of homogeneity of variance or normality. To evaluate significance, all randomisation tests utilised 10,000 iterations and recorded the number of times that the mean difference obtained from an iteration was greater than that obtained from the observed data (Manly 1997). The p-values produced from the randomisation tests were adjusted using the Benjamini-Hochberg Procedure to reduce the chance of Type I error (Benjamini & Hochberg 1995). All statistical analyses were conducted in RStudio 1.2.5 (RStudio Team 2019) and evaluated at a significance level of $\alpha = 0.05$.

5.3.3.1 Comparisons of the number of individuals and age composition

To evaluate how mixed-species groups fit into the broader patterns of grouping dynamics, the number of individuals and the age composition of single-species sightings were compared to those of mixed-species sightings. Additionally, the number of individuals and the age composition of conspecifics within mixed-species sightings were compared to those of single-species sightings of the same species. Finally, given that the relative number of individuals of each species can influence the nature of interspecific interactions, the number of individuals and the age composition of conspecifics within mixed-species sightings were compared to each other.

5.3.3.2 Frequencies of initial behavioural states

To determine if the presence of heterospecifics influences the species' behaviour, the frequencies of the initial behavioural states of each species were compared between single- and mixed-species sightings with a chi-square contingency table. Sightings with an initial behavioural state of boat avoidance or boat interaction (n=21) were excluded from this analysis.

5.3.3.3 Nature of interspecific interactions

To better understand how the relative numbers and age composition of each species relate to the nature of interspecific interactions, we evaluated the behavioural events observed during focal follows of mixed-species sightings. Mixed-species sightings were then categorised into those involving aggressive (e.g., tail slaps, forceful body contact, and chases) and/or sexual (e.g., copulation and ventral-to-ventral positioning) behavioural events (hereafter "aggressive/sexual mixed-species sightings") and those not involving such behavioural events (hereafter "non-aggressive/sexual mixed-species sightings") (Herzing & Johnson 1997, Parra 2005, Elliser & Herzing 2016a). Aggressive and sexual behavioural events were often concurrent and difficult to distinguish in the field, hence sightings involving such behaviours were combined into one category. Only mixed-species sightings observed during a focal follow lasting ≥10 minutes were analysed to ensure that adequate opportunity was had to observe any aggressive or sexual behavioural events, which were recorded *ad libitum* (Altmann 1974, Mann 1999). The characteristics of these mixed-species sightings were then analysed, firstly, by comparing the total number of individuals (i.e., both species combined) in aggressive/sexual and non-aggressive/sexual mixed-species sightings, then, by comparing the number of individuals and the age composition of each species between aggressive/sexual and non-aggressive/sexual mixed-species sightings and between species.

5.4 Results

5.4.1 Sightings summary

Both humpback and bottlenose dolphins were observed across the study area and throughout all six field seasons, resulting in a total of 1130 dolphin sightings (Figure 5.2). Of these sightings, 427 (37.8%) were of humpback dolphins only, 584 (51.7%) were of bottlenose dolphins only, and 119 (10.5%) contained both species (i.e., mixed-species groups), 18 of which were classified as mixed-species nursery groups (i.e., groups with two or more calves and where calves constituted at least 25% of group members). Accordingly, 21.8% of the 546 sightings containing humpback dolphins were mixed, as were 16.9% of the 703 sightings containing bottlenose dolphins.

5.4.2 Comparisons of the number of individuals and age composition

Mixed-species sightings contained on average 9.2 ± 4.1 individuals and were significantly larger than both single-species sightings of humpback (4.5 ± 2.5, $p < 0.001$) and bottlenose dolphins (5.9 ± 4.4, $p < 0.001$). The number of humpback dolphins in single-species sightings did not differ significantly from the number of humpback dolphins in mixed-species sightings (single-species: 4.5 ± 2.5, mixed-species: 4.6 ± 2.8, p = 0.612) (Figure 5.3a). There were no differences either in the number of humpback dolphin adults (single-species: 3.0 ± 1.7, mixed-species: 3.2 ± 1.8, p = 0.250) (Figure 5.3b), juveniles (single-species: 0.8 ± 0.9, mixed-species: 0.8 ± 1.0, p = 0.482) (Figure 5.3c), or calves (single-species: 0.6 ± 0.9, mixed-species: 0.6 ± 0.9, p = 0.954) (Figure 5.3d). In contrast, the total number of bottlenose dolphins in single-species sightings was larger than in mixed-species sightings (single-species: 5.9 ± 4.4, mixed-species: 4.6 ± 3.5, p = 0.002) (Figure 5.3a) as single-species sightings contained more bottlenose dolphin adults (single-species: 4.8 ± 3.9, mixed-species: 3.5 ± 2.7, p = 0.001) (Figure 5.3b), although there was no difference in the number of juveniles (single-species: 0.8 ± 0.9, mixed-species: 0.7 ± 0.9, p = 0.386) (Figure 5.3c) or calves (single-species: 0.4 ± 0.7, mixed-species: 0.3 ± 0.6, p = 0.284) (Figure 5.3d).

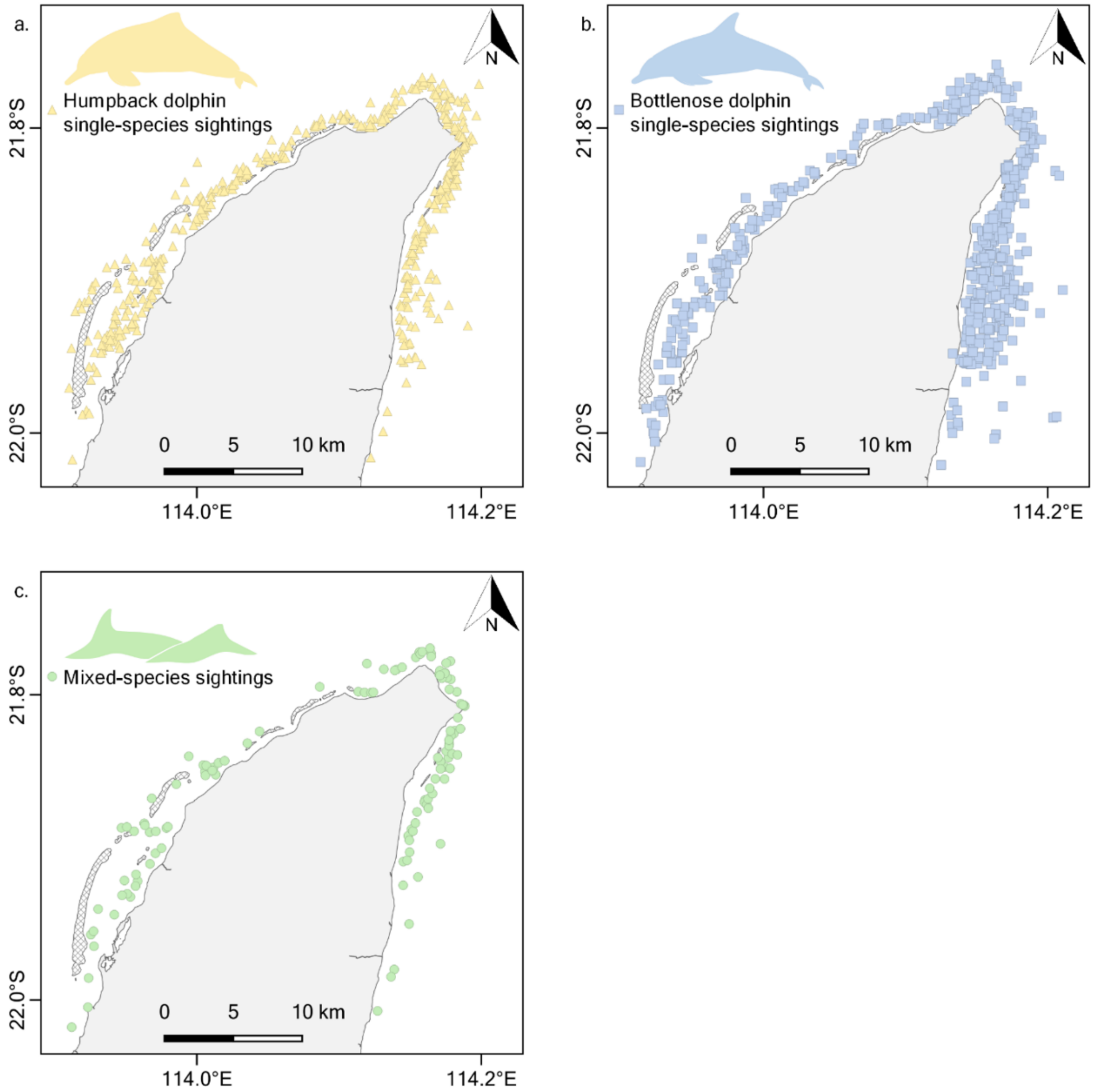

Figure 5.2 The North West Cape, Western Australia, with (a) single-species sightings of Australian humpback dolphins (*Sousa sahulensis*) (n=427), (b) single-species sightings of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (n=584), and (c) mixed-species sightings of both species (n=119) collected from April to October of 2013-2015, 2018-2019, and 2021.

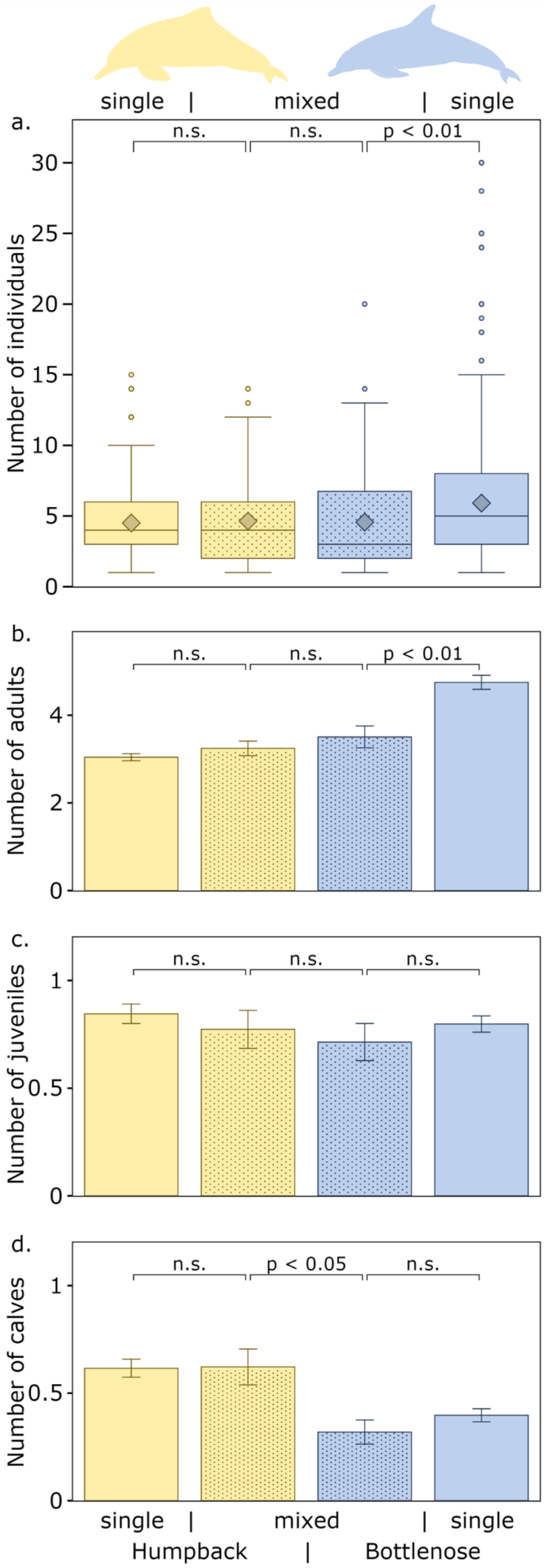

Figure 5.3 Comparisons between Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) with regards to (a) the number of individuals as well as the number of (b) adults, (c) juveniles, and (d) calves present in single- and mixed-species sightings around the North West Cape, Western Australia. The box plot shows the interquartile range with the line showing the median and the whiskers 1.5 times the interquartile range while dots represent outliers and diamonds indicate the mean. Bar plots show mean values with standard error bars. Significance between key pairs is written above the brackets

5.4.3 Frequencies of initial behavioural states

The observed initial behavioural states differed significantly between humpback dolphin single-species sightings and mixed-species sightings (χ^2_4 = 99.6, $p < 0.001$) and between bottlenose dolphin single-species sightings and mixed-species sightings (χ^2_4 = 61.8, $p < 0.001$) (Figure 5.4). Most notably, socialising was the initial observed behavioural state of only 5.1% of humpback and 10.3% of bottlenose dolphin single-species sightings but was the most common initial behavioural state of mixed-species sightings (36.1%) (Figure 5.4). Furthermore, travelling was the second most common initial behavioural state of mixed-species sightings (28.6%) but was noticeably less frequent for mixed-species sightings than for humpback dolphin single-species sightings (57.8%) and, to a lesser extent, bottlenose dolphin single-species sightings (35.1%) (Figure 5.4). Similarly, foraging was the initial behavioural state of 21.4% and 32.0% of humpback and bottlenose dolphin single-species sightings, respectively, but only 10.9% of mixed-species sightings (Figure 5.4).

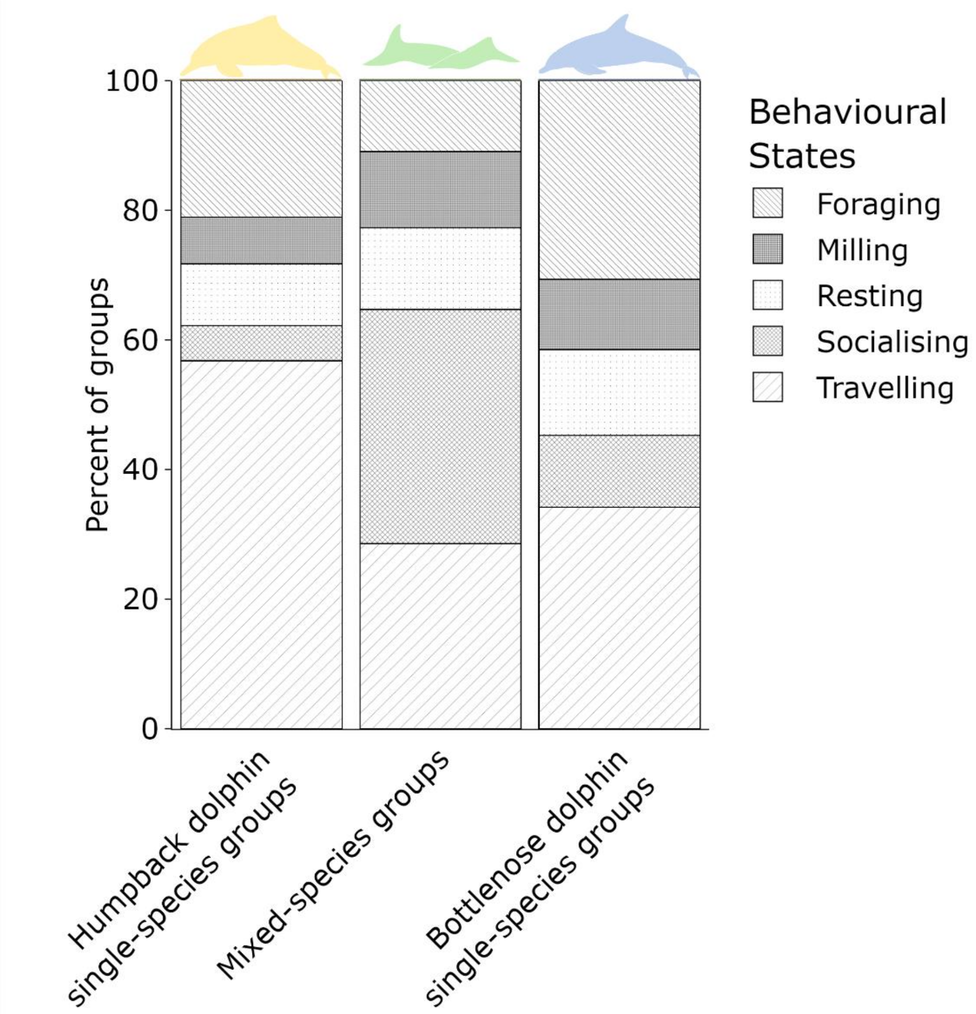

Figure 5.4 The frequency of the initial behavioural states of single-species sightings of Australian humpback dolphins (*Sousa sahulensis*), single-species sightings of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*), and mixed-species sightings of both species observed around the North West Cape, Western Australia.

5.4.4 Nature of interspecific interactions

Across all mixed-species sightings, the number of individual humpback and bottlenose dolphins did not exhibit any significant difference (humpback: 4.6 ± 2.8; bottlenose: 4.6 ± 3.5; $p = 0.872$) (Figure 5.3a), however this apparently equal representation was not observed after considering the nature of the behavioural events exhibited by the individuals during interspecific interactions.

Of 93 mixed-species sightings observed during a focal follow of ≥10 minutes, 32 (34.4%) involved aggressive and/or sexual behavioural events (Figure 5.5a). Both species were observed to perform a variety of aggressive behavioural events, including forceful body contact and tail slapping, however observed chases involved bottlenose dolphins pursuing humpback dolphins (Figure 5.6a). Sexual interactions between humpback and bottlenose dolphins were characterised by high levels of physical contact (e.g., rubbing and rolling over one another), ventral-to-ventral positioning, mounting, and erections. Additionally, avoidance behaviours, such as positioning the ventral side towards the water surface and raising the head above the water surface (Figure 5.6b), were also observed.

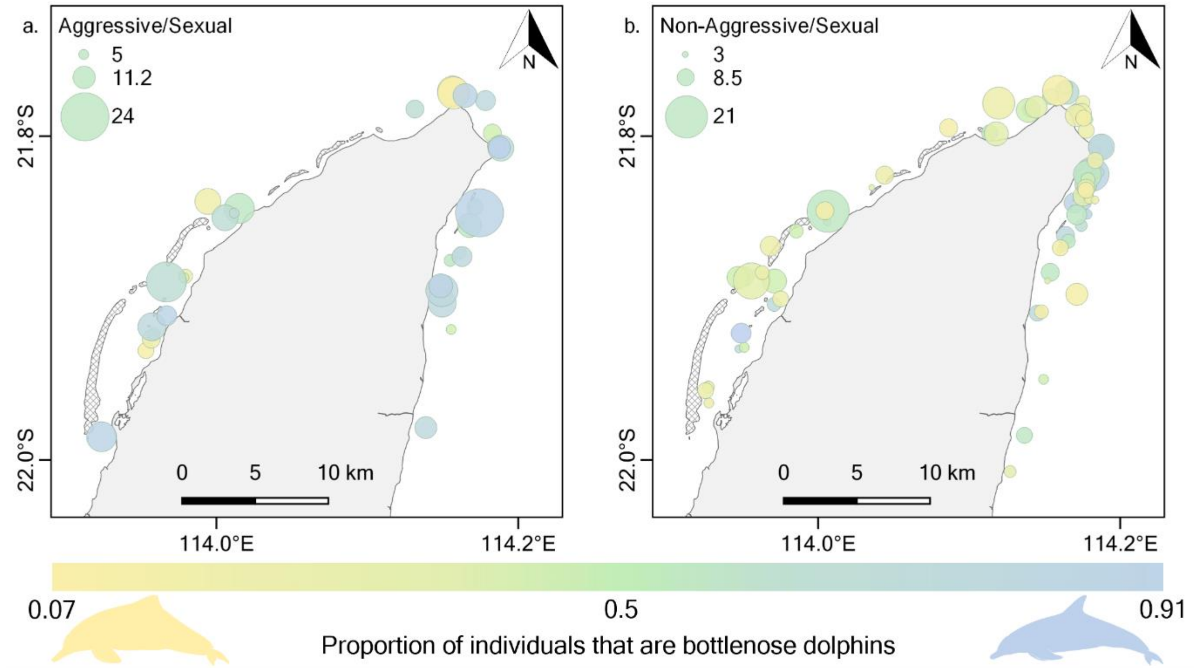

Figure 5.5 Mixed-species sightings of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around the North West Cape, Western Australia, that were observed during focal follows lasting ≥10 minutes and that (a) involved aggressive and/or sexual behaviours (n=32) or (b) did not involve aggressive or sexual behaviours (n=61). The size of each dot is proportional to the total number of individuals (i.e., both species combined) in that sighting, as indicated by the legends which display the minimum, mean, and maximum sizes for their respective plots. The colours represent the proportion of individuals that were bottlenose dolphins, as indicated by the colour bar.

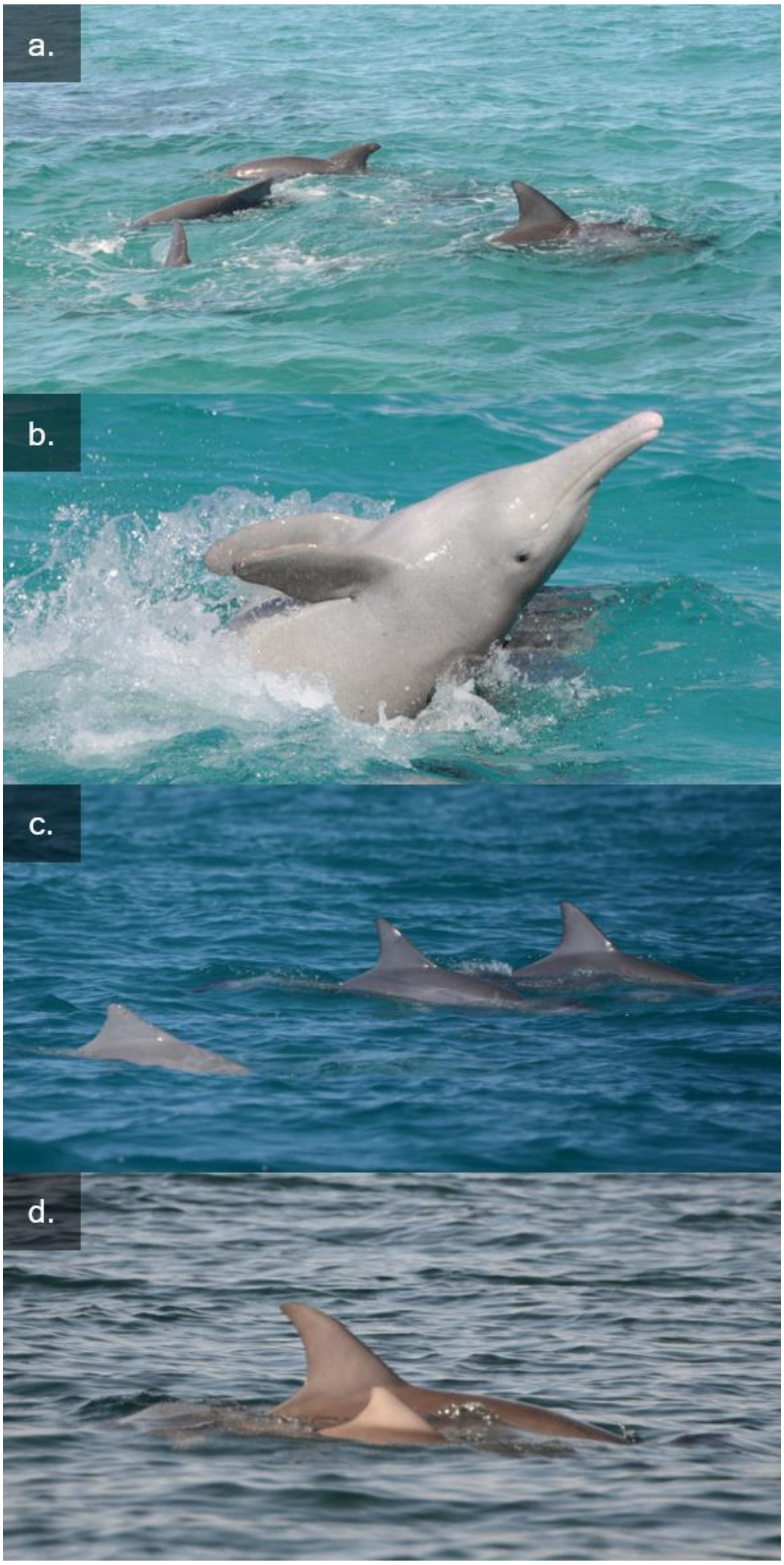

Figure 5.6 Photographs illustrating the variety of behavioural interactions between Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) during mixed-species groups observed around the North West Cape, Western Australia: (a) humpback dolphin (second from left) surrounded by bottlenose dolphins during an aggressive/sexual interaction; (b) humpback dolphin exhibiting evasive behaviour during the same aggressive/sexual interaction; (c) humpback dolphin and two bottlenose dolphins surfacing alongside while resting; and (d) humpback dolphin calf swimming closely alongside a bottlenose dolphin adult.

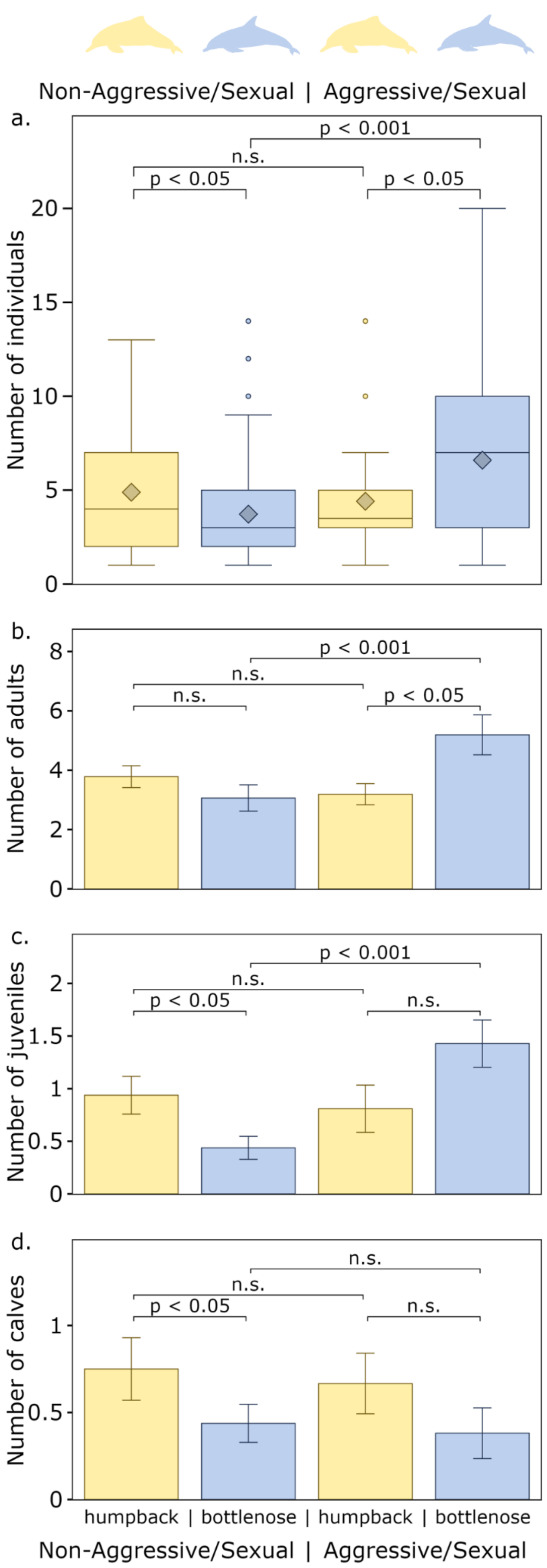

Figure 5.7 Comparisons between Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) with regards to (a) the number of individuals as well as the number of (b) adults, (c) juveniles, and (d) calves present in mixed-species sightings around the North West Cape, Western Australia, that involved aggressive and/or sexual behaviours (i.e., aggressive/sexual) or did not involve such behaviours (i.e., non-aggressive/sexual). The box plot shows the interquartile range with the line showing the median and the whiskers 1.5 times the interquartile range while dots represent outliers and diamonds indicate the mean. Bar plots show mean values with standard error bars. Significance between pairs is written above the brackets.

The remaining 61 (65.6%) mixed-species sightings, including 14 (93.3%) of 15 nursery groups observed for ≥10 minutes, did not involve any such aggressive and/or sexual behavioural events (Figure 5.5b). They did, however, involve neutral behavioural events, such as individuals swimming alongside one another without any observed direct behavioural interactions, as was often displayed during travelling and resting (Figure 5.6c), and affiliative behavioural events, including synchronous surfacing, non-aggressive tactile interactions, and playful behaviour often involving calves and juveniles. Calves were also observed swimming closely alongside a heterospecific adult in events that resembled interspecific alloparental care on four occasions: one involving a bottlenose dolphin calf and a humpback dolphin adult and three involving a humpback dolphin calf and a bottlenose dolphin adult (Figure 5.6d).

In total, mixed-species sightings involving aggressive and/or sexual behaviours contained more individuals than those not involving such behaviours (aggressive/sexual: 11.9 ± 4.4, non-aggressive/sexual: 9.4 ± 3.6, $p = 0.008$) (Figure 5.5). This was due to the larger number of bottlenose dolphins in aggressive/sexual mixed-species sightings (aggressive/sexual: 7.2 ± 4.6, non-aggressive/sexual: 3.9 ± 2.9, $p < 0.001$) (Figure 5.7a). More specifically, aggressive/sexual mixed-species sightings contained more bottlenose dolphin adults (aggressive/sexual: 5.2 ± 3.1, non-aggressive/sexual: 3.1 ± 2.5, $p < 0.001$) and juveniles (aggressive/sexual: 1.4 ± 1.0, non-aggressive/sexual: 0.4 ± 0.6, $p < 0.001$) (Figure 5.7b and c). The number of humpback dolphins present, on the other hand, was unaffected by the nature of interspecific interactions (aggressive/sexual: 4.7 ± 2.8, non-aggressive/sexual: 5.5 ± 3.1, $p = 0.436$) (Figure 5.7a). In accordance with these patterns in bottlenose and humpback dolphin numbers, in mixed-species sightings involving aggressive and/or sexual behaviours there were more bottlenose dolphins than humpback dolphins (humpback: 4.7 ± 2.8, bottlenose: 7.2 ± 4.6, $p = 0.017$), but in non-aggressive/sexual mixed-species sightings there were more humpback dolphins than bottlenose dolphins (humpback: 5.5 ± 3.1, bottlenose: 3.9 ± 2.9, $p = 0.022$) (Figure 5.5 and Figure 5.7a).

5.5 Discussion

Mixed-species groups of delphinids are widespread, yet their dynamics and potential functions have rarely been investigated (Stensland et al. 2003, Cords & Würsig 2014, Syme et al. 2021). Australian humpback and Indo-Pacific bottlenose dolphins around the North West Cape, Western Australia, were regularly observed in mixed-species groups (10.5% of all dolphin sightings were mixed), the formation of which is presumably driven by evolutionary benefits that one or both species gain from grouping with the other. Here, by assessing the relationship between group characteristics (e.g., size and age composition) and the frequency and nature of their behavioural interactions, we show that the potential functions of mixed-species groups of sympatric humpback and bottlenose dolphins around the North West Cape are most consistent with the social advantage hypothesis and, at least in certain cases, the antipredator advantage hypothesis.

5.5.1 Antipredator advantage hypothesis

The larger number of individuals in mixed-species groups could lead to a reduction in predation risk, as has been hypothesised for other species (Scott & Chivers 1990, Scott & Cattanach 1998, Heymann & Buchanan-Smith 2000, Kiszka et al. 2011a). Little information is available on predation risk around the North West Cape, however numerous humpback and bottlenose dolphins bear scars from shark bites (JS and GJP personal observations) and both species are known to share predators, including tiger (*Galeocerdo cuvier*), bull (*Carcharhinus leucas*), and white sharks (*Carcharodon carcharias*) (Heithaus et al. 2017, Parra & Jefferson 2018, Wang 2018, Smith et al. 2018). The observed mixed-species groups of humpback and bottlenose dolphins do not, however, resemble mixed-species groups that form to reduce predation risk in several aspects. Notably, humpback dolphins and, to a lesser extent, bottlenose dolphins travelled less frequently when in mixed-species groups and direct behavioural interactions between the species were frequent. This differs from spinner dolphin – pantropical spotted dolphin mixed-species groups around Mayotte (Kiszka et al. 2011a) and Indian Ocean humpback dolphin (*Sousa plumbea*) – bottlenose dolphin groups in South Africa (Koper & Plön 2016) where travelling behaviour was more frequent in mixed-species groups and no direct interactions were observed. Furthermore, the frequent occurrence of socio-sexual interactions observed in mixed-species groups of humpback and bottlenose dolphins in this study would likely lead to decreased vigilance, further arguing against the antipredator advantage hypothesis.

Certain species have been shown to form mixed-species groups when the number of vulnerable young individuals, and therefore the predation risk, is highest (Chapman & Chapman 2000). This does not appear to be the case around the North West Cape where, for both species, the number of calves was not higher in mixed-species groups. Nevertheless, calves were present in mixed-species groups, including 18 observed nursery groups. Furthermore, we observed instances of humpback and bottlenose dolphins travelling or resting alongside each other without any evident direct behavioural interactions. Thus, it seems plausible that in travelling and resting groups, particularly nursery groups, mixed-species group formation could result in increased group vigilance and, therefore, reduced predation risk. Therefore, it remains a possibility that, at least in certain cases, humpback and bottlenose dolphins around the North West Cape form mixed-species groups to gain antipredator benefits.

5.5.2 Foraging advantage hypothesis

Mixed-species groups where foraging benefits are gained often involve heterospecifics with similar diets as this leads to higher quality information concerning foraging opportunities (Sridhar & Guttal 2018). No dietary data from the study populations is available, however both species are generalists and analyses of stomach contents and observations of foraging from other locations indicate that there is potentially some interspecific dietary overlap (Amir et al. 2005, Parra 2006, Cagnazzi et al. 2011, Kiszka et al. 2014, Parra & Jedensjö 2014). Our observations of mixed-species groups do not, however, correspond to those expected from species that gain foraging benefits by forming mixed-species groups. Most notably, both species foraged less frequently when in mixed-species groups. This contrasts with mixed-species groups where foraging behaviour is a prominent feature such as those of false killer whales (*Pseudorca crassidens*) and common bottlenose dolphins off New Zealand (Zaeschmar et al. 2014) and Diana monkeys (*Cercopithecus diana*) and Campbell's monkeys (*Cercopithecus campbelli*) in the Taï Forest, Côte d'Ivoire (Wolters & Zuberbühler 2003). Furthermore, we did not observe a clear tendency of one species to follow or join the other, as is the case for common bottlenose dolphins that follow and join foraging short-finned pilot whales and Risso's dolphins (*Grampus griseus*), seemingly to obtain information about prey (Shane 1994, Bacon et al. 2017), or rock kestrels (*Falco rupicolus*) that preferentially follow "travel foraging" (i.e., searching for food while moving) chacma baboons (*Papio ursinus*) to catch insects flushed by the primates' movements (King & Cowlishaw 2009). Finally, the absence of observed intra- and interspecific cooperative foraging, combined with the tendency of humpback dolphins to forage in small groups (2-3 individuals) (Parra et al. 2011) argues against the possibility of interspecific cooperative foraging as has been observed, for example, between false killer whales and common bottlenose dolphins (Zaeschmar et al. 2013). Thus, it seems unlikely that foraging benefits drive the formation of mixed-species groups of humpback and bottlenose dolphins in the coastal waters of the North West Cape.

5.5.3 Social advantage hypothesis

The marked increase in the frequency of socialising behaviour when in mixed-species groups and the numerous, diverse behavioural interactions between the species indicate that social benefits may play a key role in the formation of mixed-species groups of humpback and bottlenose dolphins around the North West Cape. The interactions recorded between humpback and bottlenose dolphins covered a wide range of behaviours, from affiliative to aggressive. Similar variation in interspecific interactions has previously been reported between certain primate (van Lawick-Goodall 1968, Struhsaker 2010) and dolphin species (Herzing & Johnson 1997, Parra 2005, Acevedo-Gutiérrez et al. 2005, Melillo et al. 2009, May-Collado 2010) and suggests that the potential social benefits may be diverse.

5.5.3.1 Aggressive and sexual interactions

Previous research on agonistic interspecific interactions within mixed-species groups indicates a tendency for larger species to be dominant over smaller ones (Heymann 1990, Herzing & Johnson 1997, Heymann & Buchanan-Smith 2000, Psarakos et al. 2003, Parra 2005, Elliser & Herzing 2016a). Given the similarity in body size of humpback and bottlenose dolphins (Parra & Jefferson 2018, Wang 2018), it is not apparent that either species should have a noticeable physical advantage over the other. Bottlenose dolphins had, however, a clear numerical advantage during aggressive and sexual interactions and, accordingly, typically appeared to initiate such interactions with humpback dolphins – a role that is proving to be widespread with both Indo-Pacific and common bottlenose dolphins having been reported to initiate aggressive and/or sexual interactions with heterospecifics (Ross & Wilson 1996, Herzing & Johnson 1997, Stensland et al. 2003, Wedekin et al. 2004, Acevedo-Gutiérrez et al. 2005, Melillo et al. 2009, Barnett et al. 2009, Cotter et al. 2012). During interactions not involving aggressive and/or sexual behaviours, however, bottlenose dolphins were outnumbered by humpback dolphins and neither species appeared to be dominant. This pattern is suggestive of the possibility that bottlenose dolphins tend to initiate aggressive and sexual behaviours when they outnumber humpback dolphins but not when they are outnumbered. A similar dynamic has been reported in the Bahamas where male common bottlenose dolphins are dominant over male Atlantic spotted dolphins, except when the latter are more numerous, in which case they chase the common bottlenose dolphin males away (Herzing & Johnson 1997). Alternatively, it is possible that mixed-species groups start with fairly equitable numbers and that the imbalance develops as more bottlenose dolphins are drawn to the commotion from aggressive and sexual behaviours while any humpback dolphins in the vicinity stay away. Although it is not clear as to which is the cause and which is the consequence, the nature of the interspecific interactions in mixed-species groups is apparently linked to the number of bottlenose dolphins and, by extension, to the relative numbers of each species.

The socio-sexual behaviours exhibited by bottlenose dolphins towards humpback dolphins around the North West Cape are similar to those reported elsewhere. In the Bahamas, for example, immature or low-ranking male common bottlenose dolphins engage in sexual interactions with Atlantic spotted dolphins (Melillo et al. 2009) while in Zanzibar, in the western Indian Ocean, young male bottlenose dolphins display aggressive and sexual behaviours towards female Indian Ocean humpback dolphins, possibly in order to practice social behaviours or for mating (Stensland et al. 2003).

5.5.3.2 Affiliative and neutral interactions

Around the North West Cape, two thirds of the mixed-species groups of humpback and bottlenose dolphins observed for ≥10 minutes did not involve aggressive or sexual behaviours. While it is possible that the benefits from these mixed-species groups fit within the antipredator advantage hypothesis, the nature of these interactions suggest the existence of social benefits, in particular, those pertaining to the development and care of young individuals (Whitehead & Mann 2000, Spinka et al. 2001). Humpback and bottlenose dolphin calves and juveniles were observed swimming alongside each other and engaging in apparent play behaviour (e.g., leaping, chasing, and breaching). This raises the possibility that mixed-species groups provide opportunities for young dolphins to play and, thus, to develop social and physical skills (Spinka et al. 2001), as may be the case for mixed-species groups of primates (Struhsaker 2010).

Behaviours that involved potential alloparental care between humpback and bottlenose dolphins were also observed on four occasions, although it is impossible to know whether they truly represent alloparental care as it is not known if the calf and the mother benefitted (Whitehead & Mann 2000). Similar interactions resembling interspecific alloparental care have been observed previously amongst wild delphinids (Bearzi 1996, Herzing & Johnson 1997, Stensland et al. 2003, Markowitz 2004). The potential benefits and costs of interspecific alloparenting are presumably similar to those of intraspecific alloparenting, including respite from caregiving for the mother and practice parenting for the alloparent (Mann & Smuts 1998). Whether these affiliative behaviours, such as play and alloparental care, are rare or simply rarely observed is unclear and, thus, the extent to which they influence the formation of mixed-species groups is difficult to determine.

Nevertheless, they may be particularly pertinent to mothers and their young, given the presence of such affiliative behaviours in mixed-species nursery groups. Generally speaking, nursery groups may reduce predation risk and provide social benefits, such as protection from male harassment and opportunities for the development of physical and social skills (Wells et al. 1987, Weir et al. 2008, Deutsch et al. 2014). If maternal care places similar requirements on both humpback and bottlenose dolphin mothers, the benefits of forming nursery groups may extend to mixed-species nursery groups, as has been suggested for dusky (*Lagenorhynchus obscurus*) and Hector's dolphins (*Cephalorhynchus hectori*) in New Zealand (Markowitz 2004). For example, the need to protect young calves from adult male harassment could lead mothers of both species to avoid groups of individuals displaying aggressive or sexual behaviours (Pearson 2011, Cords & Würsig 2014), thus explaining the near absence of these behaviours in mixed-species nursery groups.

5.5.4 Summary

In this study we have provided evidence that humpback and bottlenose dolphins around the North West Cape form mixed-species groups primarily to gain social, and perhaps antipredator, benefits whose relevance may depend on the individuals involved and their traits (e.g., age, sex, social status, and reproductive stage). For example, we can hypothesise contrasting situations such as the following: a young male will seek opportunities to learn and practice social skills, both with con- and heterospecifics, resulting in aggressive and sexual interactions, whereas a mother with a calf will seek out other mothers and calves, be they con- or heterospecifics, to provide a safe environment for the development of her young. Future research could further unravel the complexity of these social benefits by studying these mixed-species groups on an individual, rather than a group or species, level. This would provide a more detailed understanding of what drives particular individuals to form mixed-species groups and the benefits and costs that they may experience from doing so.

Chapter 6

Variation in behavioural patterns furthers our understanding of coexistence mechanisms and the function of mixed-species groups in sympatric delphinids

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Variation in behavioural patterns furthers our understanding of coexistence mechanisms and the function of mixed-species groups in sympatric delphinids

6.1 Abstract

The coexistence of sympatric species with similar ecological requirements involves niche partitioning via interspecific differences in resource use and behaviour. Behavioural patterns of coexisting species can also be indicative of the functions of interspecific interactions, including those between species that form mixed-species groups. Here, we use Markov chain analysis applied to behavioural focal follow data of Australian humpback (*Sousa sahulensis*, hereafter "humpback dolphins") and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, hereafter "bottlenose dolphins") observed around the North West Cape, Western Australia, to investigate potential behavioural coexistence mechanisms and the functions of their mixed-species groups. During six austral winter (April to October) field seasons (2013-2015, 2018-2019, and 2021), we recorded 560 dolphin sightings from which we obtained 562 sequences of behavioural transitions: 222 humpback dolphin single-species sequences, 262 bottlenose dolphin single-species sequences, and 78 mixed-species sequences. Humpback dolphins spent more time travelling in addition to higher transitions towards travelling and longer bout lengths of travelling, while bottlenose dolphins spent more time foraging and had longer foraging bouts. These behavioural patterns indicate that humpback and bottlenose dolphins differ in their use of the study area. In particular, they suggest interspecific differences in foraging behaviour, which may serve as coexistence mechanisms. When in mixed-species groups, humpback and bottlenose dolphins altered their behavioural patterns by exhibiting higher transitions towards socialising and increasing time spent socialising, suggesting that their mixed-species groups may serve a social function. Overall, our results indicate that behavioural differences may play an important role in facilitating the coexistence of sympatric delphinids and that social benefits may be a key driver of the formation of mixed-species groups.

6.2 Introduction

Understanding the dynamics of interactions amongst co-occurring species and identifying the mechanisms that enable their coexistence is critical to community ecology (Abe et al. 1997, Tokeshi 2009, Chomicki et al. 2019). Interspecific differences in temporal and spatial patterns of resource and habitat use can enable sympatric species with similar ecological requirements to coexist (Grinnell 1924, Pianka 1974, Chesson 2000, Bearzi 2005, Tokeshi 2009). Moreover, interactions amongst sympatric species, including direct behavioural interactions (e.g., predation) and indirect interactions (e.g., competition and facilitation), can promote or hinder coexistence by affecting, positively or negatively, the species involved (Abe et al. 1997, Tokeshi 2009, Chomicki et al. 2019).

Comparative analyses of the behavioural patterns of sympatric species can further our understanding of coexistence mechanisms (Dröge et al. 2017, Karanth et al. 2017, Morris et al. 2019). For example, in addition to targeting different prey, cheetahs (*Acinonyx jubatus*) in western Zambia hunt primarily during daylight hours, apparently to avoid competition with lions (*Panthera leo*) who mainly hunt at night (Dröge et al. 2017). Assessing behavioural changes resulting from interspecific interactions can provide information on the biological significance of the interactions and is particularly important for species that regularly form mixed-species groups. Mixed-species groups are found in numerous taxa, including fishes, birds, and mammals, and have been hypothesised to provide antipredator, foraging, and/or social benefits for participating species and individuals (Stensland et al. 2003, Goodale et al. 2017, Sridhar & Guttal 2018, Syme et al. 2021). Participation in mixed-species groups can result in diverse behavioural changes. For example, plains zebras (*Equus quagga*) decrease and Grevy's zebras (*Equus grevyi*) increase their flight initiation distances when in mixed-species groups, indicating a moderating effect of heterospecific presence on risk assessment (Brubaker & Coss 2016). Carolina chickadees (*Poecile carolinensis*) change the frequency of social cohesion calls in response to the number of tufted titmice (*Baeolophus bicolor*) in mixed-species flocks (Coppinger et al. 2020). Understanding these behavioural changes is key for understanding the functions of mixed-species groups and for evaluating the potential impacts of mixed-species groups on the fitness and survival of participating species (Goodale et al. 2020).

Australian humpback (*Sousa sahulensis*, hereafter "humpback dolphins") and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*, hereafter "bottlenose dolphins") are found in sympatry throughout much of their ranges across the inshore waters of northern Australia and southern Papua (Corkeron 1990, Allen et al. 2012, Brown et al. 2012, Palmer et al. 2014, Beasley et al. 2016). Around the North West Cape, Western Australia, they exhibit habitat and temporal partitioning – humpback dolphins prefer shallower and more nearshore water than bottlenose dolphins and the latter are observed more frequently in the afternoon (Chapter 4). Despite spatial and temporal differences in occurrence, humpback and bottlenose dolphins still display considerable overlap in their habitat use and regularly form mixed-species groups (Chapters 4 and 5, Brown et al. 2012, Hunt 2018). Previous research suggests that the characteristics of these mixed-species groups are most congruent with the social advantage hypothesis as both species increase the occurrence of various forms of social interactions when in mixed-species groups (Chapter 5). Additionally, the formation of mixed-species groups might also reduce predation risk from large sharks, notably for nursery groups of mothers and calves (Chapter 5).

Questions remain, however, about the role of behaviour in facilitating coexistence, the functions of these mixed-species groups, and the impact of mixed-species group formation on their behavioural patterns.

We employed an interspecific comparative approach using Markov chain analysis to quantify the daylight behavioural patterns of single- and mixed-species groups of humpback and bottlenose dolphins observed around the North West Cape. Our aim was to, firstly, compare their behavioural patterns to determine if there are behavioural mechanisms that enable their coexistence and, secondly, to further explore the function of their mixed-species groups and evaluate the impacts of mixed-species group formation on their behaviour. Previous analyses of the behaviour of *Sousa* and *Tursiops* species (Karczmarski & Cockcroft 1999, Parra 2005, Stensland et al. 2006, Steckenreuter et al. 2012, Fury et al. 2013, Bizzozzero et al. 2019) have shown that, in general, both species primarily travel and forage and that humpback dolphins, in contrast to bottlenose dolphins, spend little time socialising. Accordingly, we hypothesise that travelling and foraging will be the predominant behaviours of humpback and bottlenose dolphins around the North West Cape and that socialising will be infrequent for humpback dolphins, but not for bottlenose dolphins. We also predict that both species will show an increase in socialising and a corresponding decrease in other behavioural states (i.e., foraging, milling, resting, and travelling) when in mixed-species groups. This prediction is based on previous research which has suggested that social benefits are the major driver of mixed-species group formation in humpback and bottlenose dolphins (Chapter 5). These sympatric species which are often found in mixed-species groups present an ideal model system to improve our understanding of the behavioural mechanisms underlying the coexistence of delphinids and the biological significance of their interactions.

6.3 Methods

6.3.1 Data collection

Data were collected in the austral winter (April to October) over six years (2013-2015, 2018-2019, and 2021) during daylight hours and good conditions (Beaufort scale ≤3, no rain or fog). Observations were made from a 5.8 m research vessel during systematic surveys following a predetermined route, during non-transect surveys, and during travel through the study area. The survey route consisted of two, opposing, zigzag transect lines that covered shallow waters (<30 m) on both sides of the North West Cape as well as an additional straight transect line on the west side of the North West Cape outside the reef (Figure 6.1).

Dolphin sightings included *singletons* (i.e., single animals) and *groups*, operationally defined as two or more individuals within 100 m of one another and engaged in similar behaviour (Hunt et al. 2017, Syme et al. 2022). This definition was applied equally to humpback and bottlenose dolphins and, thus, to mixed-species groups (Stensland et al. 2003, Syme et al. 2021). When dolphins were sighted, the research vessel approached to within 100 m and key data were recorded including the species, the initial behavioural state, and the number of individuals present.

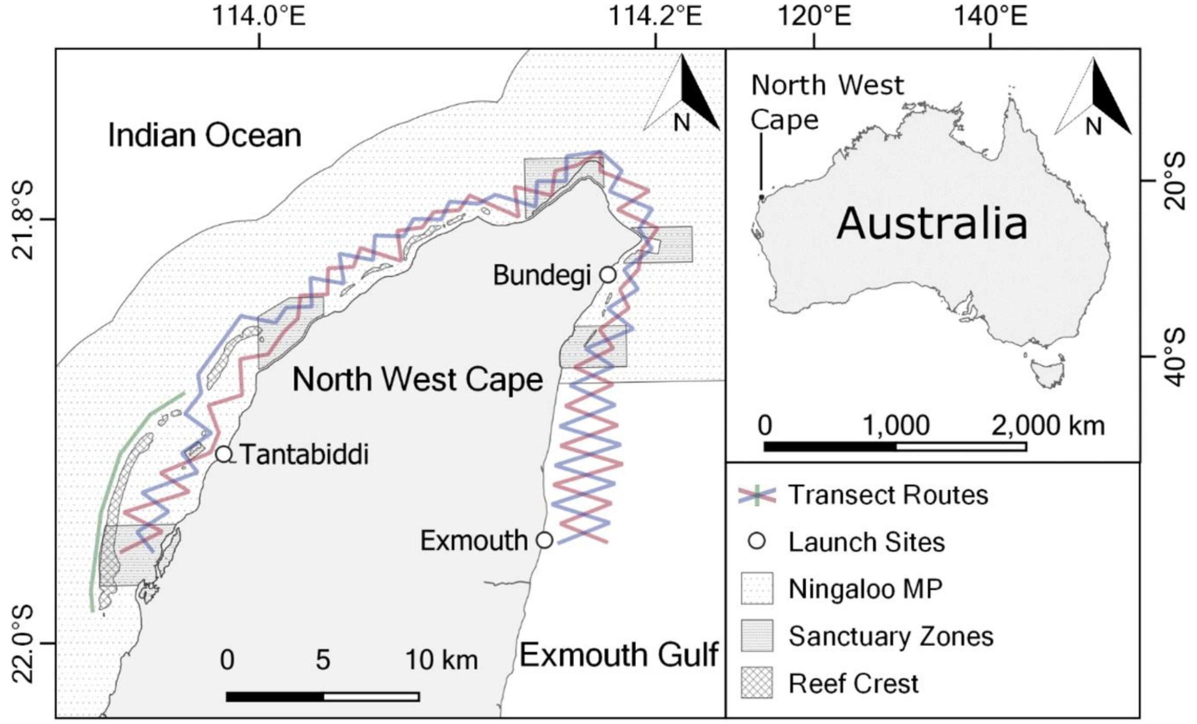

Figure 6.1 The study site, the North West Cape, Western Australia, showing the vessel launch sites and the transect routes (two opposing, zigzag routes and an additional straight route) used to survey for Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). In addition, the map shows Ningaloo Marine Park (dotted area), sanctuary zones (grey shaded areas), and reef crests (crosshatched area).

Subsequently, focal follows were conducted with continuous sampling to determine the behavioural state of the majority of the animals present which was classified as either foraging, milling, resting, socialising, or travelling (see Table 6.1 for criteria used to define behavioural states). Specifically, the behavioural state was recorded every ten minutes, unless the behavioural state changed, in which case the behavioural state was recorded at the change. Incidences when dolphins were either interacting with or avoiding the research vessel were also noted (Table 6.1). For observations of groups, group focal follows were chosen over individual focal follows as group sizes are small (Hunt et al. 2017, Haughey et al. 2020), thus allowing reliable observations of all group members, and because individuals can be hard to identify in situ and track. Focal follows ended when either the animals were lost (>10 minutes without sighting), weather conditions or low light levels no longer permitted reliable observations, or a time limit of one hour as stipulated by the ethics approval was reached.

Table 6.1 Definitions of the five behavioural states (i.e., foraging, milling, socialising, resting, and travelling) as well as descriptions of boat interaction and avoidance used during focal follows of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) around the North West Cape, Western Australia

Behavioural state	Definition
Foraging	Fast, non-directional, sometimes erratic movements with rapid acceleration Frequent, long dives at steep angle Observations of prey
Milling	Slow, non-directional movements with short dives at shallow angle, but most time spent at surface Close proximity, but few interactions
Resting	Very slow, non-directional movements at surface with low activity level Tight group formation
Socialising	Non-directional movements with dives of varying length Frequent aerial behaviours (e.g., leaping) and heads and flukes often above the water surface Close proximity, high levels of interaction including physical contact (e.g., touching, rubbing)
Travelling	Constant, directional movement with regular surfacing, shallow dive angles Group spacing varies
Boat Interaction	Interacting with boat (e.g., bow riding, wake riding)
Boat Avoidance	Rapid movement away from the boat, directional changes away from the boat, prolonged dives

6.3.2 Data analysis

6.3.2.1 Markov chains

Markov chain analysis can be used to determine if a sequence of states is random and, if it is not random, to assess the dependence of a state on preceding states (Lehner 1996, Martin & Bateson 2007). Previous studies have used Markov chain analysis to investigate the impact of tourism boat traffic on dolphin behaviour (Lusseau 2003, Stockin et al. 2008, Meissner et al. 2015, Cecchetti et al. 2018) and to assess the behavioural patterns of sympatric delphinids (Viddi & Harcourt 2016). Here, we apply Markov chain analysis to quantify and compare the daylight behavioural patterns of sympatric humpback and bottlenose dolphins in single- and mixed-species groups. More specifically, we employed time-discrete first-order Markov chains, in which the probability of a given behavioural state at a given time step depended only on the behavioural state in the immediately preceding time step. The Markov chains were created and the corresponding behavioural parameters (i.e., transition probabilities, bout lengths, budgets) were calculated in Python 3.8.0 (Python Software Foundation 2016). All statistical analyses were conducted in RStudio 1.2.5 (RStudio Team 2019) and evaluated at a significance level of $\alpha = 0.05$.

6.3.2.2 Behavioural sequences

From the focal follow data of single- and mixed-species sightings, we sampled the behavioural state at five-minute intervals to produce sequences of behavioural transitions. Sequences during which the behavioural state was unknown or the dolphins interacted with or avoided the research vessel were excluded from all analyses, thus, the five analysed behavioural states (i.e., foraging, milling, resting, socialising, or travelling) were collectively exhaustive and mutually exclusive (Lusseau 2003). Additionally, only sequences that lasted ≥10 minutes, and that, therefore, included at least two behavioural transitions, were analysed.

6.3.2.3 Transition frequencies

The behavioural sequences were classified according to which species were present (i.e., humpback dolphin single-species, bottlenose dolphin single-species, or mixed-species) and analysed to derive, for each of the 25 potential behavioural transitions, the transition frequencies. The transition frequencies represent the number of times that dolphins in behavioural state A were in behavioural state B at the next sampling interval (i.e., five minutes later), where A and B can be any of the five behavioural states.

Analysis of transition matrices depends on the assumption of stationarity, i.e., that transition probabilities remain constant over time (Lehner 1996, Lusseau 2003, Martin & Bateson 2007). To test this assumption, the transition frequencies were organised into three-way 5 x 5 x 2 contingency tables (preceding behavioural state versus succeeding behavioural state versus set of years), where, due to low sample size (Quinn & Keough 2002), time was represented by two sets of years: 2013, 2014, and 2015; and 2018, 2019, and 2021. These contingency tables were used to analyse the effect of time on the transition frequencies by comparing two log-linear models – a fully saturated model (preceding behavioural state x succeeding behavioural state x set of years) and a model of all two-way interactions – with a likelihood ratio test (Quinn & Keough 2002, Lusseau 2003). A lack of significant difference between the two models in terms of goodness-of-fit indicates that the conditional dependence between a pair of variables is the same at each level of the third (Quinn & Keough 2002). In our study, this meant that any dependence between preceding and succeeding behavioural state was the same across the sets of years and, thus, that transition probabilities were constant over time (Lehner 1996, Lusseau 2003, Martin & Bateson 2007).

The transition frequencies were then pooled across time, resulting in a two-way 5 x 5 contingency table of behavioural transition frequencies (preceding behavioural state versus succeeding behavioural state) for each of the combinations of species present (i.e., humpback dolphin single-species, bottlenose dolphin single-species, or mixed-species). To determine if the observed transition frequencies differed from random and, thus, if the behavioural patterns were sequentially dependent, we used a Fisher's exact test (Quinn & Keough 2002, Martin & Bateson 2007).

6.3.2.4 Transition probabilities

From the two-way contingency tables of transition frequencies, corresponding transition probability matrices were generated by calculating the transition probabilities between each pair of behavioural states according to the formulae:

$$p_{ij} = \frac{a_{ij}}{\sum_{j=1}^{n} a_{ij}}, \qquad \sum_{j=1}^{n} p_{ij} = 1$$

where n is the total number of behavioural states included in the analysis, i and j are the preceding and succeeding behavioural states, respectively, a_{ij} is the number of observed transitions from behavioural state i to j, and p_{ij} is the transition probability from behavioural state i to j in the Markov chain (Lusseau 2003). These transition probabilities represent how likely it is that dolphins in behavioural state A will transition to behavioural state B by the next sampling interval (i.e., five minutes later), where A and B can be any of the five behavioural states. To determine if the behavioural transitions of humpback and bottlenose dolphins varied depending on whether they were observed in single- or mixed-species sightings, we compared the behavioural transition probabilities between single-species sightings of each species and mixed-species sightings with a Fisher's exact test for proportions.

6.3.2.5 Bout lengths

For single-species sightings of each species and for mixed-species sightings, the average bout length of each behavioural state was approximated from the mean of the geometric distribution of p_{ii} according to the formula (Guttorp 1995):

$$\overline{t_{ii}} = \frac{1}{1 - p_{ii}}$$

where p_{ii} is the transition probability from behavioural state i to itself and $\overline{t_{ii}}$ is the mean number of transitions from behavioural state i to itself, i.e., the average number of transitions that a bout lasts for (Guttorp 1995, Lusseau 2003). The average bout length in minutes was then calculated by multiplying $\overline{t_{ii}}$ by the sampling interval (i.e., five minutes) (Lusseau 2003) and represents the average amount of time that dolphins spend in a given behavioural state before transitioning to another behavioural state. The average bout lengths of each behavioural state were compared between single-species sightings of each species and mixed-species sightings using Welch's t-tests to determine if the species differed in the length of time that they spent engaged in each behavioural state.

6.3.2.6 Budgets

Behavioural budgets were derived from the stationary distributions of the Markov chains using the Linear Algebra (`numpy.linalg`) module in the package `NumPy 1.22.1` (Harris et al. 2020) in Python 3.8.0 (Python Software Foundation 2016). This was possible because the Markov chain is ergodic, therefore, regardless of the initial distribution, in the long term, it converges towards a unique stationary distribution (Seneta 1973). Furthermore, because the Markov chain is both non-negative and irreducible (i.e., all states are reachable, directly or indirectly, from all other states), the transition matrix has, according to the Perron-Frobenius theorem, a positive left eigenvector, ν, which corresponds to an eigenvalue, λ, and from which the stationary distribution can be derived (Horn & Johnson 1985, Lusseau 2003). In our analysis, the stationary distribution contained five values which summed to one and which corresponded to the proportion of time that the dolphins spent engaged in each behavioural state, i.e., the behavioural budget. By creating behavioural budgets for single- and mixed-species sightings of humpback and bottlenose dolphins we were able to compare, using a Z test for proportions (Newcombe 1998, Fleiss et al. 2003), the amount of time that each species spent in each behavioural state when with and not with heterospecifics in addition to comparing the budgets of single-species sightings of the species to each other.

6.3.2.7 Cumulative budgets

To adequately evaluate the impact of mixed-species group formation on behavioural budgets, however, it is necessary to account for the amount of time that species spend in mixed-species groups. To this end, we calculated cumulative behavioural budgets for each species according to the formula (Lusseau 2003):

$$\mathrm{cumulative\ budget} = (\mathrm{a} \times \mathrm{SSB}) + (\mathrm{b} \times \mathrm{MSB})$$

where SSB and MSB are the behavioural budgets for single- and mixed-species sightings, respectively, and a and b are the proportion of time spent in single- and mixed-species sightings, respectively (hence $\mathrm{a} = 1 - \mathrm{b}$). Thus, the cumulative behavioural budget represents the proportion of time that dolphins can be expected to spend in each behavioural state given that they spend a certain amount of their time in mixed-species groups. For each species, we then compared the cumulative and single-species sightings budgets for each behavioural state with a Z test for proportions (Newcombe 1998, Fleiss et al. 2003) to determine whether participation in mixed-species groups has any impact on the overall behavioural budgets of humpback and bottlenose dolphins.

6.4 Results

6.4.1 Sightings summary

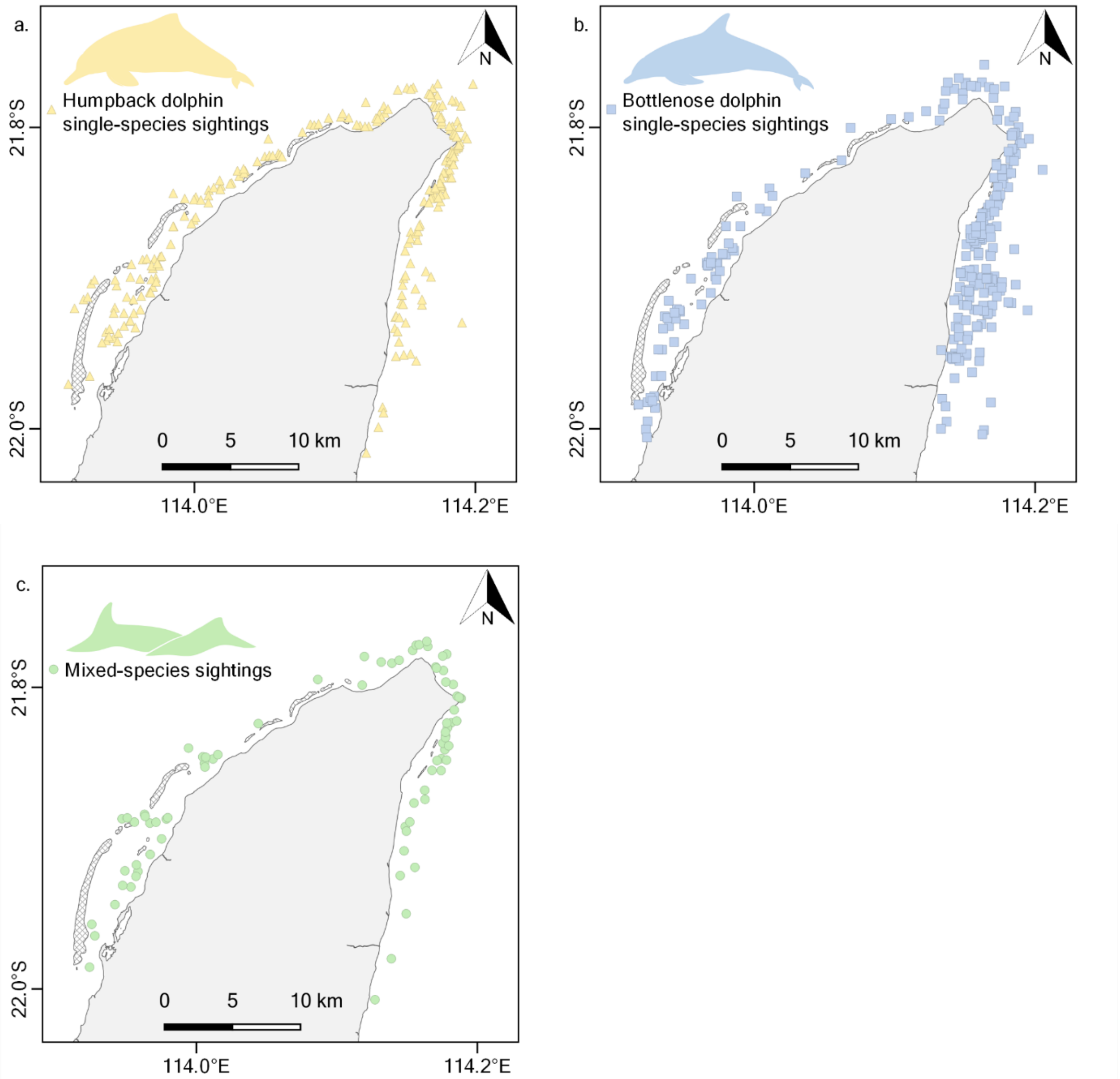

Figure 6.2 Single-species sightings of (a) Australian humpback (*Sousa sahulensis*) (n=222) and (b) Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (n=261) and (c) mixed-species sightings of both species (n=77) recorded from April to October over six years (2013-2015, 2018-2019, and 2021) around the North West Cape, Western Australia, and from which behavioural sequences were obtained for Markov chain analysis.

Across six years of surveys (2013-2015, 2018-2019, and 2021), we recorded 560 dolphin sightings (Figure 6.2) from which we obtained 562 behavioural sequences that met the requirements for analysis (i.e., ≥10 mins and involving only the five behavioural states). These sequences consisted of 222 humpback dolphin single-species sequences (mean time: 23.2 min; total time: 85.9 h), 262 bottlenose dolphin single-species sequences (mean time: 27.8 min; total time: 121.5 h), and 78 mixed-species sequences (mean time: 23.9 min; total time: 31.1 h).

Accordingly, humpback and bottlenose dolphins spent 26.6% and 20.4%, respectively, of their total observation time (single- and mixed-species sequences) in mixed-species groups. From the behavioural sequences, we obtained a total of 2741 behavioural transitions: 996 (36.3%) from humpback dolphin single-species sequences, 1388 (50.6%) from bottlenose dolphin single-species sequences, and 357 (13.0%) from mixed-species sequences.

6.4.2 Assumption of stationarity

The assumption of stationarity was met as the transition frequencies for humpback dolphin single-species sightings (G^2=17.06, df=50, p=0.382), bottlenose dolphin single-species sightings (G^2=23.170, df=50, p=0.109), and mixed-species sightings (G^2=18.14, df=50, p=0.316) were stable over time.

6.4.3 Transition frequencies

For single-species sequences of both species and for mixed-species sequences, the observed transition frequencies differed from random (humpback: $p < 0.001$; bottlenose: $p < 0.001$; mixed: $p < 0.001$; Fisher's exact test), indicating sequentially dependent behavioural patterns.

6.4.4 Transition probabilities

Humpback and bottlenose dolphins in single-species sightings differed in six behavioural transition probabilities (Figure 6.3). More specifically, four transitions were higher for humpback dolphins in single-species sightings: foraging → travelling ($p = 0.024$, Fisher's exact test), milling → travelling ($p = 0.001$, Fisher's exact test), resting → travelling ($p = 0.016$, Fisher's exact test), and travelling → travelling ($p < 0.001$, Fisher's exact test). The other two transitions were higher for bottlenose dolphins in single-species sightings: travelling → foraging ($p = 0.002$, Fisher's exact test) and travelling → socialising ($p = 0.005$, Fisher's exact test). All four transition probabilities that were higher for humpback dolphins were transitions to travelling, while the two that were higher for bottlenose dolphins were transitions from travelling (Figure 6.3).

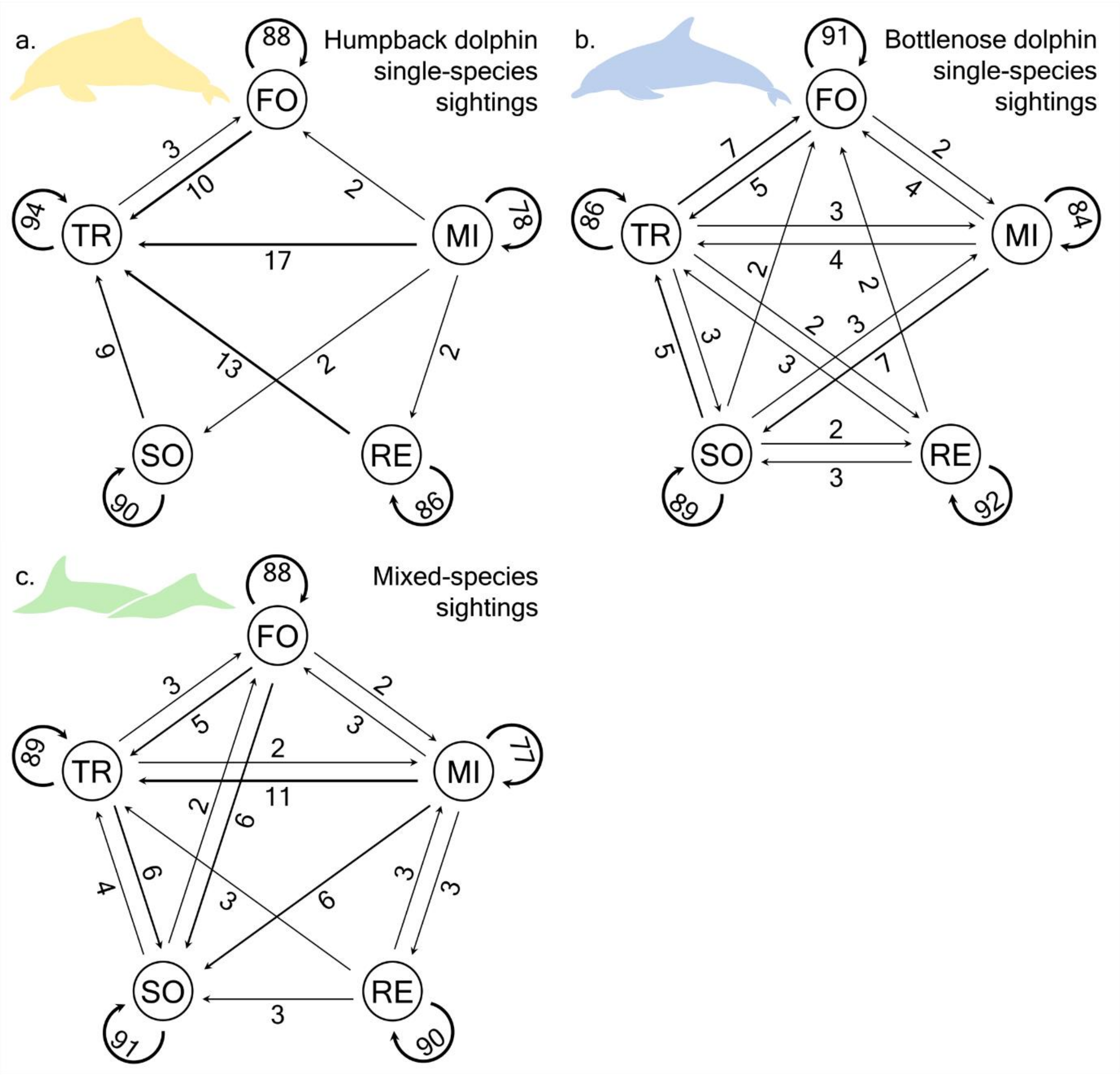

Figure 6.3 Markov chains illustrating transition probabilities between behavioural states for (a) single-species sightings of Australian humpback dolphins (*Sousa sahulensis*), (b) single-species sightings of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) and (c) mixed-species sightings of both species recorded from April to October over six years (2013-2015, 2018-2019, and 2021) around the North West Cape, Western Australia. Values are percentages and only transitions ≥2% are displayed. Behavioural states are as follows: FO, foraging; MI, milling; RE, resting; SO, socialising; TR, travelling. See Table 6.1 for criteria used to define behavioural states.

For humpback dolphins, two transitions were higher in mixed-species sightings than in single-species sightings: foraging → socialising ($p = 0.011$, Fisher's exact test) and travelling → socialising ($p = 0.001$, Fisher's exact test). Similarly, for bottlenose dolphins, the transition foraging → socialising was higher in mixed-species sightings ($p = 0.019$, Fisher's exact test). All the transition probabilities that were higher in mixed-species sightings than in single-species sightings of either species were transitions to socialising (Figure 6.3).

6.4.5 Bout lengths

Single-species sightings of humpback and bottlenose dolphins differed in the average length of behavioural bouts for all behavioural states except socialising (Figure 6.4; Table S4.1). In particular, humpback dolphin travelling bouts were 51.7 min longer than those of bottlenose dolphins ($t = 13.3$, $p = 0.003$) whereas bottlenose dolphin resting bouts were 24.2 min longer ($t = -3.6$, $p < 0.001$).

When in mixed-species groups, humpback dolphin bouts of travelling decreased significantly by 39.1 min (54.6%, $t = 6.0$, $p < 0.001$), but the bout lengths of the remaining behavioural states remained unchanged (Figure 6.4; Table S4.2). For bottlenose dolphins, all behavioural states except resting differed in bout length between single- and mixed-species sightings with socialising and travelling bouts increasing by 14.4 min (33.6%, $t = -2.8$, $p = 0.006$) and 12.6 min (36.1%, $t = -2.2$, $p = 0.031$) in mixed-species groups, respectively, and foraging and milling bouts decreasing by 14.1 min (26.1%, $t = 2.7$, $p = 0.008$) and 9.5 min (30.3%, $t = 2.4$, $p = 0.017$), respectively (Figure 6.4; Table S4.3).

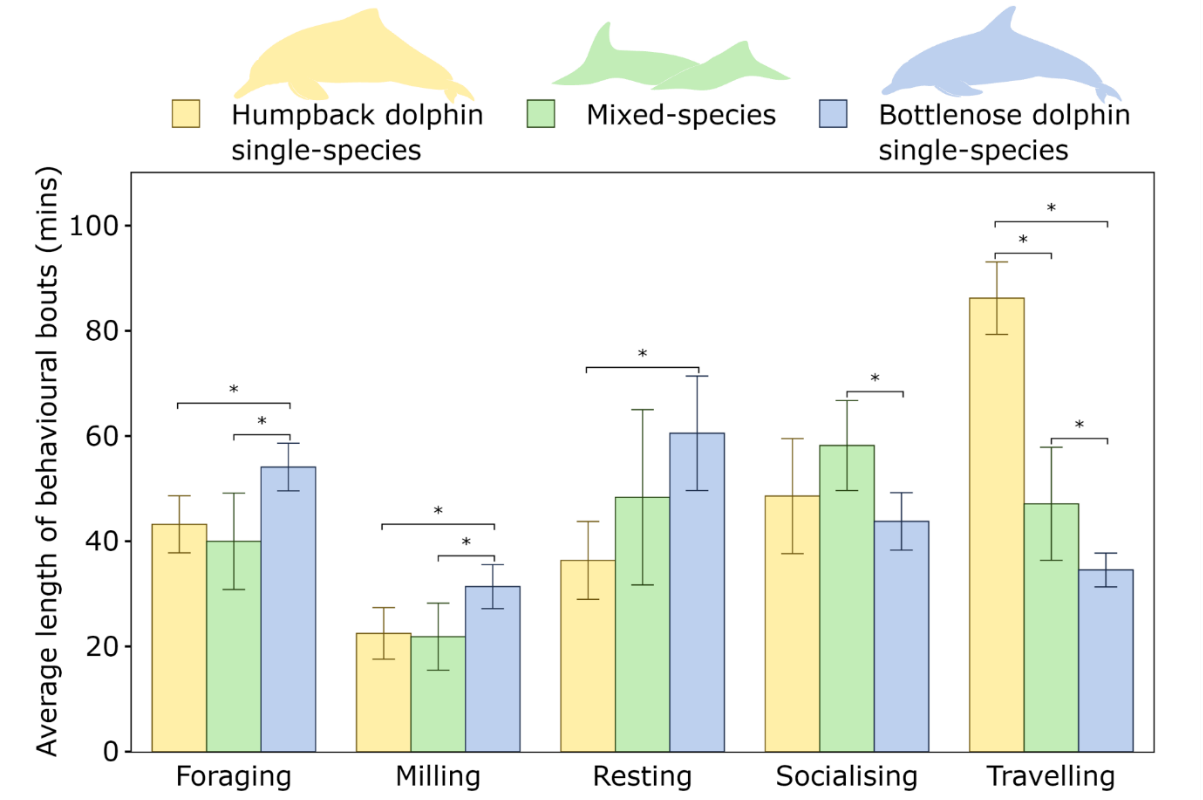

Figure 6.4 Average behavioural bout lengths derived from Markov chain analysis of single-species sightings of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) and mixed-species sightings of both species observed around the North West Cape, Western Australia. Significant differences (p<0.05) are shown by brackets with an asterisk. Error bars represent the 95% confidence interval. See Table 6.1 for criteria used to define behavioural states.

6.4.6 Budgets

The behavioural budgets, as predicted by the Markov chain model, indicated that humpback and bottlenose dolphins in single-species sightings differed in the proportion of time spent in all five behavioural states (Figure 6.5; Table S4.4). Bottlenose dolphins spent more time foraging ($Z = 7.801, p < 0.001$), milling ($Z = 6.454, p < 0.001$), resting ($Z = 4.521, p < 0.001$), and socialising ($Z = 10.319, p < 0.001$) whereas humpback dolphins spent more time travelling ($Z = 20.666, p < 0.001$).

In mixed-species sightings, humpback dolphins spent more time socialising ($Z = 16.540$, $p < 0.001$) and less time travelling ($Z = 11.806, p < 0.001$) compared to single-species sightings, but the proportion of time spent in the other behavioural states (i.e., foraging, milling, and resting) did not change (Figure 6.5; Table S4.5). Bottlenose dolphins spent more time socialising ($Z = 8.313, p < 0.001$) and travelling ($Z = 2.319, p = 0.020$) in mixed-species sightings, but less time foraging ($Z = 5.274, p < 0.001$), milling ($Z = 3.156, p = 0.001$), and resting ($Z = 3.510, p < 0.001$) (Figure 6.5; Table S4.6).

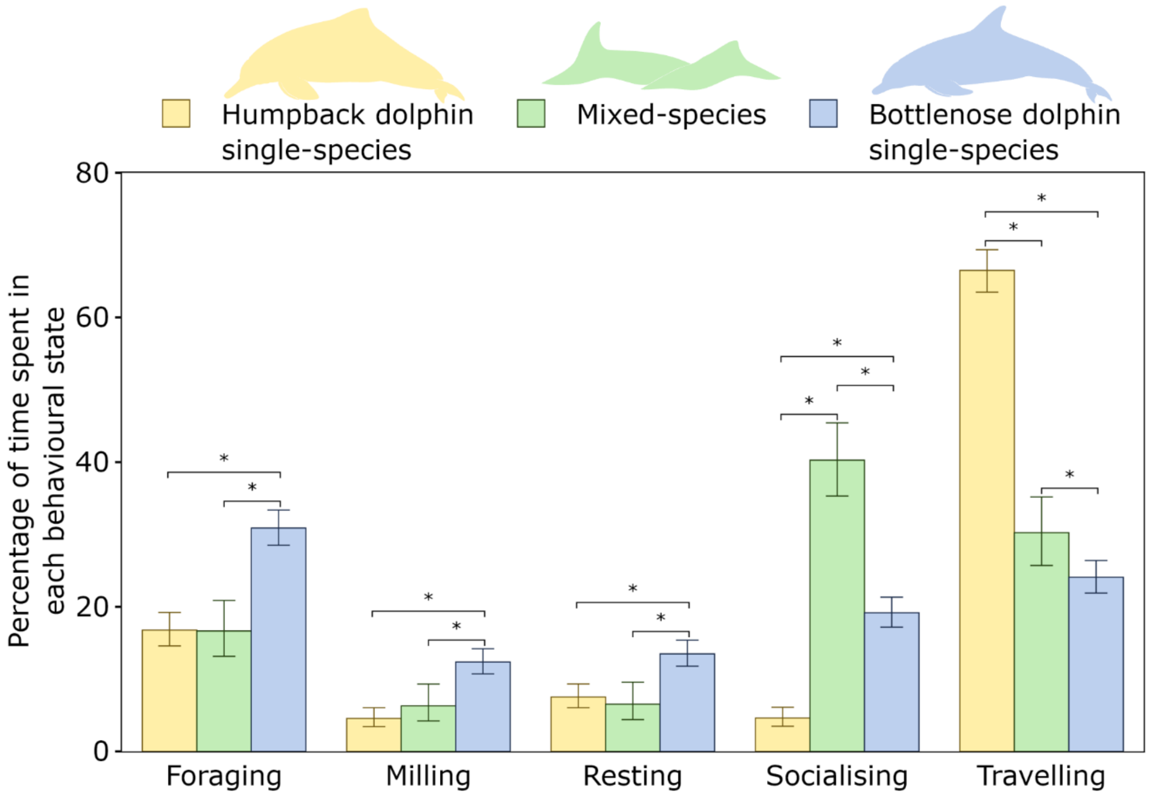

Figure 6.5 Behavioural budgets representing the stationary distributions of Markov chains of single-species sightings of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) and mixed-species sightings of both species observed around the North West Cape, Western Australia. Significant differences (p<0.05) are shown by brackets with an asterisk. Error bars represent the 95% confidence interval. See Table 6.1 for criteria used to define behavioural states.

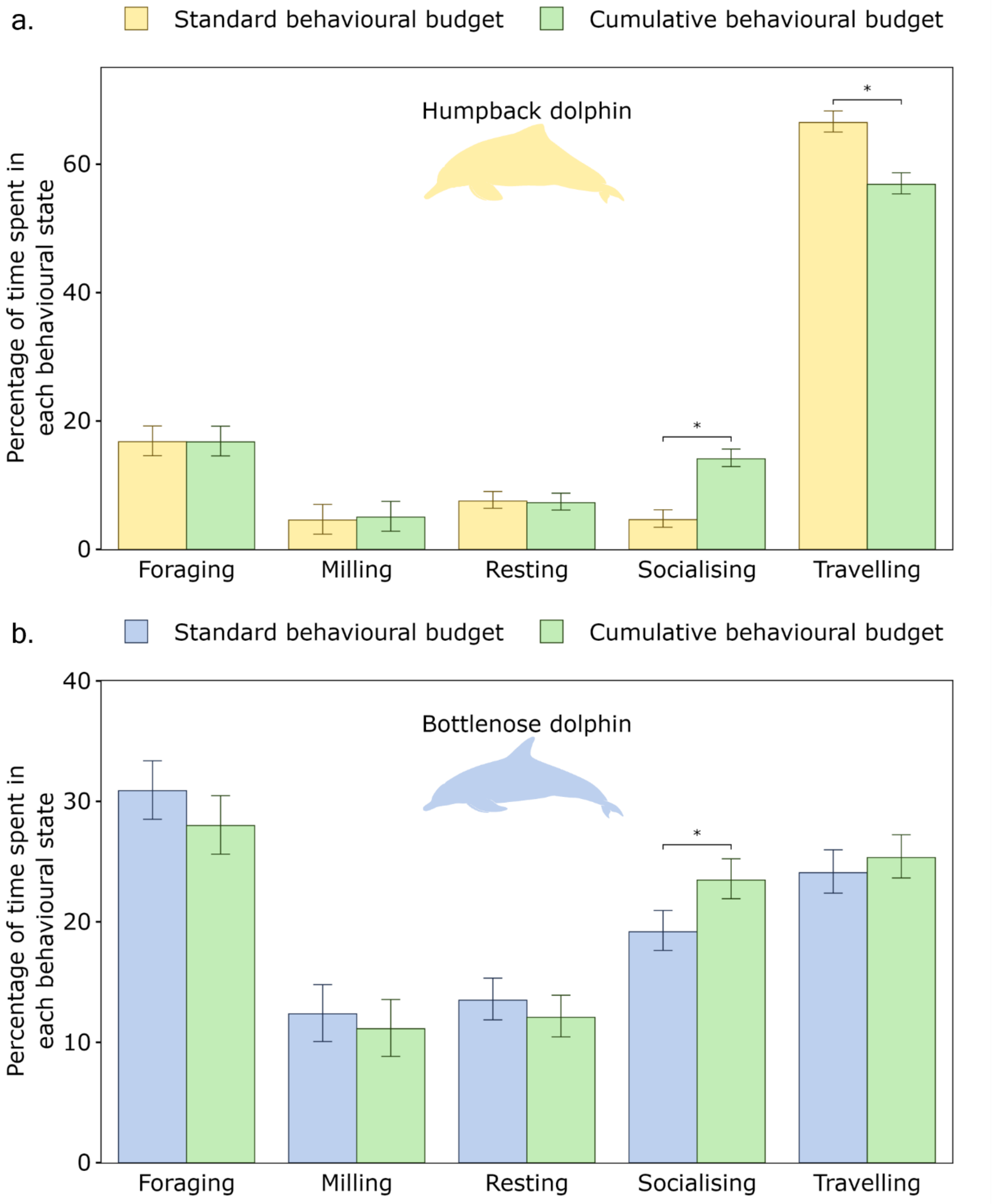

Figure 6.6 Standard and cumulative behavioural budgets of (a) Australian humpback (*Sousa sahulensis*) and (b) Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) observed around the North West Cape, Western Australia. Significant differences ($p<0.05$) are shown by brackets with an asterisk. Error bars represent the 95% confidence interval. See Table 6.1 for criteria used to define behavioural states.

6.4.7 Cumulative budgets

The cumulative behavioural budget analysis indicated that both species adjusted the time spent in particular behavioural states after accounting for the proportion of time spent in mixed-species groups (Figure 6.6; Tables S4.8 and S4.9). Specifically, as a result of participating in mixed-species groups, humpback dolphins spent more time socialising ($Z = 6.973, p < 0.001$) and less time travelling ($Z = 4.171, p < 0.001$) (Figure 6.6; Table S4.7) while bottlenose dolphins spent more time socialising ($Z = 2.606, p = 0.01$) (Figure 6; Table S4.8). For both species, the proportion of time spent in the remaining behavioural states was not affected by participation in mixed-species groups (Figure 6.6; Tables S4.8 and S4.9).

6.5 Discussion

The humpback and bottlenose dolphins that occur sympatrically around the North West Cape, Western Australia, differ in several aspects of their daylight behaviour, including behavioural transitions, bout lengths, and budgets. Moreover, both species display behavioural responses to the presence of heterospecifics in mixed-species groups. By using Markov chain analysis to study their behavioural patterns, we provide new insights into how interspecific differences in behaviour facilitate their coexistence as well as the functions of their interspecific interactions.

6.5.1 Comparison of behavioural patterns reveals coexistence mechanisms

During daylight hours, humpback dolphins spent the majority of their time travelling, followed by foraging, with little time spent in the remaining behavioural states (i.e., milling, resting, and socialising). These findings are consistent with observations of humpback dolphins in Exmouth Gulf, adjacent to our study area (Sprogis & Parra 2022) and with previous findings elsewhere that have shown that humpback dolphins (*Sousa* sp.) are rarely seen socialising and mainly travel and forage (Karczmarski & Cockcroft 1999, Parra 2005, Stensland et al. 2006). For example, in Zanzibar, the most frequent observed behaviours of Indian Ocean humpback dolphins (*Sousa plumbea*) are travelling and foraging, whereas socialising was only observed occasionally (Stensland et al. 2006). Similarly, humpback dolphins in Cleveland Bay, Queensland, and Indian Ocean humpback dolphins in Algoa Bay, South Africa, also spend little time socialising although, unlike in our study, they spend more time foraging than travelling (Karczmarski & Cockcroft 1999, Parra 2005).

The behavioural budget of bottlenose dolphins was more evenly distributed, with foraging, travelling, and socialising the most frequent behaviours observed during daylight hours. These results concur to some extent with previous studies on bottlenose dolphin behavioural budgets which indicate that, although they can vary considerably with location, sex, and diet, the predominant observed behaviours tend to be foraging and travelling (Christiansen et al. 2010, Steckenreuter et al. 2012, Fury et al. 2013, Bizzozzero et al. 2019). In Exmouth Gulf, adjacent to our study area, bottlenose dolphins show similar behavioural patterns, with travelling and foraging as the most frequent behaviours (Sprogis & Parra 2022). Any conclusions drawn from comparisons between studies must be treated with caution, however, as observed differences may be due to differences in methodology rather than differences in behaviour (Steiner 2011).

Behavioural budgets can be influenced by the quality and availability of food items (Hanya 2004, Vankosky & VanLaerhoven 2015) as well as an individual's foraging behaviour (Bizzozzero et al. 2019) and competition with sympatric species (Dröge et al. 2017, Karanth et al. 2017). Differences in behavioural patterns of sympatric species can reveal interspecific differences in habitat and resource use, both spatial and temporal, which are the main underlying constituents of a species' ecological niche (Perri & Randall 1999, Justa et al. 2019).

Around the North West Cape, the most notable observed difference in the daylight behavioural patterns of humpback and bottlenose dolphins was the prominence of travelling for humpback dolphins. This difference was evident in the higher transition probabilities to travelling and the greater length of travelling bouts displayed by humpback dolphins which resulted in a larger proportion of time spent travelling in their behavioural budget. Additionally, humpback dolphins spent approximately half as much time foraging as bottlenose dolphins and tended to forage in shorter bouts. This pattern could be explained by humpback dolphins primarily foraging outside the study area. This seems unlikely, however, as the study area encompasses the environments where humpback dolphins tend to forage, i.e., shallow, coastal waters, particularly those near estuaries and reefs (Parra 2006, Cagnazzi et al. 2011). Additionally, research in Exmouth Gulf outside and adjacent to our study area found similar patterns in behaviour (Sprogis & Parra 2022). Furthermore, the available information on the diet of humpback dolphins indicates that, like bottlenose dolphins, they are opportunistic-generalist feeders that prey on a wide variety of fish that are readily available in such environments (Amir et al. 2005, Kiszka et al. 2014, Parra & Jedensjö 2014).

An alternative possibility is that humpback dolphins preferentially forage at different times to bottlenose dolphins, such as at night, when behavioural observations were not conducted. Indo-Pacific humpback dolphins (*Sousa chinensis*) in the Pearl River Estuary, China, for example, emit more buzzes (i.e., "*short-range sonar sounds with minimum inter-click intervals shorter than 10 milliseconds*") at night, suggesting that this is when they mainly forage (Wang et al. 2015). In Menai Bay, Zanzibar, Indian Ocean humpback dolphins and bottlenose dolphins appear to use inshore areas for foraging more commonly at night, although due to a lack of information on the echolocation clicks of bottlenose and, in particular, Indian Ocean humpback dolphins, the species in this study could not be separated based on acoustic data alone and so were treated as a single population (Temple et al. 2016). Passive acoustic monitoring could be used to assess diel differences in the foraging behaviour of both humpback and bottlenose dolphins around the North West Cape, particularly at night, but also during the summer months when weather conditions are generally too poor to conduct boat-based observations (Wang et al. 2015, Temple et al. 2016, Todd et al. 2022). Additionally, further studies on the trophic interactions of these two species may be able to confirm the use of distinct foraging niches.

6.5.2 Changes in behavioural patterns indicate functions of mixed-species groups

Humpback and bottlenose dolphins both exhibited differences in their daylight behavioural patterns when in the presence of heterospecifics. In accordance with previous work (Chapter 5) and as hypothesised, humpback and bottlenose dolphins spent more time socialising when in mixed-species groups. The few studies that have compared the behavioural budgets of delphinids in single- and mixed-species groups have shown that the species involved change the proportion of time allocated to various behaviours when in mixed-species groups (e.g., Chapter 5, Acevedo-Gutiérrez et al. 2005, Kiszka et al. 2011a). For example, Acevedo-Gutiérrez et al. (2005) found that, in Costa Rica, both common bottlenose (*Tursiops truncatus*) and Guiana dolphins (*Sotalia guianensis*) socialise more frequently when in mixed-species groups. To adequately evaluate the impact of a variable on behavioural budgets, however, it is necessary to account for the amount of time that the species is affected by that variable. For example, studies on the impact of boat traffic on dolphin behavioural budgets have shown that, although dolphin behaviour may change when boats are present, the overall impact of boat traffic may not be significant if boats are only present for a small amount of time each day (Lusseau 2003, Meissner et al. 2015, Cecchetti et al. 2018). Similarly, the overall impact of mixed-species group formation on behavioural budgets will presumably be limited if species only infrequently form mixed-species groups.

In the standard behavioural budgets, bottlenose dolphins in single- and mixed-species sightings differed in the time allocated to all five behavioural states. However, because bottlenose dolphins spent only a fifth of their observation time in mixed-species groups, four of the behavioural states – foraging, milling, resting, and travelling – did not differ between the single-species and the cumulative behavioural budgets, highlighting the need to consider how much time species spend in mixed-species groups when evaluating changes in behavioural budgets. Nevertheless, as a result of mixed-species group formation, the cumulative behavioural budgets of both species were impacted, albeit disproportionately. Bottlenose dolphins slightly increased time spent socialising whereas humpback dolphins, who spent approximately a quarter of their observation time in mixed-species groups, tripled the amount of time that they spent socialising as the result of participating in mixed-species groups. Thus, around the North West Cape, mixed-species groups are frequent enough to impact certain aspects of the overall behavioural patterns of both species, most notably by increasing the time that they spend socialising. Additionally, when in mixed-species groups, both species displayed higher probabilities of transitioning to socialising from other behavioural states as well as, for bottlenose dolphins, increased lengths of socialising bouts.

The prominence of socialising when in mixed-species groups, particularly when compared to single-species groups of each species, supports previous findings that suggested that the formation of mixed-species groups of humpback and bottlenose dolphins are likely driven by social benefits that one or both species may gain (Chapter 5). A variety of interspecific behavioural interactions have been observed between these species, from aggressive chases and biting, to copulation, to non-aggressive tactile interactions, suggesting that the potential social benefits are diverse (Chapter 5). For example, young male dolphins may use interactions with heterospecifics as opportunities to practice socio-sexual behaviours while mixed-species groups may provide a safe and stimulating environment for the development of calves (Chapter 5). Similar hypotheses have been proposed for mixed-species groups of other delphinid species, including Atlantic spotted (*Stenella frontalis*) and common bottlenose dolphins in the Bahamas (Herzing & Johnson 1997, Melillo et al. 2009) and dusky (*Lagenorhynchus obscurus*) and Hector's dolphins (*Cephalorhynchus hectori*) in New Zealand (Markowitz 2004).

Interestingly, amongst other taxa, such as primates (Heymann & Buchanan-Smith 2000, Goodale et al. 2017) and birds (Sridhar et al. 2009, Goodale et al. 2017), the formation of mixed-species groups appears to be mainly driven by increased safety from predators and increased foraging efficiency rather than social benefits. Why interspecific social interactions are apparently frequent amongst delphinids but not amongst other taxa, such as primates, that are also highly social intraspecifically is unclear. The answers may lie, however, in the differences between delphinids and other taxa in terms of travel costs, predation risk, intra-guild competition, dispersal, and territoriality (Pearson 2011, Cords & Würsig 2014). For example, the high fission-fusion dynamics of many delphinid societies (Connor et al. 2000), combined with the low energetic cost of travelling (Williams et al. 1992, 1993), appears to enable wide-ranging social interactions between conspecifics (Pearson 2011, Randić et al. 2012) and may also facilitate interspecific social interactions. Comparative studies on the dynamics of mixed-species groups have so far been hindered by the limited available information on delphinid mixed-species groups (Cords & Würsig 2014, Syme et al. 2021), unclear terminology (Syme et al. 2021, 2022), and the lack of a conceptual framework for assessing their functional significance (Syme et al. 2021). As more research is conducted, it will become feasible to conduct comparative analyses, firstly, between delphinid species and, secondly, between delphinids and other taxa. Such analyses may help explain the prevalence of social benefits in delphinids mixed-species groups in contrast to other taxa.

In addition to antipredator, foraging, and social benefits, mixed-species groups may bring certain costs (Terborgh 1990, Cords & Würsig 2014). Discussion of costs has primarily focussed on feeding competition (Terborgh 1990, Cords & Würsig 2014), however, given that humpback and bottlenose dolphins spend only a small amount of time foraging when in mixed-species groups and their potential differences in foraging behaviour, feeding competition seems unlikely to be substantial. Potential costs of mixed-species groups of humpback and bottlenose dolphins may instead relate to time and energetic constraints.

Time can be an important limiting factor that affects activity budgets, group sizes, and species distributions (Dunbar et al. 2009). Increased time spent socialising necessary implies a decrease in the time spent performing one or more of the remaining behaviours, such as foraging or resting. For bottlenose dolphins, the increase in socialising when in mixed-species groups was compensated by small, non-significant decreases in the time spent foraging, milling, and resting, with all three of these behavioural states also occurring in shorter bouts when in mixed-species groups. For humpback dolphins, on the other hand, the increase in socialising came primarily at the cost of travelling, which decreased by approximately 10% in the cumulative behavioural budget and occurred in shorter bouts when humpback dolphins were in mixed-species groups. If travelling is necessary for humpback dolphins to acquire resources or avoid predation, then the decreased time spent travelling may affect fitness and survival.

There are also potential energetic costs associated with the increased time that both species spend socialising as the result of participation in mixed-species groups. During interspecific interactions, humpback and bottlenose dolphins have been observed to perform a variety of high intensity behaviours, including leaping, fast chasing, and forceful body contact (Chapter 5). For some individuals, the costs may be outweighed by the benefits. However, if species or individuals do not benefit equally from participating in mixed-species groups, then, for certain individuals, these costs may remain largely uncompensated. In mixed-species groups of saddle-back (*Saguinus fuscicollis*) and moustached tamarins (*Saguinus mystax*), for example, the latter allocate more time and energy to energetically costly boundary contests, resulting in asymmetric benefits (Peres 1992a). Around the North West Cape, the benefits of high intensity interactions involving aggressive and sexual behaviours appear to be biased towards bottlenose dolphins, who are typically the initiators of interspecific interactions (Chapter 5). If this is the case, humpback dolphins may experience energetic costs with little or no compensatory social benefits.

Our analyses, including the cumulative behavioural budgets, do not account for certain potential finer-scale patterns in mixed-species group participation. If certain individuals or classes of individuals (e.g., young males) are disproportionately represented in mixed-species groups, the impact that they experience may be more severe. Alternatively, even if an individual spends very little time in mixed-species groups, brief interactions could carry substantial costs if they result in severe injury or provoke ongoing avoidance behaviour (MacLeod et al. 2007, Williamson et al. 2022). Further work should investigate the costs and benefits of mixed-species group formation, both at the species and at the individual level (e.g., by comparing individual characteristics, such as age and sex, in relation to the frequency of participation and behaviour in mixed-species groups).

6.6 Conclusion

Interspecific comparative approaches are important for furthering our knowledge of coexistence mechanisms and interspecific interactions, two sets of ecological processes that are key to community structure and function. Differences in the behavioural patterns of humpback and bottlenose dolphins around the North West Cape suggest likely temporal partitioning in foraging activity, which would facilitate their coexistence. Changes in behavioural patterns when in the presence of heterospecifics indicate that the principal driver of mixed-species groups of humpback and bottlenose dolphins is likely to pertain to social benefits, which, in turn, may impact the fitness and survival of participating individuals. Overall, our study contributes to an improved understanding of the array of factors that facilitate coexistence and drive the formation of mixed-species groups amongst delphinids.

Chapter 7

General discussion

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General discussion

7.1 Introduction

Mixed-species groups of delphinids are widely reported, yet the majority of accounts are limited to brief observations of their occurrence. Few studies have evaluated if these apparent groups truly represent mixed-species groups or are simply chance encounters or aggregations, described their characteristics (e.g., size, age composition, and behaviour), investigated their potential functions, or evaluated their impacts on the species and individuals involved (Stensland et al. 2003, Cords & Würsig 2014, Syme et al. 2021). Furthermore, the interplay between mixed-species group formation and the mechanisms that facilitate the coexistence of sympatric delphinids (i.e., niche partitioning) are poorly understood. To advance this field of study, I developed and employed a conceptual framework for assessing the function of delphinid mixed-species groups that synthesises and builds on the various ideas, hypotheses, and study techniques that have been applied previously. To achieve this, I summarised and analysed the current information available in the literature on cetacean mixed-species groups to develop the conceptual framework (Chapter 2, Syme et al. 2021). Additionally, I assessed how delphinid groups are defined in the literature and in practice by delphinid researchers to provide greater clarity on the issue of what constitutes a group and I proposed a process for formulating biologically meaningful, yet compatible definitions that should improve our understanding of the factors that affect delphinid grouping dynamics (Chapter 3, Syme et al. 2022). I then employed the framework developed in Chapter 2 and Syme et al. (2021) on a model system consisting of the Australian humpback (*Sousa sahulensis*) (hereafter "humpback dolphin") and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) (hereafter "bottlenose dolphin") that inhabit the coastal waters of the North West Cape, Western Australia. More specifically, I collected and analysed observational data on humpback and bottlenose dolphins to evaluate their co-occurrence patterns and habitat partitioning (Chapter 4), investigate the potential benefits of their mixed-species groups (Chapter 5), and evaluate behavioural coexistence mechanisms and the functions of their mixed-species groups (Chapter 6). In this final chapter, I summarise the key findings, consider their implications, and make recommendations for future research into delphinid mixed-species groups.

7.2 Summary of results

7.2.1 Objective 1. Review the literature on cetacean mixed-species groups (Chapter 2, Syme et al. 2021)

From the literature review in Chapter 2 and Syme et al. (2021), I found 203 studies reporting cetacean mixed-species groups. These mixed-species groups involved 54 species from five Odontocete (Delphinidae, Kogiidae, Phocoenidae, Physeteridae, and Ziphiidae) and three Mysticete (Balaenidae, Balaenopteridae, and Eschrichtiidae) families and were observed in all the major ocean basins, except the Southern Ocean, in a variety of habitats, from shallow coastal waters to the open ocean. Despite the large number of studies reporting cetacean mixed-species groups, only 27 studies discussed potential functional explanations. Furthermore, most studies of the potential functions of mixed-species groups were focussed on small delphinids, with results indicating that they form mixed-species groups for a variety of antipredator, foraging, and social benefits. The studies reporting cetacean mixed-species groups employed different terms (e.g., *mixed-species group*, *interspecific association*, or *mixed-species school*), often without explicit definitions, and very few (n=5) utilised a technique to distinguish mixed-species groups from chance encounters and aggregations. Techniques used for inferring the potential benefits of mixed-species group formation were also varied, but typically involved analysing key characteristics (e.g., behaviour, location, and group size) of single- and mixed-species groups. These results confirm the conclusion of previous reviews that have indicated that mixed-species groups of cetaceans, particularly delphinids, are widespread but poorly understood (Stensland et al. 2003, Cords & Würsig 2014). To improve our understanding, I used the results of this review to construct a conceptual framework for assessing the functional significance of cetacean mixed-species groups which includes standardised terminology and key steps to follow. This framework will provide guidance for future studies of cetacean mixed-species groups, just as it guided Chapters 4, 5, and 6 of this thesis.

7.2.2 Objective 2. Assess how delphinid groups are termed and defined (Chapter 3, Syme et al. 2022)

After reviewing the literature on cetacean mixed-species groups (Chapter 2, Syme et al. 2021), there remained a key unresolved issue – how to define a mixed-species group? In the broadest sense, mixed-species groups can be described as groups of animals containing more than one species (Stensland et al. 2003, Syme et al. 2021). Thus, the issues concerning the definition of a mixed-species group can be traced back to the question of what defines a group. The literature review and online expert survey that I conducted illustrated several key issues, but also provided potential solutions. Although all four key terms (i.e., *group*, *school*, *party*, and *pod*) were used, *group* was the most frequent in operational definitions applied in the field. Similarly, various criteria were used to define delphinid groups, however spatial proximity was the most common. These trends lead to the recommendation of using the term *group* defined by spatial proximity in field studies of delphinids. I aimed to address further issues surrounding the use of spatial proximity criteria by proposing an analytical process to formulate definitions that are biologically meaningful and compatible across studies and species. The recommendations and proposed process have the potential to improve the way that we define delphinid groups and, thus, increase our ability to draw strong conclusions.

7.2.3 Objective 3. Investigate spatial and temporal occurrence patterns of humpback and bottlenose dolphins around the North West Cape (Chapter 4)

The first part of the framework for the study of cetacean mixed-species groups (Chapter 2, Syme et al. 2021) incorporates a key step: determining whether species occur together by chance (i.e., a chance encounter), by mutual attraction to a resource (i.e., an aggregation), or by attraction between species (i.e., a mixed-species group). I achieved this by analysing readily obtainable presence-absence data with a joint species distribution model (Ovaskainen et al. 2017, Tikhonov et al. 2020) which was capable of assessing co-occurrence patterns of humpback and bottlenose dolphins within the context of spatial habitat partitioning. This analysis showed that the species display habitat partitioning, with humpback dolphins occurring in shallower and more nearshore waters. Additionally, a temporal analysis indicated limited temporal partitioning, with bottlenose dolphins sighted more often in the afternoon. Despite this partitioning, the species co-occurred more often than expected by chance given shared responses to key environmental variables (i.e., water depth and distance to shore). This positive association in the species' occurrence is, I believe, indicative of attraction between the species resulting in the active formation of mixed-species groups.

7.2.4 Objective 4. Investigate the potential benefits of mixed-species groups of humpback and bottlenose dolphins around the North West Cape (Chapter 5)

The attraction between species that form mixed-species groups exists because one or more of the species gains benefits by grouping with heterospecifics. These benefits are typically placed into three hypotheses: the antipredator, foraging, and social advantage hypotheses (Stensland et al. 2003, Sridhar et al. 2009, Goodale et al. 2017, Syme et al. 2021). The second step in the conceptual framework for assessing the function of mixed-species groups is to determine what those benefits may be (Chapter 2, Syme et al. 2021). I achieved this by comparing the number of individuals, the age composition, and the behaviour of single- and mixed-species sightings of humpback and bottlenose dolphins to determine which hypothesis was most congruent with the observations. For both species, socialising was observed more frequently and travelling and foraging less frequently when in mixed-species groups. Moreover, numerous diverse interspecific behavioural interactions were observed from aggressive (e.g., chasing, biting, and forceful body contact) and sexual behaviours, to neutral (e.g., swimming alongside) and affiliative behaviours (e.g., playing and non-forceful body contact). The nature of interspecific interactions was linked to the relative numbers of the species which was, in turn, dependent on changes in the number of bottlenose dolphins present. More specifically, during interactions involving sexual and/or aggressive behaviours, bottlenose dolphins outnumbered humpback dolphins, however the reverse was true for interactions not involving such behaviours. The diversity of the observed behavioural interactions suggests that mixed-species groups may provide multiple social benefits, notably those concerning socio-sexual behaviours and the development and care of young. Additionally, given that these species share predators and the lack of direct behavioural interactions in certain mixed-species groups, the antipredator advantage hypothesis may also be relevant.

7.2.5 Objective 5. Evaluate behavioural coexistence mechanisms of humpback and bottlenose dolphins around the North West Cape and further investigate the functions of their mixed-species groups (Chapter 6)

To better understand the coexistence mechanisms of humpback and bottlenose dolphins and the functions and impacts of their mixed-species groups, I used Markov chain analysis to investigate their daylight behavioural patterns. Specifically, I used focal follow data of single- and mixed-species sightings to calculate behavioural transition probabilities (i.e., the probability that dolphins in a given behavioural state will transition to another behavioural state within a predetermined time step). I then used these probabilities to construct first-order Markov chains, from which I derived behavioural bout lengths (i.e., the average amount of time that dolphins spend in a given behavioural state before transitioning to another), and behavioural budgets. Travelling was more prominent for humpback dolphins who exhibited higher transition probabilities to travelling, had longer bouts of travelling, and spent more time travelling in their behavioural budget. Bottlenose dolphins, on the other hand, spent more time foraging and exhibited longer foraging bouts. These divergent behavioural patterns may reflect differences in foraging behaviour, with humpback dolphins potentially foraging principally at night and bottlenose dolphins during the day. Such temporal partitioning may facilitate coexistence of these species. The behavioural patterns of humpback and bottlenose dolphins also changed when in mixed-species groups with both species exhibiting higher transitions towards socialising and increasing the time spent socialising in their behavioural budgets. These changes affirm that, for humpback and bottlenose dolphins around the North West Cape, the driver of mixed-species group formation is likely related to social benefits that one or both species may gain. The changes in behavioural patterns may also result in certain costs pertaining to increased energy expenditure and disruption of normal behavioural patterns.

7.3 Overcoming the shortcomings of investigating the functions of delphinid mixed-species groups

In this study, I have used the available information on mixed-species groups of delphinids and other taxa to provide potential solutions to two of the key shortcomings that have hindered the investigation of the functions of delphinid mixed-species groups. Firstly, in the framework presented in Chapter 2 and Syme et al. (2021), I provided guidance on how to term and define mixed-species groups, a topic that I subsequently investigated further in Chapter 3 and Syme et al. (2022), where I evaluated current definitions of delphinid groups and proposed an analytical process to help counter some of the key issues that remain. Secondly, in Chapter 4, I use a novel application of joint species distribution modelling to quantitatively assess if mixed-species groups are indeed the result of attraction between species, a question that has largely remained unanswered, particularly in studies of delphinids (Chapter 2, Stensland et al. 2003, Cords & Würsig 2014, Syme et al. 2021). Here, I discuss these solutions, their implications, and recommendations for future work.

7.3.1 Terminology and definitions of mixed-species groups

Several studies have raised the issues associated with delphinid group definitions, such as the inconsistent use of terminology and the arbitrary nature of criteria (e.g., Mann 1999, Connor et al. 2000, Gibson & Mann 2009, Syme et al. 2021). To my knowledge, this study is the first, however, to analyse a large sample of definitions to identify specific issues and trends in order to make recommendations and propose potential solutions. By proposing the use of a single term to refer to cetacean mixed-species groups (Chapter 2, Syme et al. 2021) and by making recommendations on the use of terms and criteria related to delphinid grouping behaviour (Chapter 3, Syme et al. 2022), I provide well-founded, simple, yet effective guidance that can reduce inconsistency and facilitate comparisons amongst studies.

My analyses of the terms and definitions applied to groups focussed on cetaceans (Chapter 2, Syme et al. 2021) and, in particular, delphinids (Chapter 3, Syme et al. 2022). Yet, grouping behaviour, including the formation of mixed-species groups, is fundamental to the behavioural ecology of numerous, diverse taxa (Krause & Ruxton 2002, Stensland et al. 2003, Goodale et al. 2017, Majolo & Huang 2018). Group definitions used in studies of other group-living taxa, from fishes to primates, are similar in construct to those applied to delphinids (Archie et al. 2006, Croft et al. 2006, Machanda et al. 2013, Castles et al. 2014, Kasozi & Montgomery 2020). For example, studies of ungulates typically use spatial proximity to define groups

(Kasozi & Montgomery 2020). Moreover, researchers who study these taxa are faced with similar issues (e.g., inconsistent definitions and a lack of biological justification of distance thresholds) (Krause & Ruxton 2002, Miller & Gerlai 2011, Viscido & Shrestha 2015, Kasozi & Montgomery 2020). Thus, although delphinid research brings its own unique challenges, the proposed ways forward discussed in this study could be applied to other group-living taxa, just as similar techniques have been applied to ungulates (Clutton-Brock et al. 1982), primates (Ramos-Fernández 2005), and fishes (Miller & Gerlai 2011).

The discussion of current issues concerning group definitions and the proposed analytical process to determine threshold distances at which to delimit groups (Chapter 3, Syme et al. 2022) represent a first step to developing definitions that are compatible, yet biologically meaningful to the study species. Such improved definitions will assist future socio-ecological research on delphinids. Ideally, the process (Chapter 3, Syme et al. 2022) will be applied to diverse delphinid species in different locations and habitats, thus allowing for future comparative work to investigate the factors (e.g., habitat type, water depth, or predation risk) that influence the dynamics of delphinid grouping behaviour (e.g., group size and group density).

7.3.2 Distinguishing mixed-species groups from chance encounters and aggregations

To my knowledge, no other study of delphinid mixed-species groups has quantitatively determined whether apparent mixed-species groups are indeed the result of attraction between species and not simply chance encounters or aggregations (Chapter 2, Syme et al. 2021). In Chapter 4, I took advantage of recent developments in joint species distribution modelling (Ovaskainen et al. 2017, Ovaskainen & Abrego 2020) to conduct this key step. Joint species distribution models have been applied in community ecology to diverse taxa, from stream invertebrates to forest birds (Elo et al. 2021, Burgas et al. 2021). They explain and predict species occurrence as a function of environmental factors, while considering possible species associations originating from ecological interactions (e.g., competition, predation, parasitism, or mutualism) (Pollock et al. 2014, Warton et al. 2015, Ovaskainen et al. 2017, Ovaskainen & Abrego 2020). For each pair of species, joint species distribution models calculate the residual correlation, which indicates whether species co-occur more or less often than expected by chance after accounting for their responses to environmental factors included in the model (Pollock et al. 2014, Ovaskainen et al. 2017). One possible explanation for highly positive residual correlation (i.e., species association) is attraction between species.

By using joint species distribution modelling combined with observations of species together, I was able to assess if humpback and bottlenose dolphins form mixed-species groups rather than chance encounters or aggregations (Chapter 4). It is important to note, however, that there are other factors that may affect residual correlation, including unmeasured environmental predictors and other ecological interactions, and that these cannot be distinguished statistically by the model (Pollock et al. 2014, Ovaskainen et al. 2017, Tikhonov et al. 2017). The possibility that species co-occurrence is due to other ecological interactions, such as species responding similarly to shared predators and/or prey, can be eliminated with behavioural observations, as I did in Chapter 4. Nevertheless, a more robust approach that could be employed by future studies is to obtain data on the presence, distribution, and abundance of predators and prey and incorporate them as environmental factors in the models in order to quantitatively assess this possibility.

In addition to data on environmental variables, joint species distribution modelling requires presence-absence data of the target species and can be implemented with a variety of packages in several statistical software programs (Pollock et al. 2014, Warton et al. 2015, Ovaskainen et al. 2017, Tikhonov et al. 2020, Ovaskainen & Abrego 2020). Consequently, the methods that I applied are more feasible and accessible than previously used techniques (e.g., ideal gas models) that require detailed data (e.g., data on group travel speeds and group densities). Thus, the approach that I took in Chapter 4 will facilitate future research to undertake this key step when investigating delphinid mixed-species groups. These methods should ideally be applied to the wide variety of delphinid species that have been reported to form mixed-species groups (Chapter 2, Stensland et al. 2003, Cords & Würsig 2014, Syme et al. 2021) to determine whether they truly are the result of attraction between species. By answering this question, we will be able to pinpoint more accurately the drivers of the formation of delphinid mixed-species groups.

7.4 Further consideration of the social advantage hypothesis

Numerous species from diverse taxa have been reported in mixed-species groups, however most research has been conducted on mixed-species groups involving primates and birds (Heymann & Buchanan-Smith 2000, Stensland et al. 2003, Sridhar et al. 2009, Heymann & Hsia 2015, Goodale et al. 2017). Moreover, discussion of the benefits of primate and avian mixed-species groups focusses almost entirely on two hypotheses: the antipredator and foraging advantage hypotheses (Heymann & Buchanan-Smith 2000, Sridhar et al. 2009, Goodale et al. 2017). Consequently, the literature on these hypotheses is considerable, the theory is well-established, and there are numerous studies on a variety of species across a range of ecosystems. The social advantage hypothesis, however, has not been so well investigated and there remains much to learn about interspecific social interactions, the benefits that they provide and the costs that they entail.

The social advantage hypothesis has principally been applied to delphinids, which may benefit, for example, by practising socio-sexual behaviours, by providing a safe learning environment for calves, or by gaining experience from alloparenting (Chapters 2, 5, and 6, Herzing & Johnson 1997, Stensland et al. 2003, Markowitz 2004, Melillo et al. 2009, Herzing & Elliser 2013, Syme et al. 2021). Nevertheless, only 12 studies on a narrow range of delphinid species have hypothesised that the function of mixed-species groups is social (Chapter 2, Syme et al. 2021). Additionally, in Chapter 5 and 6, I provide robust evidence indicating that the main function of humpback and bottlenose dolphin mixed-species groups is social in nature. To further our understanding of the social advantage hypothesis, future studies should aim to empirically test potential social benefits, to investigate how various factors (e.g., morphology, phylogeny, and social structure) influence social benefits, and conduct comparative studies within and between taxa to help explain differences in the prevalence of interspecific social behaviour.

7.4.1 Testing the potential social benefits of mixed-species groups

The mechanisms that reduce predation risk (e.g., the confusion effect, the selfish herd effect, or more eyes and ears) and improve foraging success (e.g., mutual and non-mutual information exchange or facilitation) are well-known and the benefits that they provide have been empirically tested (Heymann & Buchanan-Smith 2000, Stensland et al. 2003, Sridhar et al. 2009). For the social advantage hypothesis, there are also proposed mechanisms that explain how individuals benefit, although they are less well-formulated and supported. For example, interspecific alloparenting may improve a female's success at raising her own calves, playful interactions between young heterospecific individuals may help their social and physical development, and young males that practice socio-sexual behaviours with heterospecifics may achieve higher social standing or may have higher reproductive success with conspecifics (Chapters 2 and 5, Herzing & Johnson 1997, Stensland et al. 2003, Markowitz 2004, Melillo et al. 2009, Syme et al. 2021). In most cases, these potential social benefits have not been empirically tested with targeted studies.

Testing whether individuals obtain social benefits and the form that those benefits take would be challenging, yet possible. For example, one could determine whether interspecific socio-sexual interactions improve a male's reproductive chances by analysing for correlations between participation in mixed-species groups and mating success or number of offspring (Stensland et al. 2003). Similarly, one could assess correlations between participation in mixed-species nursery groups and a female's success at raising calves. Such empirical tests will require detailed long-term datasets that may not always be available. In this case, an alternative is to analyse for correlations between interspecific social behaviour and key individual characteristics. For example, if it can be shown that, in mixed-species groups involving sexual behaviours, most of the participants of a given species are young males, that would support, but not prove, the hypothesis that young males practice socio-sexual behaviours on heterospecifics. Testing directly for social benefits or for patterns in individual characteristics and social behaviour would give support to the hypotheses that have been proposed and would provide insight into why interspecific social interactions occur and the benefits that they provide.

A better understanding of social benefits and their impacts may also be gained from analysing how various factors influence these benefits and the mechanisms by which they are obtained. Similar considerations can be found in the literature on the antipredator and foraging advantage hypotheses. For example, Sridhar and Guttal (2018) discuss how increased dietary overlap between birds increases both food competition and the quality of social information that heterospecifics can provide, in turn influencing the choice of partner species. It is unknown, however, how diverse factors such as morphology, phylogeny, or social structure may influence the frequency and nature of social benefits that delphinids gain from forming mixed-species groups.

For example, morphological traits have been shown to influence the propensity of cetaceans to hybridise (Crossman et al. 2016) and, along with other traits such as behaviour, vocalisations, and social structure, may affect the social benefits that delphinids obtain from mixed-species groups. Humpback and bottlenose dolphins, which regularly socialise with one another (Chapters 5 and 6), are morphologically similar (Parra & Jefferson 2018, Wang 2018), which may promote interspecific social interactions. In contrast, common bottlenose dolphins (*Tursiops truncatus*) are noticeably larger than Atlantic spotted dolphins (*Stenella frontalis*) in the Bahamas (Herzing & Johnson 1997, Melillo et al. 2009, Elliser & Herzing 2016a) and Guiana dolphins (*Sotalia guianensis*) in Costa Rica (Acevedo-Gutiérrez et al. 2005, May-Collado 2010) with whom they regularly interact socially. Moreover, social interactions have also been observed between species as divergent as common bottlenose dolphins and gray whales (*Eschrichtius robustus*) (Shane 1994) or sperm whales (*Physeter macrocephalus*) (Wilson 2013b). Moreover, morphology alone cannot explain the variation in interspecific social interactions. For example, pantropical spotted (*Stenella attenuata*) and spinner dolphins (*Stenella longirostris*), which are closely related and morphologically similar, were never observed to interact socially around the western Indian Ocean island of Mayotte (Kiszka et al. 2011a), yet were observed interacting in diverse ways, including copulation, around the Hawaiian island of Oahu (Psarakos et al. 2003). Thus, whether morphological similarity enables, promotes, or even hampers interspecific social behaviour is unclear. Furthering our understanding of how traits, such as morphology, influence the social interactions between species that form mixed-species groups will help us to better understand potential social benefits and how they affect the individuals and species involved.

7.4.2 Comparative analyses between taxa

In addition to comparisons within taxa, as discussed above, comparisons between taxa may further our understanding of the social advantage hypothesis. Amongst other taxa, such as primates and birds, mixed-species groups are rarely driven by social benefits and interspecific social interactions appear to be infrequent (Heymann & Buchanan-Smith 2000, Stensland et al. 2003, Sridhar et al. 2009, Goodale et al. 2017). For example, primates of the genera *Saguinus* and *Callimico* regularly form enduring mixed-species groups, yet interspecific social interactions are rarely observed and are mostly limited to agonistic interactions over food resources (Heymann & Buchanan-Smith 2000). In contrast, several species of delphinid exhibit a diversity of interspecific social interactions (Chapter 5, Herzing & Johnson 1997, Psarakos et al. 2003, Markowitz 2004, Parra 2005, Acevedo-Gutiérrez et al. 2005, Melillo et al. 2009) and the social advantage hypothesis is often given as an explanation for the formation of delphinid mixed-species groups (Chapter 2, Syme et al. 2021). This difference is particularly striking when comparing delphinids to primates as both taxa are highly social intraspecifically and display similarities in certain aspects of social organisation and behaviour. For example, both primate and delphinid species engage in non-reproductive sexual behaviours with conspecifics to maintain relationships, improve their social status, and/or diffuse tension (Furuichi et al. 2014), yet only certain delphinids have been reported to regularly engage in such behaviours with heterospecifics (Chapter 5, Herzing & Johnson 1997, Psarakos et al. 2003, Parra 2005, Acevedo-Gutiérrez et al. 2005, Melillo et al. 2009). Whether these differences are the result of a bias in research focus or differences in behavioural ecology is unclear.

Comparative analyses of mixed-species groups of delphinids and primates may provide insight into how social benefits are influenced by diverse factors including travel costs, dispersal patterns, territoriality, predation risk, intra-guild competition, and social organisation. The higher sociability of female bottlenose dolphins when compared to female chimpanzees has been explained by the lack of territoriality, the lower travel costs, and the lack of dispersal from natal ranges in female bottlenose dolphins (Pearson 2011). Such differences may also facilitate interspecific social interactions, leading to more complex relationships and behaviour between heterospecifics. A review by Cords and Würsig (2014) revealed key similarities and differences between delphinid and primate mixed-species groups, however, their conclusions were limited by the paucity of studies into delphinid mixed-species groups (Cords & Würsig 2014). As future research delves deeper into the functions and dynamics of delphinid mixed-species groups, comparative analyses will enable us to draw stronger conclusions about what drives differences between species and taxa in terms of the social benefits that they gain from participating in mixed-species groups.

7.5 Future research and recommendations

By employing the framework developed in Chapter 2 and Syme et al. (2021) on a model system of humpback and bottlenose dolphins around the North West Cape (Chapters 4, 5, and 6) I was able, firstly, to determine that observed mixed-species groups are the result of attraction between species and, secondly, to infer their potential benefits. In addition to the work presented in this thesis, several published studies have investigated the habitat use, demography, and social structure of the humpback and bottlenose dolphin populations of the North West Cape (Hunt et al. 2017, 2019, 2020, Haughey et al. 2020, 2021). The ensemble of this work, together with this thesis, provides the ideal foundation to conduct further in-depth research into aspects of their mixed-species groups that have not yet been investigated.

Here, I provide directions and recommendations for future research that will further our understanding of the diverse aspects of delphinid mixed-species groups that are still poorly understood including: the mechanisms that promote the formation and maintenance of mixed-species groups; the level of communication between species; and the influence of individual, population, and ecological characteristics on the dynamics of mixed-species groups. Although I focus on mixed-species groups of delphinids, particularly those of the humpback and bottlenose dolphins of the North West Cape, the research directions and questions that I discuss are applicable and of benefit to the study of mixed-species groups more broadly.

7.5.1 Formation and maintenance of mixed-species groups

Data on which species initiates mixed-species group formation by merging with heterospecifics can provide information concerning which species benefits, as the species that gains the most from mixed-species groups will presumably be primarily responsible for their formation (Cords & Würsig 2014). For example, Teelen (2007) concluded that red-tailed monkeys (*Cercopithecus ascanius*) benefit more from forming mixed-species groups with red colobus monkeys (*Procolobus rufomitratus*) than the latter because red-tailed monkeys were responsible for initiating the majority of mixed-species groups by approaching and joining red colobus monkeys. Around the North West Cape, the majority of mixed-species groups of humpback and bottlenose dolphins had already formed when they were sighted, so it was difficult to determine whether one species predominantly joined the other. Nevertheless, long focal follows of single- and mixed-species groups can provide additional observations of the species responsible for initiation and termination of mixed-species groups. Such data could provide insights into the circumstances under which humpback dolphins join or split with bottlenose dolphins and vice versa.

A related question concerns the mechanisms that enable heterospecifics to form and maintain mixed-species groups (Cords & Würsig 2014, Goodale et al. 2017). Species may be attracted intentionally or unintentionally to the calls of heterospecifics and, once the group is formed, may rely on visual and acoustic signals to maintain group cohesion (Heymann & Buchanan-Smith 2000, Goodale et al. 2017). For example, in the Amazon Rainforest, moustached (*Saguinus mystax*) and saddle-back tamarins (*Saguinus fuscicollis*) issue mutual contact calls in the morning prior to the formation of mixed-species groups (Heymann 1990). Thus, central to the formation and maintenance of mixed-species groups is communication (Goodale et al. 2017).

7.5.2 Interspecific communication

To better understand how delphinids form and maintain mixed-species groups and regulate their behavioural interactions, it would be beneficial to investigate interspecific communication. For delphinids, the primary means of communication are acoustic, visual, and tactile (Dudzinski & Gregg 2018) and, although communication may be hindered by species-specific differences, shared and modified signals may facilitate communication between species (Psarakos et al. 2003, Gorissen et al. 2006, May-Collado 2010).

Several delphinid species have been recorded vocalising in mixed-species groups (Oswald et al. 2008, May-Collado 2010, Viana et al. 2022). Moreover, acoustic communication appears to be important in delphinid mixed-species groups with certain species having been found to modulate their whistles in the presence of heterospecifics (May-Collado 2010, Viana et al. 2022). For example, common bottlenose and Guiana dolphins (*Sotalia guianensis*) modify their whistles when in mixed-species groups, resulting in whistles with intermediate structure when compared to whistles emitted in single-species groups (May-Collado 2010). Common bottlenose dolphins are also known to adjust their whistles when interacting with long-finned pilot whales (*Globicephala melas*) and Risso's dolphins (*Grampus griseus*) according to which species they are with (Viana et al. 2022). These findings illustrate the plasticity of delphinid acoustic communication and, although the reasons for these changes are still unclear, they may represent mimicry or attempts to interact acoustically with heterospecifics (May-Collado 2010, Viana et al. 2022).

No acoustic data on the humpback and bottlenose dolphins of the North West Cape were recorded during this study. However, given the importance of acoustic communication, future research should endeavour to obtain such data. Previous work in Exmouth Gulf demonstrated that humpback and bottlenose dolphins display small, but significant differences in their echolocation parameters (de Freitas et al. 2015), while in Moreton Bay, Queensland, these species differ in the physical parameters of their whistles (Schultz & Corkeron 1994). No studies have, to my knowledge, investigated the vocalisations of humpback and bottlenose dolphins in single- and mixed-species groups to elucidate the role that acoustic communication plays in facilitating the formation of mixed-species groups and mediating interspecific interactions.

Playback experiments have demonstrated that, amongst tamarins, long calls elicit a vocal response from heterospecifics and cause them to approach the speaker, indicating that these calls may play a role in mixed-species group formation (Windfelder 2001). Similarly, playback experiments have been used to investigate the responses of delphinid species to the simulated presence of heterospecifics (Curé et al. 2012, Bowers et al. 2018). Similar techniques could be applied to investigate the role of acoustic communication in the formation and maintenance of delphinid mixed-species groups. Furthermore, by determining in which situations delphinids emit certain vocalisations and how those vocalisations change, we may better understand their interspecific interactions and how they are mediated by acoustic communication. For example, in the Bahamas, Herzing (1996) found that certain types of vocalisations (e.g., “squawks” and “screams”) of common bottlenose and Atlantic spotted dolphins were associated with particular behaviours (e.g., sexual play). May-Collado (2010) suggested that changes in Guiana dolphin whistles may reflect a stress response to the antagonistic behaviour of common bottlenose dolphins. Playback experiments can be useful for understanding how, when, and why species modulate their acoustic communication in the presence of heterospecifics. For example, Gorissen et al. (2006) found that great tits (*Parus major*) imitate the song of blue tits (*Parus caeruleus*), but not vice versa, and that the stage of the great tits’ breeding cycle does not affect the occurrence of these imitations. Moreover, great tits do not respond to other great tits’ imitations of blue tit songs, indicating that these imitations serve for interspecific, and not intraspecific, communication (Gorissen et al. 2006). Further research into vocalisations of delphinids when in and not in mixed-species groups will provide insight into the extent to which they use acoustic communication to form and maintain mixed-species groups and regulate interspecific behavioural interactions.

Delphinids in mixed-species groups may also communicate via visual and tactile means. Visual communication can involve either colouration and morphological traits or the performing of particular postures and behaviours and serves a variety of purposes, from deterring predators to attracting mates (Allen et al. 2017, Dudzinski & Gregg 2018). Tactile communication comprises touching or rubbing various body parts, such as rostra, pectoral fins, and abdomens, and may be aggressive or affiliative (Connor et al. 2006, Dudzinski & Gregg 2018). Some of the postures and gestures used for visual and tactile communication appear to be shared amongst delphinids (Psarakos et al. 2003, Dudzinski et al. 2010, Cords & Würsig 2014). These include S-shaped body, head-to-head, and open mouth postures, which are generally considered to be aggressive or warning signals (Psarakos et al. 2003, Campagna 2018, Dudzinski & Gregg 2018). Pectoral fin contact, an affiliative behaviour, has been recorded amongst several species, some of which display remarkable similarity in how these behaviours are performed (Dudzinski et al. 2009). In animals, play behaviour is typically elicited by certain postures, such as bowing in dogs (*Canus familiaris*), and, if these postures are shared between species, should enable interspecific play (Fagen 1981, Spinka et al. 2001).

Several species of delphinids have been observed to perform some of these shared postures and gestures during interspecific interactions, potentially enabling them to send diverse signals, from aggressive threats to invitations to play. For example, Herzing and Johnson (1997) observed common bottlenose and Atlantic spotted dolphins performing head-to-head postures and open mouth displays during aggressive interactions in the Bahamas. In my study, observed behaviours were limited to those visible from above water, such as leaps, raising the head above the surface, and rolling over one another (Chapter 5). Understanding the role that visual and tactile communication plays in regulating interspecific interactions would require complementary analysis of underwater dolphin behaviour (Herzing & Johnson 1997, Melillo et al. 2009). A starting point would be to establish through underwater video which postures and gestures are shared by interacting species and exhibited by participants in mixed-species groups. Further research could determine the contexts in which certain postures and gestures are performed and whether the presence of heterospecifics influences their frequency or nature.

7.5.3 Individual level analyses

Research into mixed-species groups typically operates initially at a species or group level, as is the case in Chapters 4, 5, and 6. A more detailed understanding of the benefits of mixed-species groups may be gained, however, from individual level analyses. For example, it is possible to construct and analyse interspecific social networks. This has been done for common bottlenose dolphins and false killer whales (*Pseudorca crassidens*) in New Zealand and for common bottlenose and Atlantic spotted dolphins in the Bahamas, revealing associations between heterospecific individuals, including some pairs that occurred together repeatedly over several years (Zaeschmar et al. 2014, Elliser & Herzing 2016a). The dataset used in Chapters 4, 5, and 6 also contains individual photo-identification data of both species, opening the possibility of analysing interspecific social networks. If certain individuals or classes (e.g., young males) are found to participate in mixed-species groups more regularly than others, that could provide further insight into why they form mixed-species groups and future data collection could target those individuals. Moreover, continued individual identification would allow analysis of how interspecific behavioural interactions correlate to individual traits such as sex, age, and reproductive status. For example, Herzing & Johnson (1997) examined the age and sex of Atlantic spotted and common bottlenose dolphins in relation to the behavioural context of interspecific interactions (e.g., sexual play/aggression and affiliative), revealing that, in the context of sexual play/aggression, interspecific interactions typically involved males of both species and only occasionally female common bottlenose dolphins. Analysis at an individual level may be particularly important in situations where the benefits are not uniform for participating individuals, as appears to be the case around the North West Cape (Chapter 5).

7.5.4 Genetic analyses

Genetic analyses of biopsy samples could provide insight into potential hybridisation and the nature of sexual interactions between species that form mixed-species groups. Hybridisation has been reported between numerous species of cetaceans, with pairs of species that hybridise tending to be more similar in morphological and behavioural traits than those that do not (Crossman et al. 2016). Several cases of hybridisation involving *Sousa* and/or *Tursiops* species have been reported (Stensland et al. 2003, Brown et al. 2014, Crossman et al. 2016), including, potential hybridisation of bottlenose dolphins and Indian Ocean humpback dolphins (*Sousa plumbea*) in South Africa (Karczmarski et al. 1997, Koper & Plön 2016). The occurrence of sexual interactions between species in mixed-species groups, as was observed around the North West Cape (Chapter 5), raises the possibility that they result in hybrid offspring, although confirmation of this requires genetic analysis (Herzing & Johnson 1997, Acevedo-Gutiérrez et al. 2005). Testing for the presence of hybrids can also provide further information about the nature of sexual interactions between the species by determining if they are purely for practicing socio-sexual behaviours or if they result in reproduction.

7.5.5 Comparisons across study sites

At different locations, mixed-species group of the same species can differ in their frequency, characteristics, and functions. For example, mixed-species groups of redtail and blue monkeys (*Cercopithecus mitis*) in Kakamega Forest, Kenya, are more frequent than in Kibale Forest, Uganda, only 500 km away (Cords 1990). Furthermore, in Kakamega Forest, redtail monkeys are responsible for maintaining mixed-species groups and appear to benefit more than blue monkeys, while in Kibale Forest, the opposite seems to be true (Cords 1990). This variation may be attributable to ecological differences between the sites (e.g., climatic conditions or availability of food resources), differences in population structure (e.g., population density, home range sizes, or group sizes), and/or the presence of other primate species (Cords 1990). Mixed-species groups may also be influenced by anthropogenic impacts. For example, common dolphins (*Delphinus delphis*) in the Mediterranean form mixed-species groups with striped dolphins (*Stenella coeruleoalba*) more frequently in sites where they are uncommon, leading to the hypothesis that population declines are driving mixed-species group formation (Frantzis & Herzing 2002)

Humpback and bottlenose dolphin populations vary in their habitat, structure, and interactions with other species. Both species prefer shallow, inshore, tropical waters and occupy a variety of habitats, including coral lagoons, sandy embayments, and muddy estuaries (Parra et al. 2004, Parra & Jefferson 2018, Wang 2018). At other study sites around Australia, group sizes of both species are similar to those observed around the North West Cape (Chapters 4, 5, and 6, Corkeron 1990, Cagnazzi 2010, Parra et al. 2011, Fury et al. 2013, Hunt et al. 2017, Haughey et al. 2020), yet population densities are typically lower (Brown et al. 2016b, Hunt et al. 2017, Haughey et al. 2020). By studying mixed-species groups of humpback and bottlenose dolphins at other sites, such as Moreton Bay, Queensland, we will be able to conduct comparative studies to determine whether and how these ecological and demographic factors influence the frequency and nature of mixed-species groups.

An additional dynamic is presumably brought by the presence of a third delphinid species, such as the Australian snubfin dolphin (*Orcaella heinsohni*, hereafter "snubfin dolphin"), which also occurs in the shallow, coastal waters of northern Australia (Parra et al. 2011, Allen et al. 2012, Palmer et al. 2014). In Cleveland Bay, Queensland, humpback dolphins interact frequently with snubfin dolphins although, unlike in their interactions with bottlenose dolphins around the North West Cape, humpback dolphins are typically the aggressors (Parra 2005). Bottlenose dolphins have also been observed in mixed-species groups with snubfin dolphins in northwestern Australia (Allen et al. 2012, Brown et al. 2017). Evidently, both humpback and bottlenose dolphins interact, at least occasionally, with snubfin dolphins, but it is unknown how the presence of snubfin dolphins influences the way that humpback and bottlenose dolphins interact with each other.

Looking further afield, the range of the bottlenose dolphin extends from South Africa to Melanesia and Japan and overlaps with two other species of the *Sousa* genus: the Indian Ocean humpback dolphin and the Indo-Pacific humpback dolphin (*Sousa chinensis*) (Parra & Jefferson 2018, Wang 2018). Mixed-species groups of bottlenose dolphins and Indian Ocean humpback dolphins occur at several locations including Zanzibar (Stensland et al. 1998, 2003), South Africa (Koper & Plön 2016), and Mayotte (Kiszka 2007). Moreover, in Zanzibar, interactions between these species bear some resemblance to those observed in this study (Stensland et al. 2003). Further work is required to better understand mixed-species groups of bottlenose dolphins and Indian Ocean humpback dolphins and to determine whether and how bottlenose dolphins interact with Indo-Pacific humpback dolphins. Mixed-species groups of bottlenose dolphins and *Sousa* species provide an interesting opportunity to conduct comparative studies to determine the influence of various factors, including species, habitat, and location, on the potential benefits of mixed-species groups.

7.6 Conclusion

Mixed-species groups are a widespread but understudied aspect of delphinid behavioural ecology. By critically reviewing the literature, clarifying terminology, developing a conceptual framework, and applying novel methods, this thesis summarises our current knowledge of delphinid mixed-species groups and provides means to overcome some of the shortcomings that have thus far hindered research. Moreover, this thesis incorporates a study of an ideal model system consisting of the humpback and bottlenose dolphins that live, interact, and form mixed-species groups in the coastal waters of the North West Cape, Western Australia. This study provides valuable information on the frequency, characteristics, and functions of delphinid mixed-species groups. At the same time, it also raises further issues, questions, and challenges, undeniably demonstrating that there is plenty more to learn about delphinid mixed-species groups. Nevertheless, this thesis provides a solid platform to inspire and guide future studies, be they on humpback and bottlenose dolphins, other delphinid species, or other taxa, to surmount these obstacles and further our understanding of the characteristics and functions of mixed-species groups.

Supplementary Material

Appendix S1 – Chapter 2

Table S1.1 The adjectives, terms, and taxa used to create the search queries for the literature review on cetacean mixed-species groups.

Adjectives	Terms	Taxa
mixed species	group	cetacean
mixed-species	aggregation	whale
interspecific	association	dolphin
inter-specific	interaction	porpoise
interspecies	encounter	
inter-species		
heterospecific		
polyspecific		

Each *adjective* was joined with each *term* to form phrases which were then combined with the *taxa* in the following way:

(“*adjective*[i] + *term*[1 - 5]”) AND (cetacean OR whale OR dolphin OR porpoise)

This was repeated for each *adjective* to produce search queries e.g.:

("mixed species group" OR "mixed species aggregation" OR "mixed species association" OR "mixed species interaction" OR "mixed species encounter") AND ("cetacean" OR "whale" OR "dolphin" OR "porpoise")

Appendix S2 – Chapter 3

Table S2.1 Search query used for a literature review on the definitions of delphinid *groups*, *schools*, *parties*, and *pods*

Delphinid genera		Key terms	Subject area keywords
Orcaella	*Delphinus*	group	abundance
Orcinus	*Lagenodelphis*	school	assoc*
Globicephala	*Sousa*	party	behav*
Pseudorca	*Lissodelphis*	pod	conservation
Feresa	*Lagenorhynchus*		distribution
Peponocephala	*Cephalorhynchus*		ecology
Grampus			network
Sotalia			site fidelity
Steno			soci*
Tursiops			space use
Stenella			residenc*

The query is composed of three parts: the 17 delphinid genera, the four key terms, and subject area keywords. The asterisk is a wildcard character, thus soci* finds results for social, sociality, social network, etc.

The three parts (i.e., the genera, the key terms, and the subject area keywords) were joined in the following way:

TITLE-ABS-KEY (genera) AND TITLE-ABS-KEY (terms) AND TITLE-ABS-KEY (study areas)

This string was combined with limitations on language and document type to give the full query:

TITLE-ABS-KEY (orcaella OR orcinus OR globicephala OR pseudorca OR feresa OR peponocephala OR grampus OR sotalia OR steno OR tursiops OR stenella OR delphinus OR lagenodelphis OR sousa OR lissodelphis OR lagenorhynchus OR cephalorhynchus)

AND TITLE-ABS-KEY (group OR school OR party OR pod)

AND TITLE-ABS-KEY (abundance OR assoc* OR behav* OR conservation OR distribution OR ecology OR network OR "site fidelity" OR soci* OR "space use" OR residenc*)

AND LANGUAGE ("English") AND DOCTYPE ("ar") OR DOCTYPE ("ch")

Table S2.2 Online survey on the definition of delphinid groups, schools, parties, and pods

Information and Consent

In science, clear terminology provides a common basis of understanding, a solid foundation to develop concepts and theory, and facilitates scientific communication. In the literature on delphinid sociality, various definitions of group, school, party, and pod have been used to designate various concepts, often with inconsistent and unclear definitions. Variability among researchers and improper use of distinct terms generates confusion and hinders the development of comparative studies. Here we aim to investigate the definitions of these terms within our scientific community to assess which key criteria are more often used to define these terms, and work towards clearer terminology and suggestions for defining the term group and associated terms.

We would appreciate it if you would kindly take 10 – 15 minutes to complete the following survey regarding your opinions on this subject. Your responses will remain anonymous. Thank you very much for your participation.

Please see the Participant Information Sheet if you require more information.

Do you give consent to take part in this project?

- Yes, I consent
- No, I do not consent

Personal information

- What is your current role / position?
- Academic professor
- Postdoctoral researcher
- PhD student
- Masters student
- Undergraduate student
- Government researcher
- NGO researcher
- Private consultant
- other

What are your principal fields of study? (You may select more than one response)

- Ecology
- Physiology
- Behaviour
- Evolution
- Conservation
- Pathology and diseases
- Anthropogenic impacts
- other

How many years of experience do you have studying delphinids?

- less than 5 years
- 6 - 10 years
- 11 - 20 years
- more than 20 years

Which delphinid species have you mainly studied?

Definition

With regards to the study of wild delphinids, are you familiar with the term group?

- Yes
- No

Please define group.

Please list any scientific paper(s) that you use as a basis for your definition of group.

What difficulties have you experienced in applying this definition?

With regards to the study of wild delphinids, are you familiar with the term school?

- Yes
- No

Do you consider school to be a synonym of group?

- Yes
- No

Please define school.

Please list any scientific paper(s) that you use as a basis for your definition of school.

What difficulties have you experienced in applying this definition?

With regards to the study of wild delphinids, are you familiar with the term party?

- Yes
- No

Do you consider party to be a synonym of either of the following terms?

- group
- school
- neither

Please define party.

Please list any scientific paper(s) that you use as a basis for your definition of party.

What difficulties have you experienced in applying this definition?

With regards to the study of wild delphinids, are you familiar with the term pod?

- Yes
- No

Do you consider pod to be a synonym of any of the following terms?

- group
- school
- party
- none of the above

Please define pod.

Please list any scientific paper(s) that you use as a basis for your definition of pod.

What difficulties have you experienced in applying this definition?

Please be advised that once you continue you will not be able to change your answers.

Thank you for completing the survey.

If you have any additional comments, please write them below.

Table S2.3 Evaluation process used to assess the criteria employed in definitions of delphinid groups

Requirements for each criterion The definition refers explicitly to...	Criteria	Examples A group was defined as...
...the distance between the animals or the distance between the animals and some fixed point	spatial proximity	...all individuals within 10 m of any other member
...the behaviour of the animals	behaviour	...all individuals engaged in the same behaviour
...the movement and direction of the animals	movement and directionality	...all individuals that were moving in the same direction
...the number of animals that are present	number of individuals	...two or more individuals that were...
...the visual range of the observers	visual range of observers	...all individuals within visual range that were...
...interactions between the animals	interactions	...any individuals that were interacting
...the time when or the amount of time that the animals are present	temporal proximity	...individuals that were present at the same time and...
...the species that are present	species present	...individuals of the same species that were...

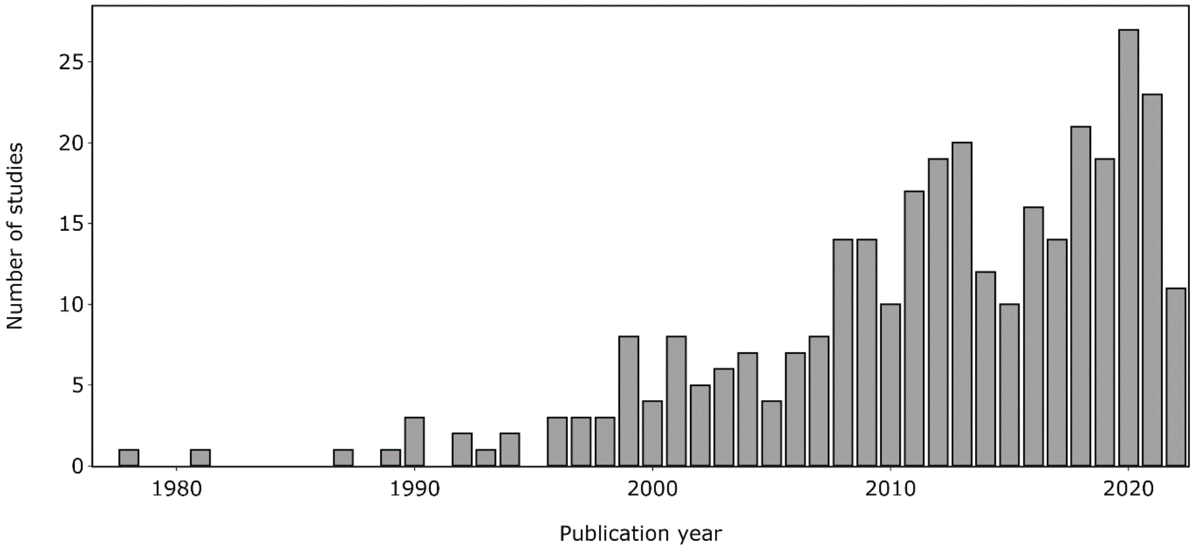

Figure S2.1 The publication year of the studies included in a review on the definition of delphinid groups

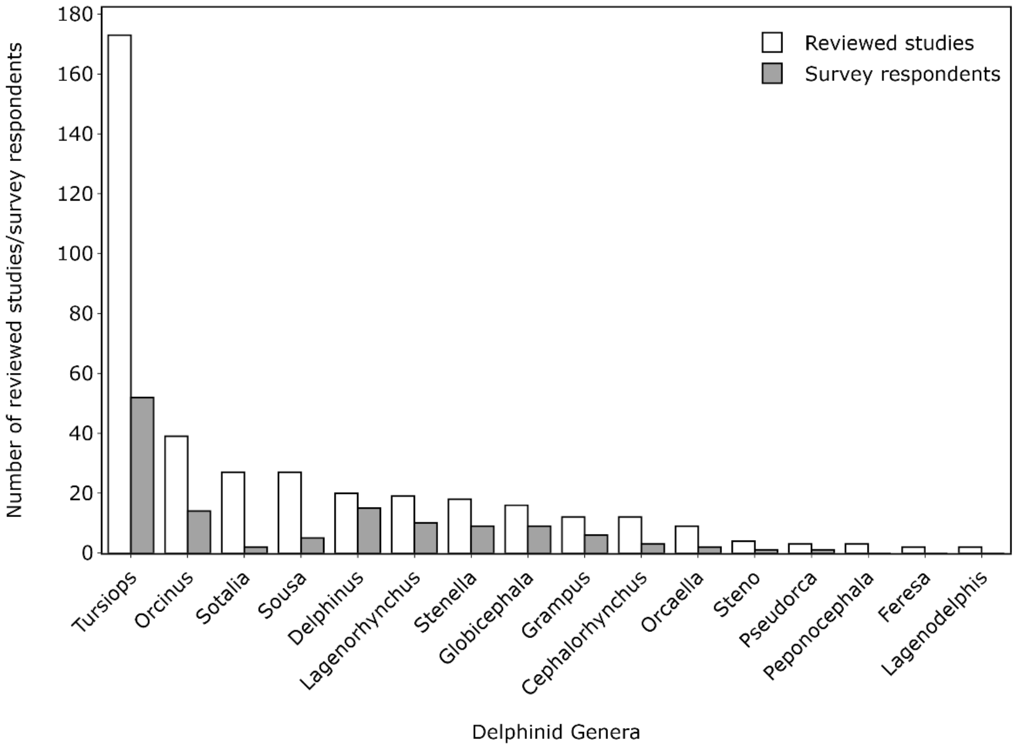

Figure S2.2 Number of reviewed studies and survey respondents that studied each of the listed delphinid genera.

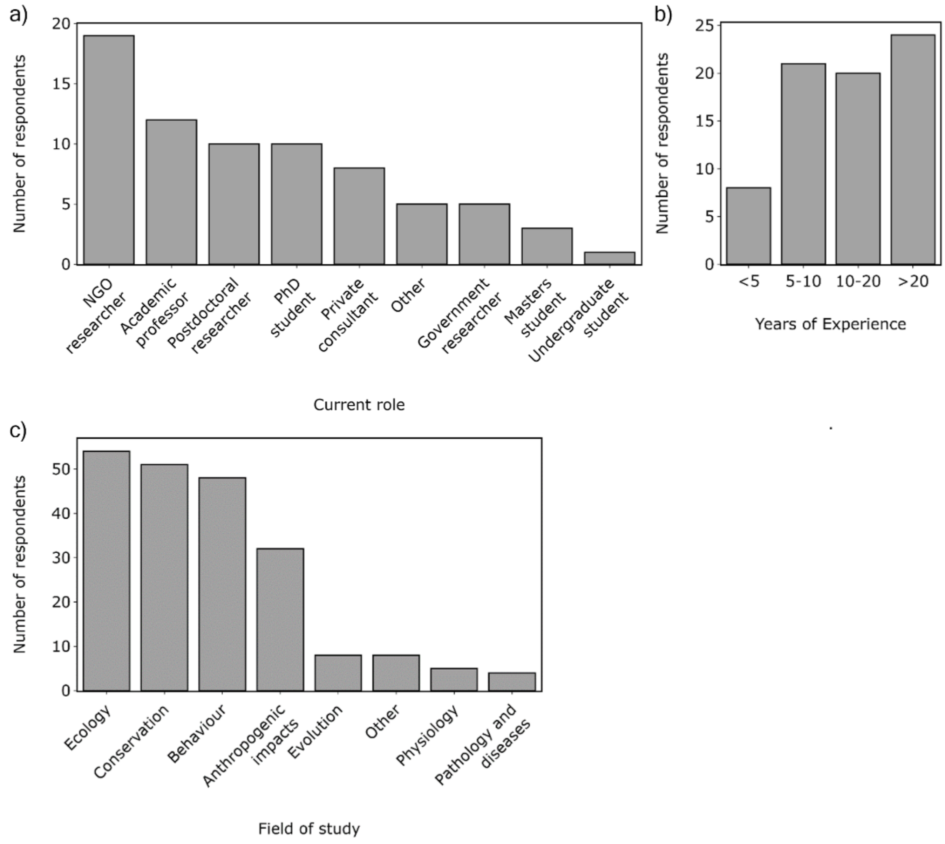

Figure S2.3 Details of the respondents to an online survey on the definition of delphinid groups showing (a) their current role, (b) their number of years of experience studying delphinids, and (c) their principal fields of study.

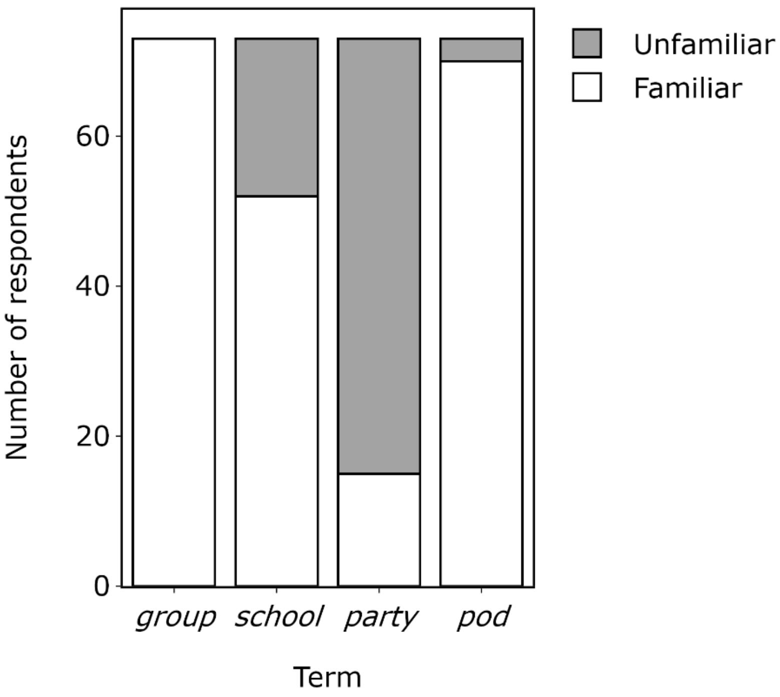

Figure S2.2 Number of respondents to an online survey of delphinid researchers who were familiar or unfamiliar with four key terms that are used to refer to delphinid groups.

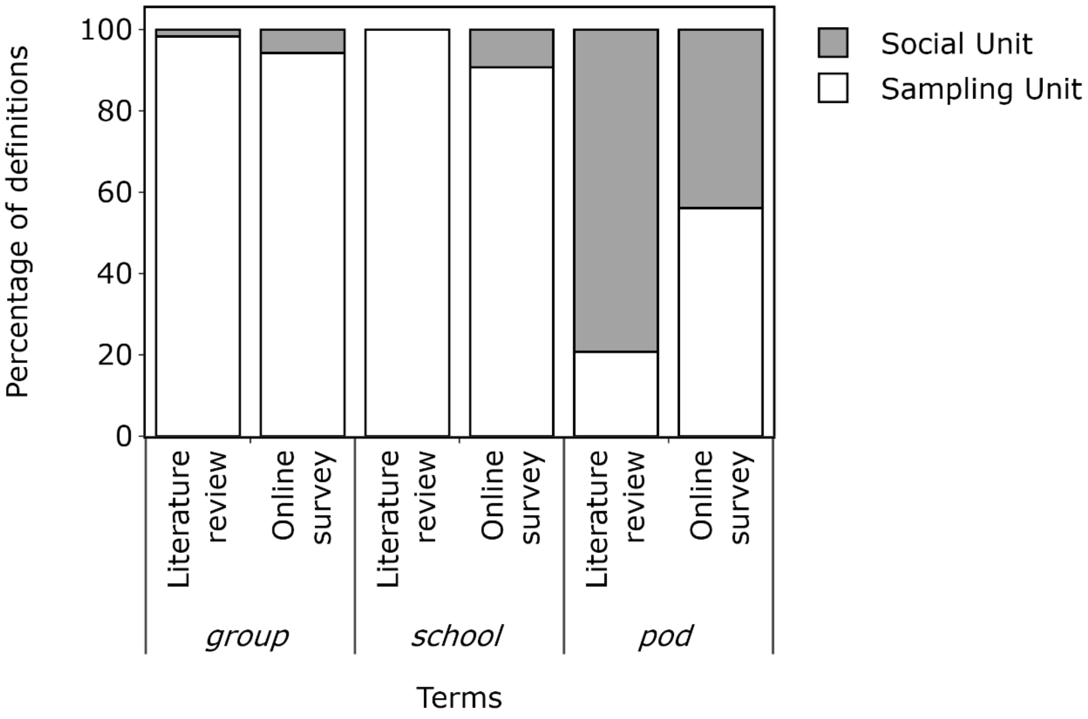

Figure S2.3 Percentage of definitions obtained from a review of the delphinid literature and an online survey of delphinid researchers that treated the terms *group*, *school*, and *pod* as sampling and social units.

Appendix S3 – Chapter 4

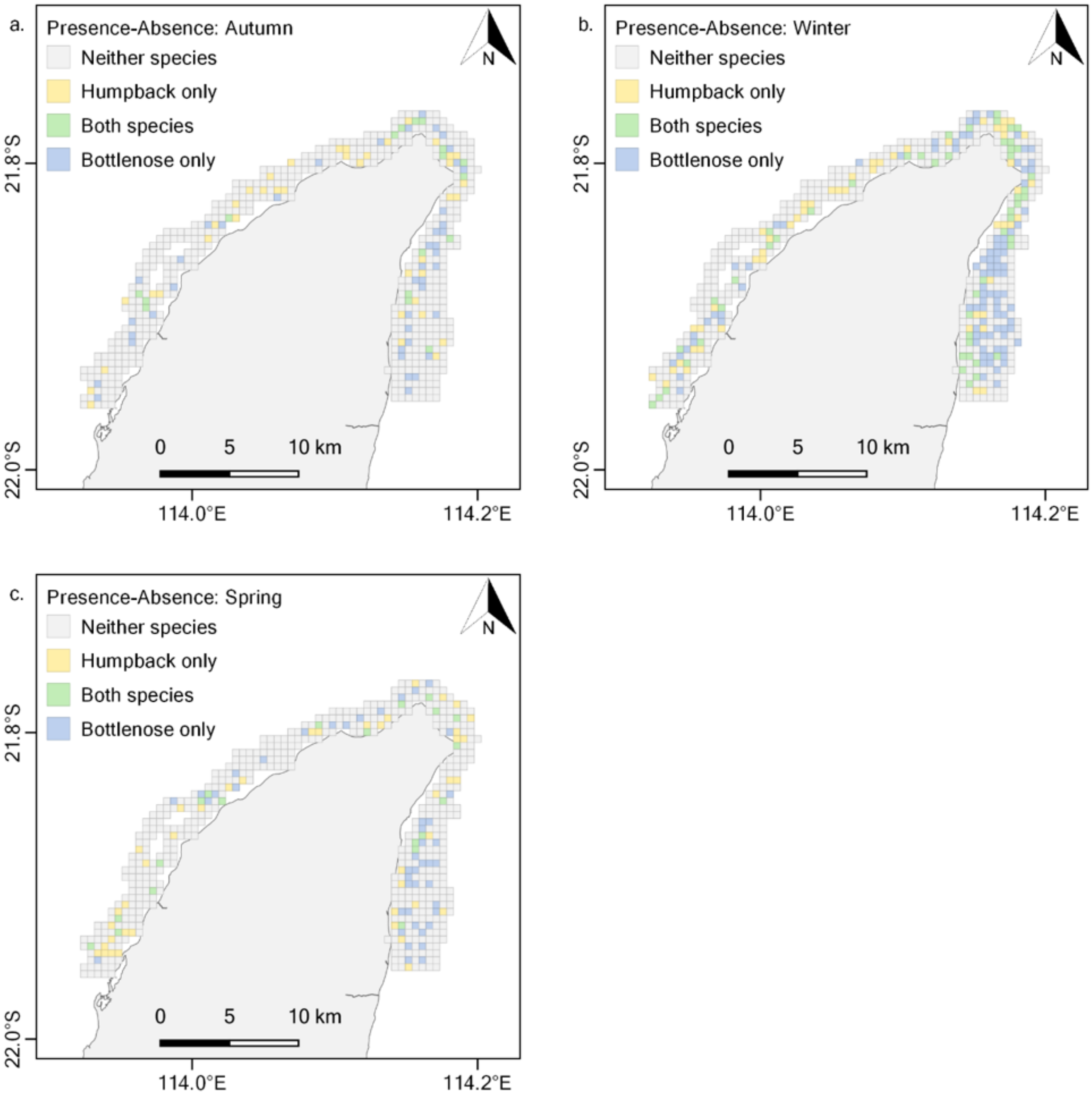

Figure S3.1 The presence-absence values of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in 540 grids of 500 x 500 m around the North West Cape, Western Australia, across three austral seasons – (a) autumn, (b) winter, and (c) spring – which were used as response variables in a joint species distribution model of their occurrence.

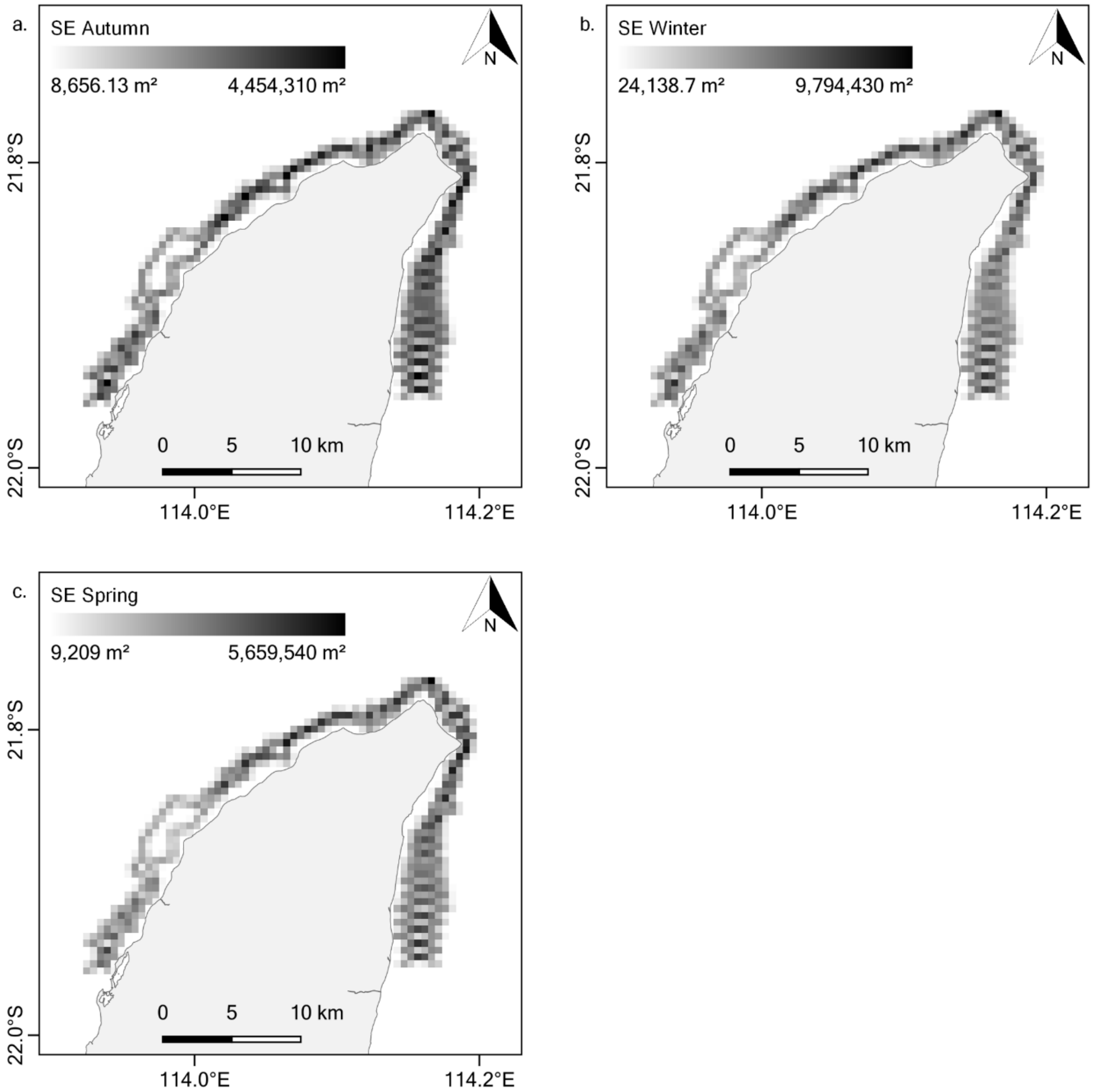

Figure S3.2 Cumulative survey effort (SE) over six years of surveys (2013-2015, 2018-2019, and 2021) across three austral seasons – (a) autumn, (b) winter, and (c) spring – in 540 grids of 500 x 500 m around the North West Cape, Western Australia, which was used as a predictor variable in a joint species distribution model of the occurrence of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). See Table 4.1 for details on how the values were calculated.

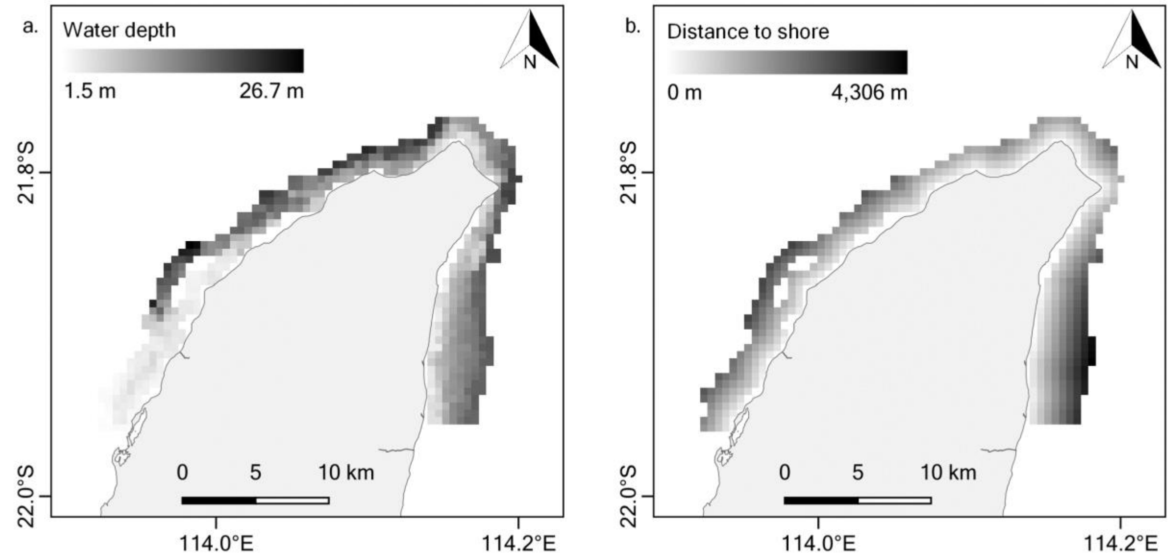

Figure S3.3 The environmental predictor variables – (a) water depth and (b) distance to shore – in 540 grids of 500 x 500 m around the North West Cape, Western Australia, which were included in a joint species distribution model of the occurrence of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*). See Table 4.1 for details on how the values were calculated.

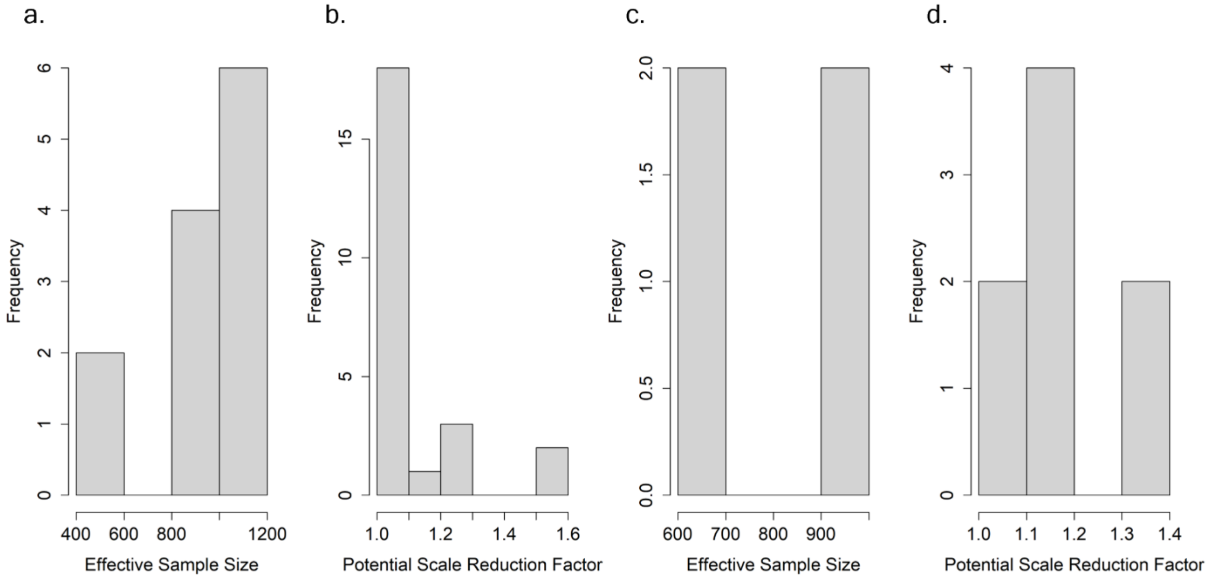

Figure S3.4 Diagnostic histograms for Markov chain Monte Carlo (MCMC) convergence for the joint species distribution model of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphin (*Tursiops aduncus*) occurrence around the North West Cape, Western Australia. The histograms show the effective sample sizes (a. and c.) and the potential scale reduction factors (b. and d.) for the beta parameters (i.e., the species responses to environmental variables; a. and b.) and the omega parameters (i.e., the species associations at the site level; c. and d.). The theoretical optimum for effective sample sizes is 1000 while potential scale reduction factors below 1.1 indicate a high level of model convergence.

Appendix S4 – Chapter 6

Table S4.1 Average behavioural bout lengths for Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in single-species sightings.

Behavioural state	Average bout length		Mean difference	95% CI	t	p	df
	Humpback	Bottlenose					
Foraging	43.2	54.1	-10.9	-18.7 to -3.1	-3.0	0.003	512.0
Milling	22.5	31.4	-8.9	-16.6 to -1.2	-2.7	0.008	156.7
Resting	36.4	60.5	-24.2	-38.5 to -9.9	-3.6	<0.001	178.7
Socialising	48.6	43.8	4.8	-6.9 to 16.5	0.8	0.443	102.6
Travelling	86.2	34.6	51.7	42.8 to 60.5	13.3	<0.001	787.0

Table S4.2 Average behavioural bout lengths for Australian humpback dolphins (*Sousa sahulensis*) in single- and mixed-species sightings.

Behavioural state	Average bout length		Mean difference	95% CI	t	p	df
	Single	Mixed					
Foraging	43.2	40	3.2	-8.0 to 14.5	0.6	0.555	110.8
Milling	22.5	21.9	0.6	-7.6 to 8.9	0.2	0.878	72.3
Resting	36.4	48.4	-12.0	-28.3 to 4.3	-1.3	0.205	39.6
Socialising	48.6	58.2	-9.6	-24.7 to 5.5	-1.4	0.177	150.5
Travelling	86.2	47.1	39.1	18.4 to 59.8	6.0	<0.001	126.6

Table S4.3 Average behavioural bout lengths for Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in single- and mixed-species sightings.

Behavioural state	Average bout length		Mean difference	95% CI	t	p	df
	Single	Mixed					
Foraging	54.1	40	14.1	0.9 to 27.3	2.7	0.008	96.8
Milling	31.4	21.9	9.5	-0.6 to 19.6	2.4	0.017	67.3
Resting	60.5	48.4	12.2	-11.1 to 35.5	1.2	0.236	54.4
Socialising	43.8	58.2	-14.4	-24.2 to -4.7	-2.8	0.006	285.8
Travelling	34.6	47.1	-12.6	-21.6 to -3.5	-2.2	0.031	77.0

Table S4.4 Comparison of behavioural budgets of Australian humpback (*Sousa sahulensis*) and Indo-Pacific bottlenose dolphins (*Tursiops aduncus*).

	Humpback	Bottlenose	Z	p-value
Foraging	16.8	30.9	7.801	<0.001
Milling	4.6	12.4	6.454	<0.001
Resting	7.5	13.5	4.521	<0.001
Socialising	4.6	19.2	10.319	<0.001
Travelling	66.5	24.1	20.666	<0.001

Table S4.5 Comparison of behavioural budgets of single- and mixed-species sightings of Australian humpback (*Sousa sahulensis*).

	Single	Mixed	Z	p-value
Foraging	16.8	16.7	0.000	1.000
Milling	4.6	6.3	1.145	0.252
Resting	7.5	6.5	0.506	0.613
Socialising	4.6	40.3	16.540	<0.001
Travelling	66.5	30.2	11.806	<0.001

Table S4.6 Comparison of behavioural budgets of single- and mixed-species sightings of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*).

	Single	Mixed	Z	p-value
Foraging	30.9	16.7	5.274	<0.001
Milling	12.4	6.3	3.156	0.002
Resting	13.5	6.5	3.510	<0.001
Socialising	19.2	40.3	8.313	<0.001
Travelling	24.1	30.2	2.319	0.020

Table S4.7 Comparison of standard and cumulative behavioural budgets of Australian humpback (*Sousa sahulensis*).

	Standard	Cumulative	Z	p-value
Foraging	16.8	16.8	0.000	1.000
Milling	4.6	5.0	0.349	0.727
Resting	7.5	7.3	0.126	0.900
Socialising	4.6	14.1	6.973	<0.001
Travelling	66.5	56.9	4.171	<0.001

Table S4.8 Comparison of standard and cumulative behavioural budgets of Indo-Pacific bottlenose dolphins (*Tursiops aduncus*).

	Standard	Cumulative	Z	p-value
Foraging	30.9	28.0	1.559	0.119
Milling	12.4	11.1	0.905	0.366
Resting	13.5	12.1	1.010	0.312
Socialising	19.2	23.5	2.606	0.009
Travelling	24.1	25.3	0.689	0.491

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