

Behavioural ecology of Irrawaddy, *Orcaella brevirostris* (Owen
in Gray, 1866), and Indo-Pacific humpback dolphins, *Sousa
chinensis* (Osbeck, 1765), in northeast Queensland, Australia: a
comparative study

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- Parra, G. J.**, P. J. Corkeron, and H. Marsh. 2004. The Indo-Pacific humpback dolphin, *Sousa chinensis* (Osbeck, 1765), in Australian waters: a summary of current knowledge. *Aquatic Mammals* **30**:195.

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ABSTRACT

Irrawaddy dolphins, *Orcaella brevirostris*, and Indo-Pacific humpback dolphins (hereafter humpback dolphins), *Sousa chinensis*, are two of the least known species of coastal dolphins found in the Indian and West Pacific Ocean region. Both species occur in sympatry throughout most of their range in Australian waters, where they have been little studied. As a result, the conservation status of Australian populations of Irrawaddy and humpback dolphins is unknown and conservation and management actions have been hampered by this lack of knowledge.

To overcome this lack of knowledge and improve the capacity to effectively conserve and manage Australian populations of Irrawaddy and humpback dolphins, this study aimed to contribute information on different aspects of their behavioural ecology. As both species co-occur throughout most of their range in Australian waters, an additional aim of this study was to analyse the degree of ecological separation between them. This comparative approach served two purposes: 1) to provide species-specific information on different aspects of the behavioural ecology (e.g., habitat use, social structure) of these species, and 2) to provide insights into the mechanisms promoting their coexistence.

Boat-based surveys were carried out in different areas along the east coast of Queensland between 1999-2002, focusing mainly in one area, Cleveland Bay Dugong Protected Area (hereafter referred as Cleveland Bay), where populations of both species are known to co-occur and where weather and logistical considerations allowed for almost year-round boat-based observations.

Analysis of data on the spatial distribution of Irrawaddy and humpback dolphin schools along different areas along the east coast of Queensland indicated that the distribution of Irrawaddy and humpback dolphins was strongly influenced by proximity to the coast, with both species occurring closer to land than would be expected under a random scenario. When comparing between species, Irrawaddy dolphins occurred closer to river mouths than humpback dolphins, but this interspecific difference was not constant across study areas. Based on the spatial distribution of both species in the areas surveyed, I found that the existing protected areas may not include the most critical habitats for Irrawaddy and humpback dolphins.

In Cleveland Bay, I found that Irrawaddy and humpback dolphins were present year round between 1999 and 2002. There was no evidence of variation in their occurrence with year or season. Irrawaddy and humpback dolphins used coastal

waters of Cleveland Bay mainly for foraging activities indicating this area represents an important feeding area within their home range.

I also found that Irrawaddy and humpback dolphins exhibit significantly different school dynamics, with Irrawaddy dolphins forming larger schools (mean \pm SE = 5.3 ± 0.35) than humpback dolphins (mean \pm SE = 3.5 ± 0.19). School of both species were mainly composed of adult individuals and, in proportion to the total number of animals within a school, Irrawaddy dolphins had a greater number of adults than humpback dolphin schools. Differences in school size and composition may be attributed to socioecological and phylogenetic factors. There is evidence from my studies that social as well as behavioural constraints may be responsible for these differences in school sizes.

Analysis of the relative use of space by both species using kernel methods showed that Irrawaddy and humpback dolphins do not use Cleveland Bay uniformly. The representative ranges (95% kernel range) of Irrawaddy and humpback dolphins were similar in size and location covering mainly the area between the Port of Townsville and the mouth of the Black River. The area around the Port of Townsville was used heavily by both species and represented a core area of use (50% kernel range) for both Irrawaddy and humpback dolphins. Irrawaddy dolphins had another core area between the mouths of the Bohle and Black Rivers. The behaviour of Irrawaddy and humpback dolphins within and outside their core areas was dominated by foraging and travelling activities. The 95% representative ranges of Irrawaddy and humpback dolphins showed considerable spatial overlap (81%). Additionally, the Utilization Distributions (UDs) of both species showed strong correlation ($r_s = 0.55$, $P < 0.05$), indicating strong concordance in the utilization patterns of shared areas by both species.

Despite considerable overlap and concordance in space use patterns, Irrawaddy and humpback dolphins showed different habitat preferences. Within their representative range Irrawaddy dolphins preferred shallow (0-2 m) waters with seagrass meadows, and occurred closer to river mouths than humpback dolphins. Humpback dolphins showed preference for deeper waters (2-5 m deep), followed by waters close to the coast, shallow waters (1-2 m deep) with no seagrass, and dredge channels (5-15 m deep). I propose that these differences in habitat preference are important factors promoting the coexistence of Irrawaddy and humpback dolphins.

I photo-identified 63 Irrawaddy dolphins and 54 humpback dolphins in Cleveland Bay. Analysis of monthly and annual sighting rates of identified animals indicated most individuals were not permanent residents in the bay, but most used the area from year to year. Irrawaddy and humpback dolphins identified in more than one year were mainly identified and re-identified during the dry season between May and September when greater survey effort was carried out. The low standard distance deviations of Irrawaddy and humpback dolphins sighted on eight or more occasions indicated that individuals of both species tended to come back to specific areas within Cleveland Bay. The observed sighting patterns of individual Irrawaddy and humpback dolphins fitted exponential models of emigration + reimmigration, indicating that some animals are permanent residents while others reimmigrate into the study area after certain periods of time. I suggest site fidelity patterns may reflect fluctuations in prey resource availability and levels of predation risk within Cleveland Bay.

The ranges of individual animals of both species sighted on eight or more occasions were similar in size; length and location. Individual ranges of both species extended over similar areas, covering mainly the stretch of coastline southeast and northwest of the Port of Townsville. This pattern of interspecific overlap in range patterns indicated a lack of species-specific territories.

Analysis of association patterns among identified individuals indicated that Irrawaddy and humpback dolphins were more frequently seen with a particular companion than would be expected by chance. Cluster analysis showed that individual Irrawaddy dolphins may form strong associations with more than one individual. Strong associations between humpback dolphins appeared to be limited to pairs of animals. The social model that best described this relationship suggested that at any one time an individual Irrawaddy dolphin had two types of associates: “constant companions” and “casual acquaintances”. The mean number of associates (constant companions + casual acquaintances) suggested by the model was approximately eight, of which four were constant companions. The fit of all social models to the data from humpback dolphins suggested a complex pattern of associations between individual humpback dolphins that may involve various associates with different levels of temporal stability. Differences in the social systems of both species could be explained by their different phylogenetic relationships among the Delphinidae and/or exposure to different levels of predation risk.

Photo-identification data collected between 1999-2002 and open mark-recapture models provided abundance estimates of Irrawaddy and humpback dolphins inhabiting the coastal waters of Cleveland Bay. Based on the open population model that best fitted the data, I estimated that less than a hundred individuals of each dolphin species used Cleveland Bay between 1999 and 2002. Based on historical data, it is certain that both species have been subject to anthropogenic mortality in the past due to entanglement in shark nets set for bather protection, and in commercial gillnets. A power analysis of the abundance estimates of both species and their associated variation indicated that, even with relatively unbiased and precise abundance estimates ($CV = 0.08$), population trends will be extremely difficult to detect within the space of a few years unless decreases in population size are worryingly high ($> 20\%$ p.a.). Because of their small population sizes, Irrawaddy and humpback dolphins are particularly vulnerable to local extinction. Detection of population trends should not be a necessary criterion for enacting conservation measures of both species.

My observations on the interspecific interactions among individuals of both species showed that encounters between Irrawaddy and humpback dolphins are common and predominantly of an aggressive/sexual nature in Cleveland Bay. The individuals involved in aggressive/sexual interactions appear to be mainly adult-male humpback dolphins and adult-female Irrawaddy dolphins with calves. During these encounters, humpback dolphins were dominant in initiating chasing, and seeking physical contact with Irrawaddy dolphins, while the latter tried to swim away or showed resistance to the interaction. I suggest the predominant aggressive/sexual interactions observed may reflect: 1) a physical training or skill development function that would have beneficial effects for future interactions between male humpback dolphins and their female conspecifics; 2) a mechanistic basis for some competitive interactions and patterns of resource partitioning between these two species of coastal dolphins; and 3) a relative scarcity of female humpback dolphins.

This study is the first comprehensive investigation of Irrawaddy and humpback dolphins in the Australian/Papua New Guinean region. The information collected provides a preliminary scientific basis for their future conservation and management. Given the certainty that the continuing loss of global biodiversity will be particularly severe in coastal ecosystems, the conservation and management of Irrawaddy and humpback dolphins will need to be intensive and adaptive. The potential for the conservation and management of Irrawaddy and humpback dolphin

populations along the Queensland coast is relatively good. However, in view of the concerns raised in this study about the long-term survival of these two species, and evidence that Australian populations of Irrawaddy and humpback dolphins represent different species/subspecies from populations elsewhere, future research directed at enhancing our ecological knowledge throughout Queensland and other areas of their range in Australia will be essential to inform their conservation.

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Chapter 1

The importance of comparative behavioural ecology studies in the conservation of coastal dolphin communities

In this chapter, I justify the importance of behavioural ecology studies for the conservation of coastal dolphins. I then describe the advantages of conducting comparative studies to define species-specific requirements and understand community structure. I provide background information on my study species, Irrawaddy and Indo-Pacific humpback dolphins, and outline the significance of this study for their conservation. Finally, I outline the aims and specific objectives of this thesis.

Chapter 1. The importance of comparative behavioural ecology studies in the conservation of coastal dolphin communities

1.1 Behavioural ecology studies: a critical resource for dolphin conservation

Delphinids represent a unique component of marine biodiversity. They are the most diverse and widespread of marine mammals, and (together with most cetaceans, and dugongs) the only mammals that live their entire lives at sea. In addition, delphinids represent one of the most socially-diverse and complex group of mammals, have cognitive abilities found only in few mammals species and, as upper level predators, play a significant role in the structure and function of marine communities (Bowen 1997, Connor et al. 1998, Whitehead et al. 2000b). For many humans, dolphins also have considerable economic value (e.g., dolphin watching industry), cultural and spiritual significance (e.g., subsistence hunting, local folklore), and symbolic value (e.g., to conservationists) (Whitehead et al. 2000b).

As long-lived upper level predators, most marine mammals, including dolphins, have evolved life history strategies predicated on extremely high levels of survivorship, particularly adult survivorship. Thus, they are unable to withstand high rates of natural (e.g., predation) or anthropogenic mortality (e.g., incidental catch in gillnets). Dolphins have long life spans, late maturity, low reproduction rates, low fecundity, and long parental care. These characteristics result in slow rates of population growth and vulnerability to rapid population declines (Taylor 2002). There is serious concern about the continued existence of many dolphin species in the wild, because of the increasing pressure of human activities on their natural environment. For example, as a result of unsustainable levels of mortality in gillnets, all populations

of Hector's dolphins (*Cephalorhynchus hectori*) in South Island, New Zealand, are considered endangered by the IUCN (Martien et al. 1999, Slooten et al. 2000).

Our lack of knowledge about the behavioural ecology of most dolphin species is one of the major obstacles to their effective conservation and management. The study of an organism's behavioural ecology can contribute greatly to its conservation and management (Sutherland 1998, Caro 1999, Anthony and Blumstein 2000).

Behavioural ecology aims to understand the way in which behaviour contributes to the survival and reproduction of individual animals under different ecological conditions (Krebs and Davies 1993). Thus behavioural ecology studies collect information on the behaviour, habitat use, movement patterns, and ecological interactions of individuals. In combination, these factors contribute to an individual's survival and reproductive success, and are vital for the conservation and management of any target species. For example, the design and location of areas to protect declining populations of dugongs (*Dugong dugong*) along the east coast of Queensland, Australia, relied heavily on information regarding their foraging behaviour, habitat requirements, and movement patterns (Marsh et al. 1999).

Among the great diversity of habitats that are inhabited by dolphins in the marine environment, the coastal area is most at risk from human activities (McIntyre 1999, Moore 1999). As a result, some species of coastal dolphins are among the most threatened species of cetaceans. However, they are also among the least known species of delphinids (Reeves et al. 2003). Human population growth has accelerated in coastal areas. In 1994, 37% of the world's population (5.62 billion) lived within 100 kilometers of a coastline, and 49% lived within 200 km from the coast (Cohen et al. 1997). Thus the conservation and long-term survival of coastal dolphins requires a comprehensive understanding of their behavioural ecology. Lack of knowledge about

the behavioural ecology of most coastal dolphins can be detrimental to their long-term survival as this uncertainty often leads to delays in conservation and management actions, calls for more research to be carried out, and/or implicit acceptance of the continuation of anthropogenic threats (Slooten et al. 2000, Thompson et al. 2000). For example, while concerns about the survival of riverine populations of Irrawaddy dolphins, *Orcaella brevirostris*, had been expressed since 1996 (Perrin et al. 1996), uncertainty about their ecology, behaviour, and mortality rates and causes, prevented any effective conservation initiatives. All Irrawaddy dolphin populations were considered *Data Deficient* by the IUCN until 2002. Recently, thanks to major efforts to study their distribution, abundance and habitat preferences (Stacey and Leatherwood 1997, Krieb 1999, 2002, Stacey and Hvenegaard 2002, Smith et al. 2003), all riverine populations of Irrawaddy dolphins are considered *Critically Endangered* and conservation actions are now underway and directed specifically at local populations.

Knowledge about the behaviour and ecology of coastal dolphins is essential to understand the functioning of their communities, their relationships with their environment, the effects of natural and human disturbance, and to develop more effective tools for their monitoring, recovery and protection. A better understanding of coastal dolphin communities also informs policy and management decisions regarding their status and conservation threats. In this context, studies on the behavioural ecology of rare or poorly known species of coastal dolphins are urgently needed, to provide the necessary information for interpreting current and future anthropogenic threats on populations and their environment.

1.2 Comparative studies: identifying species specific requirements

Studies on some of the best-known delphinids, including bottlenose dolphins (*Tursiops* spp.), and killer whales (*Orcinus orca*), have shown that their behavioural ecology can vary to a great extent within and among species. For example, studies of sympatric killer whales have shown great differences in their foraging behaviour and dispersal patterns. Resident populations of killer whales feed on fish, travel in long-term stable groups, and individuals never disperse from their natal group (Baird 2000). In contrast, transients specialize on marine mammal prey and disperse from their natal group. Similarly, there is substantial evidence for intra and interpopulation differences in the foraging behaviour, habitat use, movement patterns, and social structure of bottlenose dolphins (Shane et al. 1986, Connor et al. 2000b). These intra- and interspecific variations in behaviour indicate that we need to be cautious about generalizing behavioural traits from one population or from one species to another.

The conservation of coastal dolphins has primarily been driven by studies on bottlenose dolphins. Bottlenose dolphins are widespread throughout coastal tropical and temperate waters of the world. Studies on these species have provided the most detailed information available about the behavioural ecology of any delphinid. As a result, bottlenose dolphins have been used frequently as focal (i.e., flagship, umbrella, keystone, or indicator species) species and models for the development of inshore dolphin conservation strategies (e.g., Wilson et al. 1999, Thompson et al. 2000, Wilson et al. 2004). Although this approach is currently appropriate given the lack of information for most other species, it does not provide a sound scientific basis for the conservation of poorly known coastal delphinids that occur in similar environments. Focusing conservation and management strategies on a single focal species risks harming others that may not share common requirements (Simberloff 1998).

In the light of the increasing threats faced by inshore species, as well as the great variability and plasticity found in their behaviour and adaptations, it is obvious that their conservation would benefit from taking these biological differences into account. Comparative studies of intraspecific and interspecific patterns among delphinids will be fundamental in this process. These studies provide the means to identify species-specific features (e.g., social structure) and requirements (e.g., habitat preferences) that will aid in the development of multispecies conservation approaches. Additionally, comparative studies also have the power to provide theoretical insights into the ecological interactions structuring dolphin communities that co-occur in the same immediate habitat (e.g., sympatric coastal dolphins).

1.3 Interspecific comparisons: understanding coexistence

All natural ecosystems are composed of assemblages of coexisting species. The ecological interactions (e.g., competition and predation) occurring between these coexisting species have a strong influence on the structure and functioning of animal communities, and thus are in part responsible for maintaining species diversity (Chesson 2000). Therefore, understanding the ecological and behavioural mechanisms that mediate the coexistence of species is of central importance to ecology and conservation biology.

The coexistence of similar species in ecological communities can be explained via a suite of different mechanisms (Tokeshi 1999, Chesson 2000). Most of these mechanisms are characterized by different forms of resource partitioning, mainly along the axes of space, time and diet. Thus, the traditional approach to the study of species coexistence has been to measure the degree of overlap in resource use along these axes between sympatric species. Based on quantitative differences along these axes, coexistence among sympatric mammals has been commonly explained by

resource partitioning in the form of space use and habitat selection (Kotler and Brown 1988, Johnson and Franklin 1994, Johnson et al. 2000, Jones and Barmuta 2000, Kalcounis-Ruppell and Millar 2002), and differences in food habits (Tatara and Doi 1994, Medina 1997, Neale and Sacks 2001, Juarez and Marinho 2002, Loveridge and Macdonald 2003). In this sense, environmental heterogeneity plays a key role in promoting species coexistence by providing different opportunities for species to segregate in space and time (Chesson 1985, Tilman and Kareiva 1997, Tokeshi 1999).

Many species of delphinids co-occur in the same immediate habitat. They may even occur in mixed-species schools. For instance, in the Gulf of Corinth, Greece, four dolphin species including striped dolphins (*Stenella coeruleoalba*), short-beaked common dolphins (*Delphinus delphis*), Risso's dolphins (*Grampus griseus*) and bottlenose dolphins (*Tursiops truncatus*) occur in sympatry and interspecific interactions are common and apparently complex (Frantzis and Herzing 2002). In the Bahamas, Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins have overlapping ranges and different types of association interactions (e.g., affiliative and/or aggressive) between both species have been recorded (Herzing and Johnson 1997). Similar coexisting assemblages involving different oceanic dolphin species have also been found in the Gully-Nova Scotia (Gowans and Whitehead 1995); the Galapagos (Smith and Whitehead 1999); Gulf of Mexico (Mullin et al. 1994); the eastern tropical Pacific (Au and Perryman 1985); and the western tropical Indian Ocean (Ballance and Pitman 1998).

Despite the recognition of these coexisting communities, few studies have gone beyond recording their occurrence. Studies need to be carried out to provide insights into the mechanisms that promote such coexistence (e.g., Gowans and Whitehead 1995, Barros and Cockcroft 1999). The reason for this lack of study is that

most behavioural ecology studies on delphinids have focused on a single species instead of assemblages of coexisting species. As a result questions such as “how much do coexisting delphinids overlap or differ in their resource use?” remain unanswered. Understanding how delphinids occupying similar environments coexist is a fundamental step towards the conservation and management of multispecies communities.

1.4 Irrawaddy and Indo-Pacific humpback dolphins: the research subjects

This thesis is about the behavioral ecology of coexisting populations of Irrawaddy dolphins, *Orcaella brevirostris* (Owen in Gray, 1866), and Indo-Pacific humpback dolphins, *Sousa chinensis* (Osbeck, 1765), two of the least known species of coastal dolphins found in the Indian and West Pacific Ocean region (Fig. 1.1 and Fig. 1.2). Because of rapidly increasing human populations throughout the coastal areas of this region, the prospects for the long-term survival of Irrawaddy and Indo-Pacific humpback dolphins are considered poor (Perrin et al. 1996). A recent collection of reviews regarding the current state of knowledge throughout the range of these species indicated that, although great advances have been made towards improving our knowledge on these two dolphin species, both remained poorly studied throughout most of their geographical range (Jefferson and Smith 2002, Thomas and Jefferson 2004). This was particularly the case for Australian populations of both species (see Chapter 2).

This study aimed to contribute information about the behavioural ecology of Irrawaddy and Indo-Pacific humpback dolphins in Australian waters, where the conservation status of both species is unknown. Irrawaddy and Indo-Pacific humpback dolphins occur in sympatry throughout most of their range in Australian

waters (Fig 1.2), therefore an additional aim of this study was to analyse the degree of ecological separation between them. This comparative approach served two purposes: 1) to provide species-specific information on different aspects of the behavioural ecology (e.g., habitat use, social structure) of these species, and 2) to provide insights into the mechanisms promoting their coexistence. This approach has the potential to enhance our ability to conserve and manage both species by taking into account biological differences between them and by advancing our understanding of the forces structuring their communities.

In recognition of the poor state of knowledge of both species in Australian waters, I began this study by reviewing all available data on their distribution and conservation threats in this region. These reviews reaffirmed the importance of the coastal waters along the east coast of Queensland as important habitat for both species and the urgent need for ecological studies in Australia (Parra et al. 2002, Parra et al. 2004). Accordingly, I carried out boat-based surveys to collect data on different aspects of the behavioural ecology of Irrawaddy and Indo-Pacific humpback dolphins along the east coast of Queensland. I focused mainly in one area, Cleveland Bay, where populations of both species are known to co-occur and where weather and logistical considerations allowed for almost year-round boat-based observations. Through the remainder this introductory chapter, I present the specific objectives of this study and explain the outline of this thesis.

a) Irrawaddy dolphin, *Orcaella brevirostris*



b) Indo-Pacific humpback dolphin, *Sousa chinensis*



Figure 1.1 Irrawaddy dolphin (a) and Indo-Pacific humpback (b) dolphins from Cleveland Bay, Queensland, Australia.

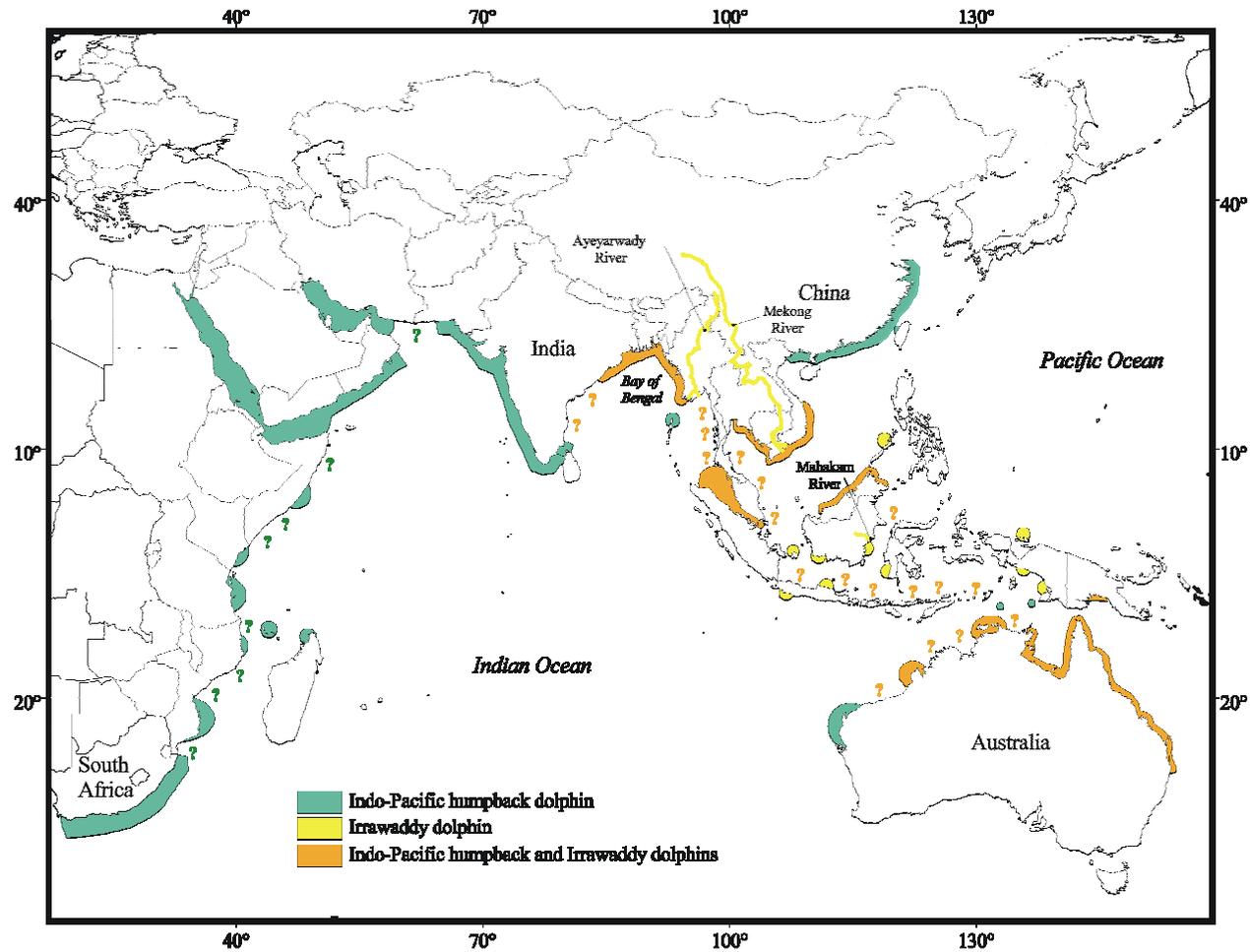


Figure 1.2 Approximate geographic distribution of Irrawaddy and Indo-Pacific humpback dolphins based on Jefferson and Karczmarski (2001); Stacey and Leatherwood (1997); Stacey and Arnold (1999). (?) indicate areas of probable, but unconfirmed distribution of Indo-Pacific humpback dolphins; and (?) indicate areas of probable but unconfirmed distribution of both species.

1.5 Research aims and thesis structure

This thesis had two major aims:

1. To improve our ability to conserve and manage Australian populations of Irrawaddy and Indo-Pacific humpback dolphins
2. To provide insights into the underlying mechanisms mediating the coexistence of Irrawaddy and Indo-Pacific humpback dolphins

In order to achieve these aims, my study had eight specific objectives each related to a chapter of my thesis. The structure of how each of these objectives and chapters relates to my two aims is represented in Figure 1.3. (page 16)

Objective 1. Review the current state of knowledge of Irrawaddy and Indo-Pacific humpback dolphins in Australian waters (Chapter 2)

In Chapter 2, I provide a review of the ecology and conservation status of Irrawaddy and Indo-Pacific humpback dolphins, with emphasis on Australian populations. I identify their major conservation threats and research needs in Australian waters.

Objective 2. Investigate the spatial distribution patterns of Irrawaddy and Indo-Pacific humpback dolphins in northeast Queensland (Chapter 3)

In Chapter 3, I use data collected during boat-based line transect surveys in two areas along the northeast Queensland coast to investigate the spatial distribution patterns of Irrawaddy and Indo-Pacific humpback dolphins. I use Geographic Information Systems (GIS), randomization techniques and Mantel tests to examine the relationship between the spatial distribution of Irrawaddy and Indo-Pacific humpback dolphins and three simple, readily quantified, environmental variables: distance to land, distance to river, and water depth. The spatial distribution patterns in relation to the environmental variables are used as a framework to assess the level of

protection offered in the study areas to Irrawaddy and Indo-Pacific humpback dolphins.

Objective 3. Investigate the occurrence patterns and school dynamics of Irrawaddy and Indo-Pacific humpback dolphins in Cleveland Bay (Chapter 4)

In Chapter 4, I use information collected in Cleveland Bay between 1999 and 2002, to identify patterns in the occurrence and school dynamics (i.e., school size and age composition) of Irrawaddy and Indo-Pacific humpback dolphins. I determine if their patterns of occurrence, school size and age composition are related to seasonal changes in the environment. Comparisons are made to determine interspecific differences and similarities in occurrence and school dynamics. This chapter also outlines the main methodology used for the boat-based surveys in Cleveland Bay.

Objective 4. Determine the space use patterns and habitat preferences of Irrawaddy and Indo-Pacific humpback dolphins in Cleveland Bay (Chapter 5).

Chapter 5 provides a quantitative assessment of the relative use of space and habitat preferences of Irrawaddy and Indo-Pacific humpback dolphins in Cleveland Bay. I identify areas of high and representative use, the behavioural activities associated with these areas, and the degree of interspecific overlap and concordance in space use. I also assess interspecific differences in habitat preferences.

Objective 5. Assess the site fidelity, residence times, and ranging patterns of Irrawaddy and Indo-Pacific humpback dolphins in Cleveland Bay (Chapter 6).

In Chapter 6, I use sighting data of identified individuals of both species to compare their sighting patterns, residence times, and range sizes. I determine annual and monthly sighting patterns for each identified individual, and their fidelity towards specific areas within Cleveland Bay. I use exponential mathematical models and the sighting data to assess the temporal patterns of residence, and residence times inside

and outside Cleveland Bay. I use minimum convex polygon techniques to assess range sizes and overlap within and among individual Irrawaddy and Indo-Pacific humpback dolphins. This chapter also outlines the photo-identification methodology used during the boat-based surveys carried out in Cleveland Bay.

Objective 6. Investigate the social structure of Irrawaddy and Indo-Pacific humpback dolphins (Chapter 7)

Chapter 7 provides an assessment of the association patterns between identified individuals of Irrawaddy and Indo-Pacific humpback dolphins. I assess the temporal variation in association patterns and apply mathematical models representing different social organizations to assess the type of association that best describes the social structure of Irrawaddy and Indo-Pacific humpback dolphins.

Objective 7. Estimate the population size of Irrawaddy and Indo-Pacific humpback dolphins inhabiting Cleveland Bay (Chapter 8)

In Chapter 8, I use open mark-recapture population models to estimate the abundance of Irrawaddy and Indo-Pacific humpback dolphins in Cleveland Bay. I review and evaluate model assumptions. Finally, I discuss the implications of the abundance estimates obtained to the conservation of these two dolphin species.

Objective 8. Describe behavioural interspecific interactions that may occur between Irrawaddy and Indo-Pacific humpback dolphins (Chapter 9)

Chapter 9 provides the first description and quantitative assessment of behavioural interactions between free ranging Irrawaddy and Indo-Pacific humpback dolphins. I suggest possible explanations for these interactions and their potential implications for the structure and functioning of coexisting communities of Irrawaddy and Indo-Pacific humpback dolphins.

Finally in Chapter 10, I provide a summary of the major results of this study and discuss these results in relation to their contribution to the conservation and management of Irrawaddy and Indo-Pacific humpback dolphins. I discuss how my results have contributed towards the understanding of the coexistence of Irrawaddy and Indo-Pacific humpback dolphins, and outline and prioritize future research directions for their conservation and management.

All data chapters (Chapters 3-9) of this thesis have been written in a format to facilitate publication in peer review journals as recommended by the James Cook University PhD Thesis Guide within the Handbook for Research Higher Degree Students 2000. Therefore, some overlap between each of these chapters has been unavoidable. Additionally, as it is unrealistic to expect a reader to read the whole thesis in one sitting, this overlap allows each chapter to be read as a stand-alone document. The title page of each chapter is on separate blue coloured paper to allow reader to locate chapters with ease. All tables have been placed at the end of each chapter to minimize interruption to the flow of the text. The table pages are printed on yellow colour paper to make them easy to locate.

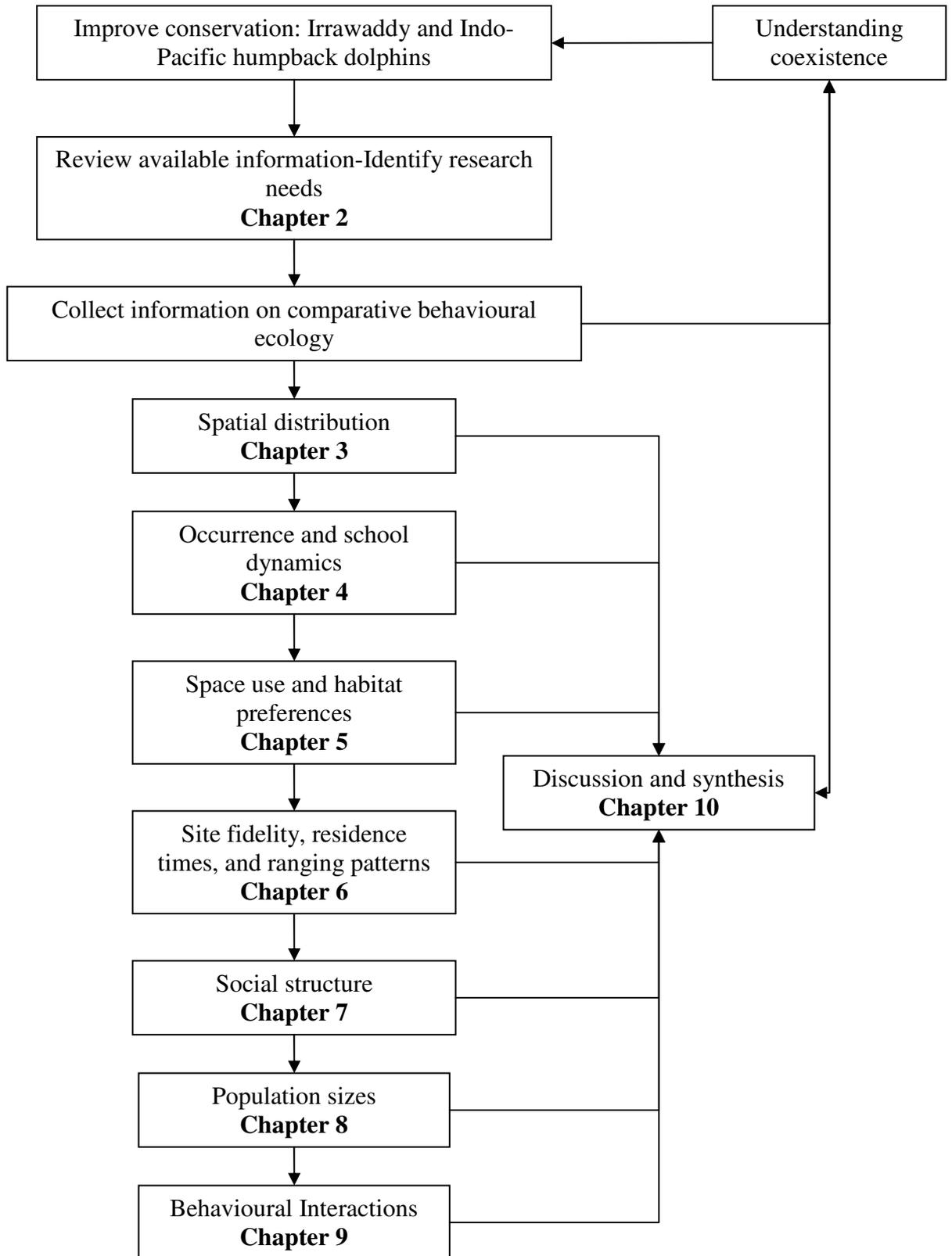


Figure 1.3 Diagram of thesis structure.

Chapter 2

Irrawaddy and Indo-Pacific humpback dolphins in Australian waters: a review of current knowledge

In this chapter, I provide a review of the ecology and conservation status of Irrawaddy and Indo-Pacific humpback dolphins, with emphasis on Australian populations. I identify their major conservation threats and research needs in Australian waters.

Chapter 2. Irrawaddy and Indo-Pacific humpback dolphins in Australian waters: a review of current knowledge

2.1 Introduction

As explained in Chapter 1, coastal ecosystems are coming under increasing pressure from expanding human populations and associated coastal zone development (Clark 1998, Hinrichsen 1998). Given their close proximity to human concentrations, many coastal cetaceans are especially vulnerable to human activities in, and adjacent to, the coastal zone. The conservation of these species often requires the mitigation and regulation of a variety of threats, including incidental catches in gillnets, shark nets set for bather protection, habitat degradation, and pollution (Perrin et al. 1996, Perrin 1999).

Irrawaddy dolphins, *Orcaella brevirostris*, and Indo-Pacific humpback dolphins, *Sousa chinensis*, occur in the tropical-subtropical waters of the Indo-West Pacific region (see Figure 1.2 in Chapter 1). Irrawaddy dolphins range from the Bay of Bengal in India, to the northeastern Australian coast (Stacey and Arnold 1999). Riverine populations of Irrawaddy dolphins occur in the Ayeyarwady (formerly known as the Irrawaddy River), Mekong, and Mahakam rivers. They can also be found in completely or partially isolated brackish or freshwater bodies including Chilka Lake and Songkla Lake. Indo-Pacific humpback dolphins are strictly marine and have been recorded from the west shores of South Africa, India, Thailand, northern East China Sea and southwards to the Australian northern coast (Jefferson and Karczmarski 2001).

Because of the increasing pressure from expanding human populations throughout the Indo-Pacific especially in coastal zones, the protection of high quality habitat for coastal populations of Irrawaddy and Indo-Pacific humpback dolphins

appears uncertain (Perrin et al. 1996). Despite these concerns, both species have been little studied throughout their range. Most studies about the behaviour and ecology of Indo-Pacific humpback dolphins have been carried out in South Africa (Saayman and Tayler 1979, Karczmarski et al. 1997, Karczmarski 1999, Karczmarski and Cockcroft 1999, Karczmarski et al. 1999a, Karczmarski et al. 1999b, Karczmarski et al. 2000a, Karczmarski et al. 2000b, Atkins et al. 2004) and China (Jefferson and Leatherwood 1997, Parsons 1998a, Jefferson 2000, Hung and Jefferson 2004). Studies on Irrawaddy dolphins have focused mainly on the ecology of riverine populations (Kreb 1999, 2002, Smith and Hobbs 2002), whereas the coastal, and estuarine populations remain largely unknown (Freeland and Bayliss 1989, Dolar et al. 2002).

In Australia, Irrawaddy and Indo-Pacific humpback dolphins have been recorded mostly in the northern regions including the coastal waters of Queensland, Northern Territory, and Western Australia (Fig. 2.1). Australian waters have long been recognized as a stronghold for populations of Irrawaddy and Indo-Pacific humpback dolphins, as Australia is one of the few developed nations in the Indo-Pacific region with a sparsely populated coastline (Perrin et al. 1996). However, both species have been little studied in Australia and the capacity to conserve and manage local populations is limited. The Action Plan for Australian Cetaceans (written in 1994) listed Irrawaddy and Indo-Pacific humpback dolphins as “insufficiently known”, a category that may include “endangered” or “vulnerable” species by virtue of their inshore distribution and close proximity to potentially detrimental human activities (Bannister et al. 1996)

In this chapter, I review the current knowledge on Indo-Pacific humpback dolphins in Australian waters and the relevance of this information to their conservation. The information available is limited, and much research is needed

before the status of Irrawaddy and Indo-Pacific humpback dolphins can be assessed properly. This thesis addresses this knowledge gap. In order to develop effective conservation measures for both species in Australian waters, an understanding of their distribution, habitat preferences, movement patterns, relative abundance and levels of anthropogenic mortality is required as a matter of urgency. At present, it appears that populations are small and localized, and are under pressure from human activities in coastal areas.

2.2 Review of current knowledge

2.2.1 Taxonomy

Genetic and morphological evidence suggest that Irrawaddy and Indo-Pacific humpback dolphins belong to the family Delphinidae (Arnold and Heinsohn 1996, LeDuc et al. 1999). However, the position of both genera within the family Delphinidae is still unresolved. Irrawaddy dolphins have been considered a member of the family Monodontidae, which includes the beluga *Delphinapterus* and narwhal *Monodon*. However, a cladistic analysis of osteological and morphological data (Arnold and Heinsohn 1996) as well as genetic data (Gretarsdottir and Arnason 1992, LeDuc et al. 1999) all provides strong support for inclusion of *Orcaella* within the family Delphinidae. The genetic data further suggest that *Orcaella* is closest to the killer whale *Orcinus* (Arnason and Gullberg 1996, LeDuc et al. 1999). Indo-Pacific humpback dolphins were thought initially to be related to *Sotalia*, a small delphinid that inhabits coastal and riverine waters of South America, and *Steno*, an oceanic dolphin species (Perrin 1989). However, molecular studies suggest that Indo-Pacific humpback dolphins are more related to tropical oceanic dolphin species including those of the genera *Stenella*, *Delphinus*, *Tursiops*, and *Lagenodelphis* (LeDuc et al. 1999).

The taxonomic status, systematic relationships, and population structure of both species at the intraspecific level, also remains unresolved. In the case of Irrawaddy dolphins, the present consensus is to recognize *O. brevirostris*, as the only species in this genus (Rice 1998). However, studies of skull morphology, including specimens throughout the species range, indicated taxonomic separation of Australia/New Guinea populations at the subspecies or even species level (Beasley et al. 2002a). Beasley, Robertson and Arnold, in a study recently accepted for publication, review all the morphological and genetic data and propose that the Australian/New Guinea populations be recognized as a distinct species, which they formally describe (Beasley and Arnold, personal communication, 2005).

There are different points of view regarding the taxonomy of the Indo-Pacific humpback dolphin genus, *Sousa*, ranging from acceptance of three nominal species *S. chinensis* (Pacific Ocean), *S. plumbea* (Indian Ocean), and *S. teuszii* (Atlantic Ocean) (Ross et al. 1994, Rice 1998) to recognition of only a single, variable species, *S. chinensis* (Ross et al. 1995, Cockcroft et al. 1997). Recent studies on skull morphology support the division of the genus into the *chinensis*, *plumbea*, *teuszii* forms, however patterns of cranial variation were conservative and no taxonomic revision were recommended (Jefferson 2004). Current genetic studies of the genus *Sousa* indicate that Indo-Pacific humpback dolphins in Australian waters may represent a different species/subspecies from populations elsewhere (Rosenbaum et al. 2003).

In summary, there is accumulating evidence that Irrawaddy and Indo-Pacific humpback dolphins in Australia/Papua New Guinean waters may represent different species/subspecies from populations elsewhere. In this context, Irrawaddy and Indo-Pacific humpback dolphins have extremely high biodiversity value as they are

expected to be recognised as the only endemic species of dolphins found in Australian/Papua New Guinean waters.

2.2.2 Distribution

Irrawaddy and Indo-Pacific humpback dolphins occur in sympatry throughout most of their range in Australian waters (Fig. 2.1). Irrawaddy dolphins have been recorded from Broome (17° 57'S, 122° 14'E) in Western Australia, along the northern coastline near Darwin and the Gulf of Carpentaria, and off the eastern coast as far south as the Brisbane River (27° 32'S, 152° 49'E) (Stacey and Arnold 1999). Indo-Pacific humpback dolphins have a similar range extending from approximately the Queensland - New South Wales border (31° 27'S, 152° 55'E) in the east to Exmouth Gulf (21° 56'S, 114° 07'E) in the west (Corkeron et al. 1997). Strandings, museum specimen records, and unpublished aerial and opportunistic boat survey sightings of Irrawaddy and Indo-Pacific humpback dolphins in Australian waters support this general distribution (Fig. 2.1, Appendix 1 to 4).

Sightings which extend the range of Indo-Pacific humpback dolphins have been reported in Ningaloo Reef (Preen 1995) and Shark Bay (Preen 1995) (Fig. 2.1). Sightings of Indo-Pacific humpback dolphins in the Ningaloo Reef region appear to be common (G. Ross, Environmental Protection Agency, personal communication, 2002) whereas in Shark Bay, the site of an extensive long-term study of inshore bottlenose dolphins, sightings are rare (P. Berggren, University of Stockholm, personal communication, 2002). Off the east and northern coast of Queensland the distribution of both species appears to be continuous, with the range of Indo-Pacific humpback dolphins extending further southeast into Moreton Bay. Indo-Pacific humpback dolphins are permanent residents in Moreton Bay, while Irrawaddy dolphins are occasional visitors to this area (Paterson et al. 1998, Chilvers et al. 2005).

The paucity of records for areas between the Gulf of Carpentaria in the north, and Ningaloo Reef in the west is likely to be a result of the remoteness and lack of research effort in this region, rather than a hiatus in the distribution of both species. The occurrence of both of these species in these areas requires further investigation.

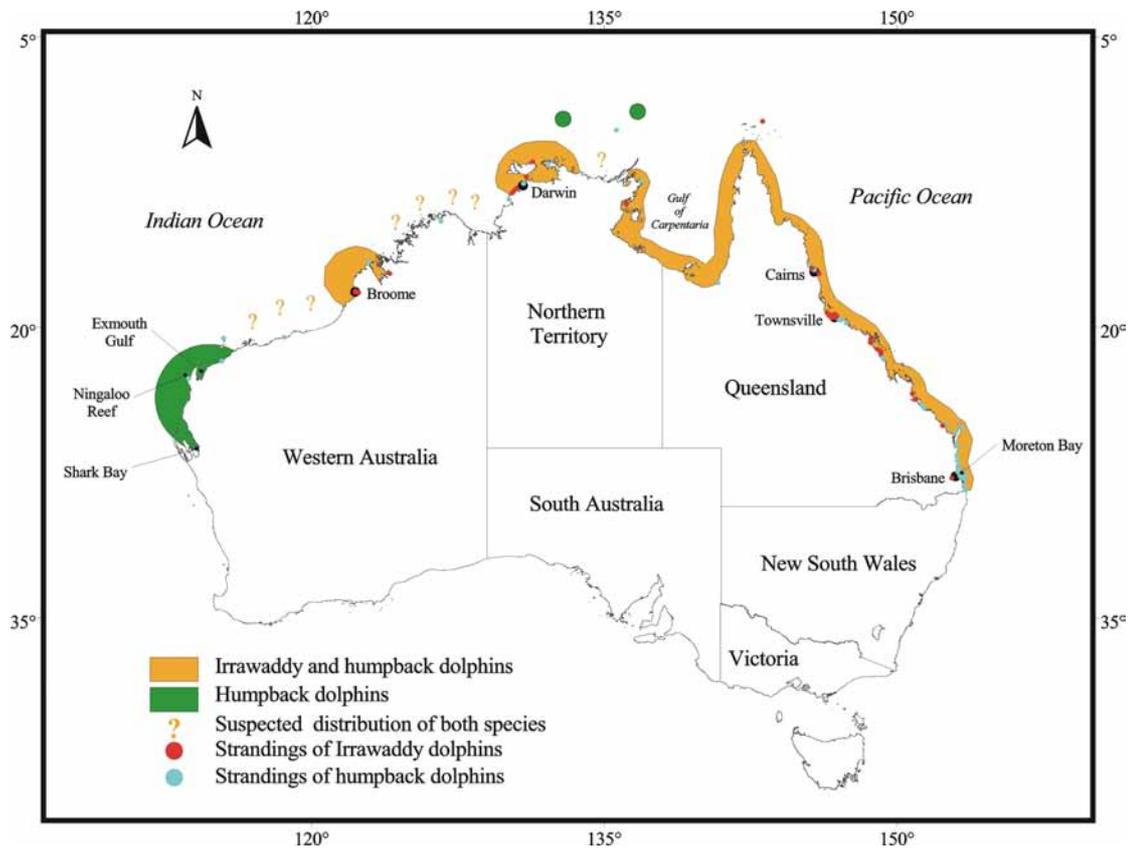


Figure 2.1 Distribution of Irrawaddy and humpback dolphins in Australian waters. The known distribution of both species is based on information reviewed in Parra (Parra et al. 2002, see Appendixes 1 to 4, 2004). Question marks indicate areas of probable, but unconfirmed, distribution. Stranding data were obtained from museum and wildlife agencies (see Appendixes 1 and 4).

2.2.3 *Habitat*

Within Australian waters, Irrawaddy and Indo-Pacific humpback dolphins are typically associated with shallow, coastal and estuarine waters. Most schools of Irrawaddy dolphins seen during opportunistic aerial surveys of Dugongs (*Dugong*

dugon) along the Great Barrier Reef Region east coast of Queensland were seen within 10 km from the nearest point of land, in waters less than 10 meters deep, and within 10 km from the nearest river mouth (Parra et al. 2002). Similarly, sightings of Indo-Pacific humpback dolphins in the same region occurred mainly in waters within 10 km from the nearest coast and shallow areas (i.e., areas less than 2 m deep at low tide, Corkeron et al. 1997). The apparent preference of both species for coastal shallow water habitats in Australian waters is consistent with what has been described for other marine populations of these species throughout their ranges (Appendix 5 and 6).

Bathymetry has been suggested as one of the main factors limiting Indo-Pacific humpback dolphins to coastal waters. In Algoa Bay, South Africa, Karckzmarski (Karczmarski et al. 2000a) suggested that the 25 m isobath represents the critical depth for Indo-Pacific humpback dolphins. Coastal Irrawaddy dolphins have rarely been sighted in waters deeper than 20m, indicating that depth may also play a role in the inshore distribution of this species (Appendices 5 and 6). While both species are generally reported to remain close to the coast in shallow waters, occasional sightings in offshore (>10 km from the coast) and deep (> 20m) waters have been reported (Appendices 5 and 6). Along the East coast of Queensland, Indo-Pacific humpback dolphins have been recorded up to 55.6 km from the coast (Corkeron et al. 1997), while Irrawaddy dolphins have been sighted up to 23 km from the coast and in waters up to 30 meters deep (Parra et al. 2002). A possible explanation for the occurrence of both species offshore and in deeper waters is the physiographic attributes of the coastlines and continental shelves where these sightings have occurred. The continental shelf along the east coast of Queensland is broad and shallow, and reefs, sandflats and continental islands are common. Thus, as

dolphins move away from the coast, they will remain in shallow water and not necessarily too far away from the nearest coast (i.e., mainland or island). Therefore dolphins do not have to travel long distances over relatively deep and exposed waters before re-entering shallow waters (Corkeron et al. 1997, Parra et al. 2002). In chapters three and five of this thesis I use data collected in different areas along the Queensland coast to investigate the spatial distribution patterns and habitat preferences of Irrawaddy and Indo-Pacific humpback dolphins in relation to the bathymetry of the area and proximity to the coast.

2.2.4 Abundance

There are no current estimates of population sizes or trends for Irrawaddy and Indo-Pacific humpback dolphins in Australian waters. Freeland and Bayliss (1989) estimated a population of 1000 Irrawaddy dolphins in one area of the Gulf of Carpentaria by an aerial survey. This estimate, however, has been questioned as a result of the difficulties in identifying dolphin species from the air in turbid waters and it is likely to be an over-estimate (Marsh et al. 1989, Stacey and Arnold 1999, Parra et al. 2002). The only available abundance estimates of Indo-Pacific humpback dolphins are for Moreton Bay, a large embayment (approx. 1315 km²) located in southeast Queensland. The population size estimates for Moreton Bay in the mid 1980s, covering two different time periods, were 163 (1984-1986, 95% confidence intervals = 108-251) and 119 individuals (1985-1987, 95% confidence intervals = 81-166) (Corkeron et al. 1997). Based on the small and declining number of sightings of Indo-Pacific humpback dolphins during aerial surveys of the Great Barrier Reef region between 1987-1995, Corkeron et al. (1997) suggested Indo-Pacific humpback dolphins are probably declining in Australian waters. This thesis (see Chapter 8) provides the first comprehensive assessment of the population size of Irrawaddy

dolphins at a local level in Australian waters, and also provides the first point of comparison to previous estimates of humpback dolphin numbers in the region.

The few available estimates of abundance for both species throughout their range indicate that, in general, populations of both species currently tend to be small (Appendices 5 and 6). Riverine populations of Irrawaddy dolphins are all below 100 individuals (Smith et al. 2003). Abundance estimates of coastal populations of Irrawaddy dolphins are not available. Population estimates of Indo-Pacific humpback dolphins range from a couple of hundred in South Africa (Karczmarski et al. 1999b, Keith et al. 2002, Guissamulo and Cockcroft 2004) and Mozambique to a thousand animals in the Pearl River estuary in China (Jefferson 2000).

2.2.5 Social Organization

Throughout their range, Irrawaddy and Indo-Pacific humpback dolphins tend to occur in schools of fewer than 10 animals, with schools of more than 10 individuals observed occasionally (Appendices 5 and 6). The few available records of school size of both species in Australian waters reflect a similar pattern. Schools of more than ten Indo-Pacific humpback dolphins seem to be related to opportunistic aggregations of animals feeding behind trawlers (Corkeron 1990, Jefferson 2000) and to reproductive seasonality (Karczmarski et al. 2000a). The occasional occurrence of large schools of Irrawaddy dolphins (>10 individuals) seems to be associated with socializing behaviour. Most of the large schools observed along the east coast of Queensland during aerial surveys involved individuals in a very tight formation with extensive physical contact (Parra et al. 2002).

There are no studies detailing the association patterns among individual Irrawaddy dolphins, thus their social structure remains unknown. Indo-Pacific humpback dolphins appear to have a fluid social system, with individuals associating

for just short periods of time, with the exception of mothers and calves (Karczmarski 1999, Jefferson 2000). In chapter seven of this thesis, I provide a detailed analysis of the social structure of Irrawaddy and Indo-Pacific humpback dolphins by looking at the association patterns among identified individuals and their variation with time.

2.2.6 Movements

Photo-identification studies on Indo-Pacific humpback dolphins in Hong Kong/Pearl River Estuary and Xiamen, China, suggest that most Indo-Pacific humpback dolphins are resident in areas around large river systems and that linear movements of tens of kilometres are common (Jefferson 2000). Ranging patterns of 27 individuals from Hong Kong waters varied from 29 km² to 395 km² (mean= 128.1 km² ± 97.47 km²) encompassing only a small portion of the estimated 1800 km² population range in this area (Hung et al. 2004). No movements of 100 kilometres or more have been recorded in this area (Jefferson 2000). In contrast, Indo-Pacific humpback dolphins in Algoa Bay, South Africa have low site fidelity, and the majority of animals seem to be involved in long-range movements, approximating at least a couple of hundred kilometres (Karczmarski et al. 1999a, 2000a). However, movements over 1000 km seem unlikely, as extensive reviews of photo-identification catalogues from areas wide apart (>500 km) yielded no matches (Karczmarski et al. 2000a). Differences in ranging patterns between Indo-Pacific humpback dolphin populations from Hong Kong and South Africa appear to be shaped by differences in habitat and availability of food resources (Hung et al. 2004). Karczmarski suggested that the patchiness of restricted inshore prey resources along the South African coastline may force dolphins to range over great distances in search of food, while the more available prey resources in the Hong Kong/Pearl River estuary area may allow dolphins to range less extensively (Hung et al. 2004).

Stacey and Arnold (1999) reviewed the early, mainly anecdotal reports on movements of Irrawaddy dolphins. The only account of ranges in the literature comes from interviews with fisherman in the Ayeyarwardy River, who reported home ranges of about 35 km (Smith et al. 1997). In riverine environments dolphins seem to aggregate in deep pool waters during the dry season and move into tributaries during the rainy season (I. Beasley, personal communication, 2004). In this study (see Chapter 6) I present data on the movement patterns of Irrawaddy and Indo-Pacific humpback dolphins including site fidelity, residence times, range size, and range overlap.

2.2.7 *Feeding habits*

Studies on diet composition and foraging behaviour of both species throughout their range are limited (Appendices 7 and 8). Minimal data exist for Australian populations of both species, with only a single study addressing this ecological aspect (Heinsohn 1979). Heinsohn's study is the only one detailing the diet habits of marine Irrawaddy dolphins. Based on the few studies of diet composition throughout the range of both species, Irrawaddy and Indo-Pacific humpback dolphins appear to be opportunistic-generalist feeders, eating a wide variety of coastal, estuarine and reef-associated fishes both on the bottom and within the water column (Appendices 7 and 8). While fish is the main food for both species, all stomach contents of Irrawaddy dolphins from Australia included cephalopod remains, which do not seem to form part of the main diet of Indo-Pacific humpback dolphins. These differences might reflect some of the morphological differences between both species and may indicate some differences in their diet.

The available data also suggest some dietary overlap when the species occur in sympatry. Comparison of stomach contents from Irrawaddy dolphins in Australian

waters and Indo-Pacific humpback dolphins elsewhere, indicates that diet overlap occurs at the family and genus level including sardines (Clupeidae: *Sardinella sp.*), Anchovies (Engraulidae), grunts (Haemulidae: *Pomadasys sp.*), ponyfishes (Leiognathidae: *Leiognathus sp.*), croakers (Sciaenidae: *Johnius spp.*) and whittings (Sillaginidae: *Sillago sp.*) (see Appendices 7 and 8).

The feeding behaviours of Indo-Pacific humpback dolphins indicate that cooperative feeding is limited. In South Africa, large groups generally disperse widely (1-100m) to feed. Individuals move in various directions with no obvious pattern, and capture fish on an individual basis (Karczmarski et al. 1997). Smaller groups remain closer (1-20m) while feeding (Karczmarski et al. 1997).

Saayman and Tayler (1979) noted that feeding activities of Indo-Pacific humpback dolphins increased during the rising tide in Plettenberg Bay, South Africa. In the Bazaruto archipelago on the coast of Mozambique, southern Africa, Indo-Pacific humpback dolphins feed during the ebb tide in the channels created between sandbanks, beaching themselves after concentrating fish against a sandbank (Peddemors and Thompson 1994). In Algoa Bay, feeding behaviour increased during high tide (Karczmarski and Cockcroft 1999).

In Australian and Hong Kong waters, Indo-Pacific humpback dolphins feed behind fishing trawlers (Corkeron 1990, Parsons 1998a, Jefferson 2000); and have also been seen feeding close to gillnets which might act as a barrier to facilitate prey capture (Jefferson 2000). Trawlers seem to be very important as aggregating points for Indo-Pacific humpback dolphins, as well as representing an important source of food (Jefferson and Leatherwood 1997). On the contrary, observations of Irrawaddy dolphins in association with trawlers are few with only two cases reported in the literature, both in Malaysia (Dolar et al. 1997, Beasley 1998).

2.2.8 *Life history*

There are no cross-sectional studies of the life history of Irrawaddy and Indo-Pacific humpback dolphins in Australian waters, mainly due to the lack of fresh carcasses. Based on age studies and captive animals, both species may live for more than 20 years (Heinsohn 1979, Marsh et al. 1989). Irrawaddy dolphins reach near adult size (2.1 m) in 4-6 years in northeastern Australia (Marsh et al. 1989).

Most of the information available on Indo-Pacific humpback dolphins' life history comes from populations in South Africa (Cockcroft 1989) and Hong Kong (Jefferson 2000). In South Africa, the gestation period of Indo-Pacific humpback dolphins lasts 10-12 months, lactation may last >2 years, sexual maturity is reached at 10 years of age for females and 12-13 year for males, and a 3 year calving interval has been suggested (Cockcroft 1989). In Hong Kong, length at birth is assumed to be about 100 cm; a gestation period of 11 months is presumed, and females reach sexual maturity at 9-10 years of age (Jefferson 2000).

2.3 Conservation threats

2.3.1 *Habitat degradation and loss*

Due to their coastal and estuarine distribution, Irrawaddy and Indo-Pacific humpback dolphins are particularly vulnerable to human activities in and adjacent to coastal areas. Most of Australia's northern coastline is relatively unpopulated by people. However, the concentration and rapid population growth along the urban coast of Queensland, extending from Cooktown to Brisbane, has increased pressure on coastal resources. The potential impact of the urban area along the Queensland coast puts pressure on the future of Irrawaddy and Indo-Pacific humpback dolphins in Australian waters. The maintenance of high quality habitat will be a major challenge

for the conservation of Irrawaddy and Indo-Pacific humpback dolphins along the coast of Queensland.

2.3.2 *Overfishing*

Depletion of local food resources is likely to have a negative effect on coastal populations of marine mammals over the next century (DeMaster et al. 2001). Most of the Australian fisheries catch is taken close to the coast in waters less than 50m deep (Resource Assessment Commission 1993) and commercial fisheries are at or near full exploitation (Kearney et al. 1996). Bottom trawling is widely recognized as a major threat to the structure and functioning of coastal ecosystems (Turner et al. 1999, Blaber et al. 2000). Trawling is the main fishing method used to catch prawns in Australia and represents one of the major extractive activities permitted within parts of the large, multiple-use marine parks in the ranges of Irrawaddy and Indo-Pacific humpback dolphins in Australia (Gribble and Robertson 1998, Pitcher et al. 2000). Trawling activities can also influence the behaviour, social structure and habitat use of coastal dolphins, leading to the existence of separate communities with different ecological needs, thus posing challenges for management (Chilvers and Corkeron 2001).

Recent changes in the zoning of the Great Barrier Reef Marine Park will alleviate the depletion of prey resources. First, the Representative Areas Program of the Great Barrier Reef Marine Park (<http://www.reefed.edu.au/rap/>) increased the percentage of the 344,400 km² Great Barrier Reef Marine Park, zoned as 'no-take' to 33% from mid 2004. Second, the new Great Barrier Reef Coast Marine Park established in November 2004, extends the Great Barrier Reef Marine Park zoning from low water to high water or to the seaward edge of the mangrove forests. The use and entry provisions to these inshore areas will be the same as the adjacent Great

Barrier Reef Marine Park. Finally, trawling effort within the Great Barrier Reef Marine Park has been substantially reduced through the East Coast Trawl Management Plan (Huber 2003).

2.3.3 *Directed takes*

There is no evidence of direct killing of Irrawaddy and Indo-Pacific humpback dolphins in Australian waters. Australian law prohibits direct killing of any cetacean species in Australian waters. Nonetheless, illegal fishing operations are known to occur within the Australian Fishing Zone and there is anecdotal evidence of foreign fishing vessels with dolphin meat on board. Whether these kills are the result of a directed fishery or incidental take is unknown.

2.3.4 *Incidental takes*

Human-related mortality of Irrawaddy and Indo-Pacific humpback dolphins in Australian waters is thought to be largely attributable to inshore gill-nets set across creeks, rivers and shallow estuaries for barramundi (*Lates calcarifer* Bloch, 1970) and threadfin salmon (*Polynemus sheridani* Macleay, 1884 and *Eleutheronema tetradactylum* Shaw, 1804) (Hale 1997), and in shark nets set for bather protection (Paterson 1990). However, there are no estimates of the magnitude of these indirect takes or of their trends over time.

Fisheries observers on gillnet vessels operating in northern Australian waters between 1981-1985 reported one Indo-Pacific humpback dolphin among the cetacean species incidentally taken (Harwood and Hembree 1987). Between 1967 and 1992 at least 544 cetaceans were caught in shark nets set for bather protection along the Queensland coast (Paterson 1990). A recent analysis of the effects of this program on non-target species (Gribble et al. 1998) estimated that between 1962 and 1995, an

average of 19.2 dolphins of all species were caught per year, decreasing to 12.5 animals per year from 1992-95. The species composition of most dolphin catches prior to 1992 is unknown. However, out of 24 dolphin catches in the Townsville region between 1968-1976, 15 were Irrawaddy dolphins (Heinsohn 1979). Eleven of 18 confirmed Indo-Pacific humpback dolphins collected from shark nets along the Queensland coast between 1968-2001 were caught in nets off Cairns and Townsville, northern Queensland (Heinsohn 1979, Haines and Limpus 2002). Although at a state level captures of both species appear to be small, most captures occurred in localized areas and could be expected to have a detrimental effect on local populations.

Net attendance rules and gear modifications have been introduced in the inshore gillnet fishery to reduce the incidental take of non-target species (e.g., turtles, dugongs, whales and dolphins), but enforcement is lacking in remote areas (Hale 1997). The Queensland Shark Control Program implemented strategies to reduce the impact of the program on non-target species including the use of acoustic alarms, mixed use of nets and drumlines, overall reduction in the number of nets, and establishment of marine mammal rescue squads (Department of Primary Industries 2001). There is no evidence to assess whether any of these measures have provided any benefit to the conservation of Irrawaddy and Indo-Pacific humpback dolphins.

2.3.5 *Pollution*

The transport of agricultural and urban-sourced pollutants into coastal waters of the Queensland coast has been identified as a major threat to the coastal water quality in the region (Haynes and Michalek-Wagner 2000). High concentrations of heavy metals and persistent organic compounds containing halogens have damaging effects on marine mammals (Tanabe et al. 1994, Tanabe 2002). A range of organohalogen pollutants (natural and anthropogenic) were detected in the blubber of

four bottlenose dolphins (*Tursiops* spp.), one common dolphin (*Delphinus* spp.) and seven dugongs (*Dugong dugon*) from north-east Queensland (Vetter et al. 2001), however no data are available for Irrawaddy and Indo-Pacific humpback dolphins.

2.3.6 Vessel traffic

Acoustic studies on Indo-Pacific humpback dolphins in Moreton Bay, southeast Queensland, showed that the dolphins' acoustic communication and group cohesion are affected by boat traffic and noise (Van Parijs and Corkeron 2001). In Algoa Bay, South Africa, Indo-Pacific humpback dolphins exhibited behavioural changes associated with vessels following them (Karczmarski et al. 1997), and inshore powerboat traffic has been identified as a serious disturbance in this area (Karczmarski et al. 1998). Post mortem investigation of stranded Indo-Pacific humpback dolphins from Hong Kong suggest that some deaths may have been caused by boat strikes (Parsons and Jefferson 2000). Irrawaddy dolphins in the Mahakam River surfaced less in the presence of boats and vessel traffic is considered a serious threat to local populations (Kreb and Rahadi 2004). In Queensland, the number of recreational vessels (motor and sail) registered has increased from 102,853 in 1990 to more than 150,500 in 2000 with registrations increasing by at least 10% per year (Queensland Environmental Protection Agency 1999, 2000). As more people have boat access to coastal areas and estuaries, the risks associated with vessel traffic (e.g., boat strikes, behaviour disruption, habitat displacement) can be expected to increase.

2.3.7 Wildlife tourism

Tourism based on free-ranging dolphins, including boat-based tours, shore-based observation, swim interactions, and hand-feeding, is one of the most popular icons of marine tourism along Australia's coastline (Birtles et al. 2001).

In Australia, observations and interactions appear to be limited to Indo-Pacific humpback dolphin at a few locations in Queensland. Four boat-based operators promote dedicated dolphin-watching trips that include Indo-Pacific humpback dolphins, two in Moreton Bay Marine Park and another two in Hervey Bay Marine Park, southeast Queensland (Birtles et al. 2001). Swimming with and hand-feeding of Indo-Pacific humpback dolphins occurs at Tin Can Bay, southeast Queensland. This activity developed from a relatively unknown local practice, to a growing tourist attraction receiving up to 300 visitors per day (Mayes 1999). The activity was officially approved by the State Minister of the Environment in 1999, when policy changes limited the amount of fish fed to the dolphins, reduced the total number of contact hours, increased education and interpretation materials, and ensured a volunteer or an interpretation officer was always present during times of interaction (Mayes 1999). However, monitoring compliance with these guidelines remains limited.

Although, the level of wildlife tourism involving Indo-Pacific humpback and Irrawaddy dolphins in Australian waters is low, it is expected to increase. Precautionary measures are needed to ensure that the continued development expected in this industry will not adversely affect coastal dolphin populations in Australian waters. In the 52nd meeting of the International Whaling Commission in Adelaide, Australia, the scientific Sub-Committee on Whale Watching recommended that hand-feeding programs of wild cetaceans be prohibited (International Whaling Commission 2001). However, closure of such activities is politically difficult to achieve, particularly in isolated regional areas which are dependant on the income generated.

2.3.8 *Conservation Status*

At present, the population status of Irrawaddy and Indo-Pacific humpback dolphins in Australian waters cannot be assessed due to the lack of biological data. The limited information available suggests that populations are small, localized, and probably declining (Corkeron et al. 1997, Hale et al. 1998). The small population sizes estimated in this study for Cleveland Bay, north Queensland (see Chapter 8), indicate Irrawaddy and humpback dolphins are particularly vulnerable to local extinction.

Extremely large (thousands of km²) multiple-use marine parks in Western Australia, the Northern Territory, and Queensland cover a substantial portion of the known and presumed habitat of Irrawaddy and Indo-Pacific humpback dolphins in Australian waters. These parks include the Shark Bay and Ningaloo Reef Marine Park (Western Australia), Cobourg Marine Park (Northern Territory); and the Great Barrier Reef, Hervey Bay and Moreton Bay Marine Parks (Queensland). The conservation success of no-take zones (i.e., areas that allow access but prohibit all extractive activities) within large multiple-use marine protected areas is likely to be low for highly mobile marine mammals (Preen 1998), unless they coincide with areas which consistently support high numbers of animals (Marsh 2000). Thus, the understanding of the distribution and relative abundance of coastal dolphins in Australian waters needs to be improved before effective conservation initiatives can be designed to ensure the persistence of viable populations of Irrawaddy and Indo-Pacific humpback dolphins. This study fills a gap of information about the ecology of Irrawaddy and Indo-Pacific humpback dolphins, and provides a preliminary scientific basis for their future conservation and management in Australian waters, at least in the Great Barrier Reef region.

Precautionary measures should be adopted, while further work on abundance estimates, population structure, and levels of human-caused mortality is carried out on a wider scale in Australian waters. In this context, it is considered important that the agencies responsible for environmental management take a more strategic, pro-active, comprehensive and coordinated approach to marine mammal research and management, than has been attempted to date (Preen 1998). A realistic research plan with defined mechanisms for securing the future of long-term research and monitoring is urgently needed, if Australia is to meet its national and international obligations with regard to the conservation of Irrawaddy and Indo-Pacific humpback dolphins (see future research recommendation in Chapter 10).

2.4 Chapter summary

- Data from stranding databases, museums, and unpublished sightings by wildlife agencies and aerial surveys showed that Irrawaddy and humpback dolphins are widely distributed along coastal waters of Queensland, Northern Territory and Western Australia.
- Both species are commonly observed close to the coast in sheltered, shallow estuarine waters. Because of their coastal distribution, the major threats to Irrawaddy and humpback dolphins in Australian waters are: 1) entanglement in gillnets set in shallow waters for fishing purposes; 2) entanglement in shark nets set for bather protection; and 3) habitat degradation and loss due to coastal zone development, pollution, boat traffic, and overfishing of prey resources.
- The population status of Irrawaddy and Indo-Pacific humpback dolphins in Australian waters cannot be assessed due to the lack of biological data. The information available from the few studies throughout their geographical range

indicates that both species occur in discrete, geographically localized populations and are susceptible to anthropogenic threats. Information on the behavioural ecology of both of these species in Australian waters is urgently needed in order to improve conservation and management efforts.

- This study fills a gap of information about the ecology of Irrawaddy and Indo-Pacific humpback dolphins, and provides a preliminary scientific basis for their future conservation and management in Australian waters, at least in the Great Barrier Reef region.

Chapter 3

Spatial distribution of Irrawaddy and Indo-Pacific humpback dolphins in northeast Queensland, Australia: implications for their conservation

In this chapter, I use data collected during boat-based line transect surveys in two areas along the northeast Queensland coast to investigate the spatial distribution patterns of Irrawaddy and Indo-Pacific humpback dolphins. I examine the relationship between the spatial distribution of Irrawaddy and Indo-Pacific humpback dolphins and three simple, readily quantified, environmental variables: distance to land, distance to river, and water depth. The relationships established are used as a framework to assess the level of protection offered in the study areas to Irrawaddy and Indo-Pacific humpback dolphins.

Chapter 3. Spatial distribution of Irrawaddy and Indo-Pacific humpback dolphins in northeast Queensland, Australia: implications for their conservation

3.1 Introduction

The spatial distribution patterns exhibited by animals result from numerous external (e.g., environmental, anthropogenic) and internal processes (e.g., population dynamics, intraspecific interactions) (May 1984, Borcard et al. 1992, Legendre 1993). All approaches to reserve design and implementation implicitly assume some knowledge of the spatial distribution of organisms (Pressey and Cowling 2001). The better we understand the spatial distribution of the species of interest, the greater our opportunities for managing human activities in order to facilitate their conservation (Turner et al. 1995, Hooker et al. 1999, Macdonald and Rushton 2003).

The extent to which fisheries affect coastal ecosystems is of increasing concern (Jackson et al. 2001, Pauly et al. 2002, Ormerod 2003). Coastal delphinids are among the marine fauna often directly affected by fisheries (Caswell et al. 1998, Pichler and Baker 2000, Chilvers and Corkeron 2001). Attempts to regulate fisheries impacts on delphinids generally include some spatial component (Bräger et al. 2002). However, along much of the world's coastlines, our knowledge of the distribution and status of delphinids remains poor (Van Parijs et al. 2002). Even though a spatial approach has been used to regulate fisheries impacts on some marine mammals (e.g., Hooker et al. 1999, Marsh et al. 1999, Marsh 2000) techniques incorporating quantitative estimates of the manner in which dolphins use space into decisions regulating fisheries activity are in their infancy (Bräger et al. 2003).

Irrawaddy dolphins (*Orcaella brevirostris*, Owen in Gray, 1866), and Indo-Pacific humpback dolphins (hereafter humpback dolphins, *Sousa chinensis*, Osbeck,

1765), are found in tropical and subtropical waters of the Indian and western Pacific Oceans (Stacey and Arnold 1999, Jefferson and Karczmarski 2001). As a result of increasing pressure from expanding human populations and associated coastal zone development throughout the Indo-Pacific region, the long-term prospects for the survival of Irrawaddy and humpback dolphins are poor (see Chapter 2, Perrin et al. 1996, Smith and Jefferson 2002). Despite these concerns, relatively little is known regarding the ecology and population status of both species throughout most of their range. The exception to this is off the coast of South Africa, (Karczmarski et al. 1999b, Karczmarski et al. 2000a, Keith et al. 2002), and in Hong Kong waters (Jefferson 2000) where humpback dolphins have been relatively well studied.

As discussed in Chapter 2, the distributions of Irrawaddy and humpback dolphins overlap throughout much of their range from the coastal waters off the Bay of Bengal to the northern coast of Australia. Both species show similar habitat preferences, occurring mainly in shallow, coastal, estuarine waters (Stacey and Arnold 1999, Jefferson and Karczmarski 2001). In Australian waters, Irrawaddy and humpback dolphins are known to co-occur throughout an extensive part of their range including coastal waters of Western Australia, Northern Territory, and Queensland (Corkeron et al. 1997, see Chapter 2, Parra et al. 2002, Parra et al. 2004). Very little is known on their ecology and status within Australian waters (Parra et al. 2002, Parra et al. 2004) even though both species are listed as *Data Deficient* under the Australian Cetacean Action Plan (Bannister et al. 1996), and are regarded as species of priority for management and research by the Great Barrier Reef Marine Park (Great Barrier Reef Marine Park Authority 2000).

Here, I combined Geographic Information Systems (GIS) and non-parametric statistics which include space as a variable (Legendre and Fortin 1989, Legendre

1993) to analyse the patterns of spatial distribution of Irrawaddy and humpback dolphins in two selected areas of northeast Queensland, Australia (Objective 2 of this thesis, see Chapter 1). I use these techniques in order to explore the relationship between the observed distribution of the dolphins and three simple, readily quantified, environmental variables in a way that accounts for autocorrelation in the data. I then assess the conservation implications of the spatial distribution patterns of both species in relation to the current threats and zoning of the Great Barrier Reef Marine Park.

3.2 Methodology

3.2.1 Study areas

The two study areas are located within the inner shelf zone of the Far Northern and Central Sections of the Great Barrier Reef Marine Park, northeast Queensland (Fig. 3.1). The Far Northern Section study area (hereafter FNS) consists of three adjacent bays open to the north: Princess Charlotte, Bathurst and Ninian Bays. Four major rivers flow into Princess Charlotte Bay, two small creeks into Bathurst Bay; no rivers flow into Ninian Bay (Fig. 3.1a). The Central Section study area (CS) is located in the Cardwell region (Fig. 3.1b). This stretch of coastline is made up of one large bay open to the north, Rockingham Bay, and the Hinchinbrook Channel, which separates the mainland from Hinchinbrook Island. Missionary Bay on the northern side of Hinchinbrook Island was also included in the surveys. Several tidal creeks and four major rivers flow into this region.

3.2.2 Fieldwork

Standard shipboard line transect surveys (Hiby and Hammond 1989) were conducted in both study areas between October and November 2001. Two boats were used: a 20 metre, modified trawler in the FNS and a 15 metre barge in the CS. Both

boats had elevated viewer platforms at 5 m (CS) and 6 m (FNS) above sea level. Surveys occurred in calm sea conditions: Beaufort 3 or less and swells less than 1.5 m. All surveys took place between 06:00 and 14:00 hours. The survey regions were stratified into two areas: inshore (< 10 km from the coast) and offshore (10-20 km offshore). Only one to four random lines were run in each offshore area. Within each inshore survey area, transects were perpendicular to the coast, 10 km long, spaced approximately 3 km apart, and were connected by shorter transect lines ranging between 2 to 4 km long (Fig.3.1). Each transect line was surveyed once. While the ship was moving at a speed of 10 km/h along the transect line a team of three observers, located on top of the viewer platforms, searched for dolphin schools ahead and on each side of the boat with the aid of 7 x 50 binoculars fitted with a compass and reticle markings. A school was defined as dolphins with relatively close spatial cohesion (i.e., each member within 100m of any other member). While on search effort, one of the observers maintained a constant search of the area near the boat with unaided eye and binoculars. Once a dolphin school was sighted search effort was stopped to identify species, assess school size, and record behaviour. Sighting distances to dolphin schools were estimated from the compass bearings and reticle readings from the horizon and land (i.e., when land instead of horizon was behind the dolphin school in question) (Buckland et al. 1993, Lerczak and Hobbs 1998). The corresponding distance to land was measured using readings from digital maps on the onboard chartplotter Global Positioning Systems (GPS). Sighting information and environmental conditions were recorded and updated throughout the survey. Survey effort and number of sightings for both study areas are summarized in Table 3.1.

Note: all tables have been placed at the end of this chapter to minimize interruption to

the flow of the text. The tables are printed on yellow colour paper to make them easy to locate.

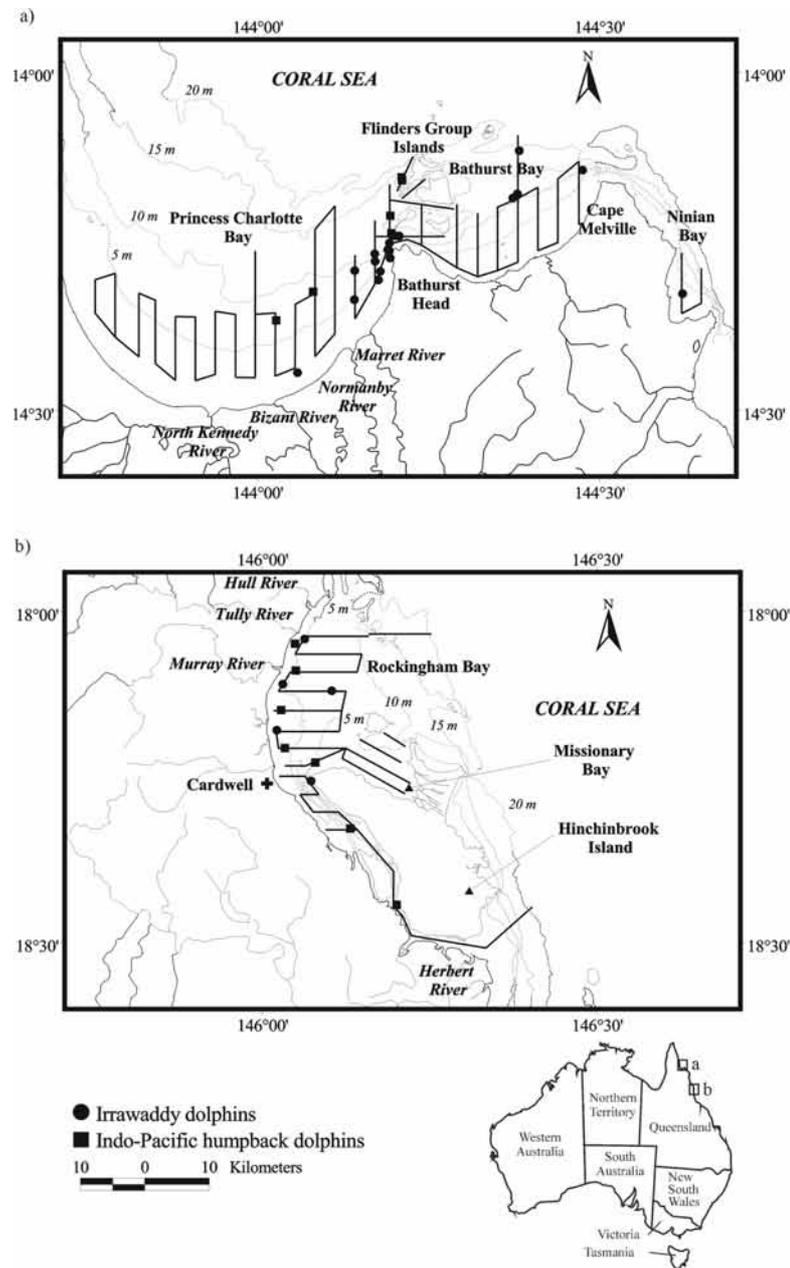


Figure 3.1 Map indicating dolphin sighting locations: (a) Far Northern Section study area (Irrawaddy dolphin sightings = 17, humpback dolphin sightings = 7); (b) Central Section (Irrawaddy dolphin sightings = 5, humpback dolphin sightings = 7). Transect lines are indicated by solid lines and isobaths by broken line.

3.2.3 *Spatial analysis*

ArcView Geographic Information Systems software (GIS) was used to construct a spatial database for each study area integrating dolphin sightings locations in relation to coastline, river mouths, and bathymetry. Geographically referenced digital data for the Queensland's coastline and estuaries (scale 1:100000) was obtained from the Australian National Mapping Agency. Digital data of water depth were obtained from the Great Barrier Reef depth model (scale 1:100000) (Lewis 2001). For areas where data points are dense, the water depth (according to the depth model) is 90% of the time within 5 m from the nearest real water depth (Lewis 2001).

From these digital data, three spatial layers were constructed for the following environmental variables: distance to land (i.e., mainland and islands), distance to river, and water depth. The distance to land spatial layer was constructed using a Euclidean distance function (ESRI 1996b) to compute the shortest distance to the nearest shoreline. The distance to river was estimated using a cost distance function (ESRI 1996b) that computed the shortest distance to the nearest river mouth taking into account the presence of land in-between (e.g., islands, capes). Additional manual editing of underrepresented water depths in inshore areas was carried out with the aid of digital georeferenced nautical charts obtained from the Australian Hydrographic Office. To ensure that sampling of environmental variables fell within the area surveyed, a buffer of 1 km, the approximate maximum radial distance at which dolphins were detected, was constructed along the sides of each transect and further sampling taken from this buffer. Spatial layers were sampled at a cell resolution of 500 x 500m. To minimize inaccuracies in distance calculations, all spatial layers were projected into Universal Transverse Mercator (UTM) Zone 55.

Analysis of spatial data was based on the location of each dolphin school when first seen while on search effort. Dolphin school locations were estimated from boat position, bearings and reticle readings from horizon or land recorded in the field. With selective availability disabled from Global Positioning Systems (GPS) position errors are reduced to $\pm 10\text{m}$ (Hulbert and French 2001). I also measured the accuracy of our distance to land measurements from the digital maps in the GPS chartplotter navigation system by comparison with measurements from available nautical charts. Corrections were then applied to all estimates of the locations of dolphin schools. Distance formulae which take into account the curvature of the earth were used to improve the accuracy of the location estimates of dolphin schools (Lerczak and Hobbs 1998).

3.2.4 Randomization tests

To determine if the dolphins occurred closer to land, river mouths and in shallower waters than would be expected by chance, one-tailed randomization tests were carried out on the observed distribution of each dolphin species (Manly 1997). The randomization test involved comparing the mean values of environmental variables observed at Irrawaddy (μ_i) and humpback dolphin (μ_h) locations with mean values obtained from random locations (μ_r) within the study area (i.e., $H_0: \mu_i - \mu_r \geq 0$, $H_0: \mu_h - \mu_r \geq 0$). This procedure was repeated multiple times (10000), and the significance of the test evaluated by recording the number of times the mean value from random locations was greater than the observed value (Manly 1997).

To assess differences between the spatial distribution of Irrawaddy and humpback dolphins in relation to the environmental variables measured, a two sample randomization test was conducted ($H_0: \mu_i - \mu_h = 0$) (Manly 1997). This type of

randomization compares the difference of the mean distances to land, mean distances to river and mean water depths at which each species was observed, with the difference obtained by randomly allocating the observed values among the two species. All randomization procedures were repeated 10000 times for appropriate precision (Manly 1997). Resample and randomization test functions in the POPTOOLS version 2.5 Excel add-in were used (available at <http://www.cse.csiro.au/poptools>).

3.2.5 *Mantel Tests*

Although randomization tests are informative regarding the spatial distribution of dolphin schools, they do not overcome some of the problems caused by the spatial autocorrelation and intercorrelation among variables inherent in species-environment relationships (Fortin and Jacquez 2000, Schick and Urban 2000). Species attributes (e.g., distribution, abundance) and environment variables measured at the same sampling locations might show strong correlations simply because both share a common spatial structure created by biotic (e.g., reproduction, migration) and abiotic (e.g., climate, geology) factors (Legendre and Fortin 1989, Legendre 1993). In the presence of spatial autocorrelation, classical parametric statistics can result in incorrect conclusions regarding species-environment relationships (Leduc et al. 1992, Legendre 1993, Hinch et al. 1994, Dunham and Rieman 1999, Nash et al. 1999). To assess how much of the observed spatial variation in dolphins distribution was explained by the environmental variables measured, while accounting for spatial autocorrelation in the data, I used simple and partial Mantel tests (Mantel 1967).

The Mantel test is a correlation approach that calculates a statistic similar to Pearson's r between two dissimilarity or distance matrices (Legendre and Fortin 1989, Legendre 1993). A simple Mantel test considers the relationships between predictor

(e.g., environmental variables) and dependant variables (e.g., species distribution), as well as their relationship with their location in space, by summarizing space as a geographic distance matrix (Schick and Urban 2000, Urban et al. 2002). A partial Mantel test considers the correlation between environmental variables and species distribution while controlling for the effect of space (i.e., spatial autocorrelation) and any intercorrelation that might exist with other variables (Schick and Urban 2000, Urban et al. 2002). The test statistic r_M ranges between -1 to +1, but does not have to be large in absolute value to be significant (Legendre and Fortin 1989). Because the elements of a distance matrix are not independent, a Mantel test of significance is evaluated via permutation by randomly rearranging the rows and columns of the distance matrices. Mantel statistics are recomputed for these permuted matrices, and the distribution of values for the statistic is generated via many iterations (e.g., 10000) (Manly 1997, Legendre and Legendre 1998).

To explore the overall relationship between the spatial distribution of dolphins and the environmental variables in multivariate terms, one-tailed ($H_0: r_M \leq 0$) simple and partial Mantel tests were carried out, in which the Mantel statistic r_M was computed between three dissimilarity matrices: one for dolphin occurrence (i.e., presence/absence of dolphins), one for environment, and one for space. The dissimilarity matrix of dolphin occurrence was summarized as a binary contrast matrix where sampling sites similar in dolphin occurrence, irrespective of species, were coded as 0 and dissimilar sites were coded as 1 (Schick and Urban 2000, Urban et al. 2002). Univariate correlations were also tested by separating the environmental dissimilarity matrix into its constituent variables (distance to land, distance to river, and water depth). Simple and partial Mantel tests were used to account for the effect

of each variable on dolphin occurrence, while controlling for space and any intercorrelation that may have existed between variables.

Finally, to test if there was any difference in the spatial distribution patterns between the two dolphin species in relation to the environmental variables, a distance matrix of dolphin species' composition was constructed. Here sampling sites similar in dolphin species' composition (i.e., presence/absence of Irrawaddy and/or humpback dolphins) were coded 0 and dissimilar sites were coded as 1. Multivariate and univariate Mantel tests for the correlation of environment variables, dolphin composition and space were carried out.

In order to avoid an uncontrolled inflation of overall Type-I error rates in the multiple correlation tests, the False Discovery Rate (FDR) correction procedure for multiple testing (Benjamini and Hochberg 1995) was used to adjust P-values and then compared at $\alpha = 0.05$. This correction procedure is more powerful than any other classical multiple comparison P-value adjustment (Benjamini and Hochberg 1995, Thissen et al. 2002). Examination of confidence limits around effect sizes (differences between means, correlation coefficients) are more informative than P-values in hypothesis testing, as they describe the possible effect sizes that could reasonably be expected in the population based on the empirical data, and assists in the distinction between statistical significance and biological significance (Yoccoz 1991, Thomas 1997). Therefore, and following suggestions on presentation and interpretation of statistical results by Anderson et al. (2001) and Colegrave and Ruxton (2003), observed effect sizes and their corresponding confidence intervals were reported together with P-values. Statistical significance of results were evaluated at $\alpha = 0.05$. However, if examination of effect sizes and confidence intervals indicated plausible substantial differences or correlations, the results were considered significant.

Confidence intervals of differences between means were obtained by non-parametric bootstrapping using the bias corrected and accelerated method (BCa) (Efron and Tibshirani 1993).

All computations related to simple and partial Mantel tests were carried out in the R software for statistical computing and graphics version 1.70 (Ihaka and Gentleman 1996) with the aid of a coded R-Library package developed at the Nicholas School of the Environment, Duke University (Goslee and Urban unpublished; R library available on request from Sarah Goslee, USDA-ARS PSWMRU, Building 3702, Curtin Road, University Park, PA 16802). Bootstrapping calculations for confidence intervals of differences between means were conducted using the R-package “boot”.

3.3 Results

3.3.1 Overall distribution

Irrawaddy dolphins were sighted in all three bays in the FNS, but most of the sightings occurred around Bathurst Head in Princess Charlotte Bay (Fig. 3.1a). Humpback dolphins were seen in Princess Charlotte Bay only in the vicinity of Bathurst Head, and around the east side of the Flinders Group Islands. Over 50% of the sightings of both species occurred in waters within 15 km from land, 20 km from the nearest river mouth and in waters less than 15 m deep (Table 3.2, Fig. 3.2). Overall, Irrawaddy and humpback dolphins tended to occur closer to land, but further away from rivers and in deeper waters than the FNS average. Irrawaddy dolphins occurred closer to rivers and in shallower water than humpback dolphins, while both occurred at similar distances to land (Fig 3.2).

In the CS, both species were sighted throughout most of the study area including Rockingham Bay and the Hinchinbrook Channel (Fig. 3.1b). Most sightings

of both species in the CS occurred within 5 km from land, 10 km from the nearest river mouth and in waters less than 10m deep (Table 3.2, Fig. 3.2). Irrawaddy dolphins occurred closer to rivers and in shallower waters than humpback dolphins, while humpback dolphins occurred slightly closer to land than Irrawaddy dolphins (Fig. 3.2).

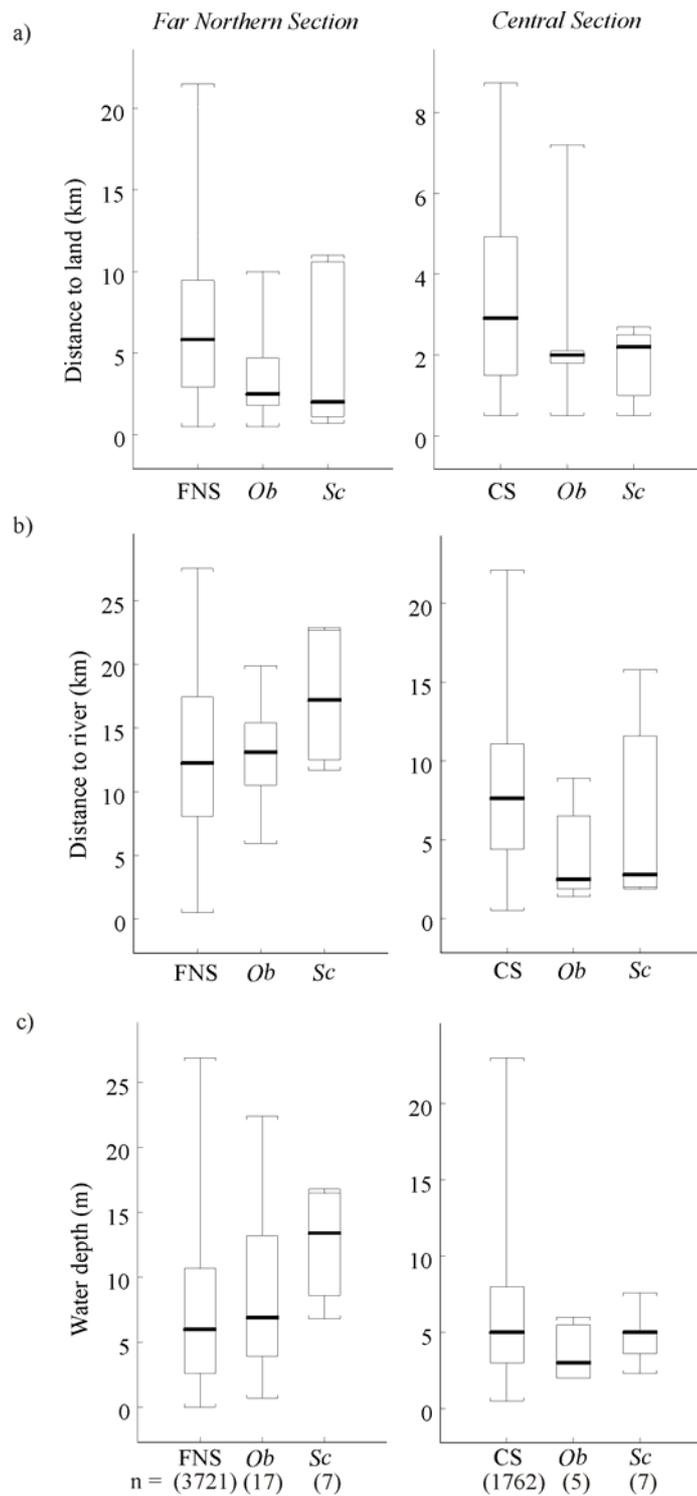


Figure 3.2 Boxplots of the distance to land (a), distance to river (b), and water depth (c) associated with each dolphin species (Irrawaddy dolphins = Ob, humpback dolphins = Sc) sighting location and study area (FNS =Far Northern Section, CS= Central Section). The midline represents the median; the box represents the interquartile range which contains 50% of values. Vertical lines indicate the data range.

3.3.2 Randomization tests: dolphins' distribution in relation to study area ($H_0: \mu_i - \mu_r \geq 0, \mu_h - \mu_r \geq 0$)

The randomization test for the FNS indicated that Irrawaddy and humpback dolphins occurred closer to land than would be expected by chance (Table 3.3). The small observed effect size and wide confidence intervals around distance to river and water depth for Irrawaddy dolphins indicated no detectable pattern of spatial distribution in relation to these variables. Confidence limits on the effect size of distance to river and water depth for humpback dolphins indicated they were likely to occur further away from rivers and in deeper water than the FNS average.

In the CS, Irrawaddy dolphins occurred in waters closer to rivers and shallower than would be expected under a random scenario, while humpback dolphins occurred closer to land (Table 3.3). Despite non-significant results in relation to water depth, the span of the confidence interval over only negative differences suggested that humpback dolphins were also likely to be found in slightly shallower waters than the CS average.

3.3.3 Randomization tests: dolphins' distribution in relation to each other ($H_0: \mu_i - \mu_h = 0$)

The two sample randomization test indicated a significant difference between the mean distances to river at which both species were sighted in the FNS, with Irrawaddy dolphins occurring closer to rivers than humpback dolphins (Table 3.4). Confidence limits on the effect size of water depth, which showed mainly negative differences, also indicated Irrawaddy dolphins were more likely to be found in shallower waters in the FNS than humpback dolphins. Two sample randomization

tests showed no significant difference between the means of distance to land, distance to river and water depth at which each species were observed in the CS (Table 3.4).

3.3.4 Mantel tests: correlation between dolphin distribution and environmental variables ($H_0: r_M \leq 0$)

The three simple Mantel tests (above diagonal, Table 3.5) for the FNS and CS indicated a significant correlation between dolphin occurrence and the environmental variables measured. However, the analysis also revealed that the distribution of dolphins in the FNS, and the environmental variables in both study areas were spatially autocorrelated. Once the spatial autocorrelation of the environmental data was accounted for with partial Mantel tests (below diagonal, Table 3.5), the correlation between dolphin occurrence and environmental variables remained significant, indicating the environment had a patterning effect on the spatial distribution of the dolphins. The spatial autocorrelation found within the dolphin occurrence matrix in the FNS disappeared once the effect of the environment was removed. This result indicated that the spatial autocorrelation found in the dolphins' distribution data was a result of correlation with the environmental matrix and not the result of spurious correlations with some unquantified variables (e.g., dolphins' social structure).

Once the environmental dissimilarity matrix was separated into individual matrices, simple (first column, Table 3.6) and partial Mantel tests controlling for spatial autocorrelation (column 3) and any intercorrelation (column 4) between variables, indicated that the spatial distribution of dolphins in the FNS was influenced by all environmental variables, while in the CS distance to land and distance to river emerged as the most important variables affecting their spatial distribution. Although no statistically significant correlation was found for water depth in the CS, confidence

intervals indicate that this correlation is likely to be positive, suggesting that water depth may also have an effect on the spatial distribution patterns of dolphins in this area.

3.3.5 Mantel tests: correlation between dolphin species'

composition and environmental variables ($H_0: r_M \leq 0$)

In the FNS, significant correlations between the dolphin species' composition at each sampling site and the multivariate environment matrix were detected, before and after controlling for the spatial structure in environmental data (Table 3.7). This correlation suggests that in the FNS there was some measurable interspecific difference in the spatial distribution of Irrawaddy and humpback dolphins in relation to the environmental variables investigated. Once the multivariate environmental dissimilarity matrix was separated into its constituent variables (Table 3.8), the results indicated that the only variable that had an effect on dolphin species' composition in the FNS was distance to river. This correlation indicates specific differences in the spatial distribution of the dolphins in relation to distance to river in the FNS, with Irrawaddy dolphins occurring closer to rivers than humpback dolphins. Confidence limits around r_M for distance to land in the FNS showed a slight tendency for the correlation to be positive; suggesting possible differences in the spatial distribution of Irrawaddy and humpback dolphins in relation to this variable. In relation to water depth, the confidence interval of the correlation spanned over negative and positive values, providing no indication of the likely effect of this variable on dolphin species' composition in the FNS.

Mantel tests for the CS indicated no differences between the spatial distribution of Irrawaddy and humpback dolphins in relation to distance to land, distance to river and water depth. Multivariate (Table 3.7) and univariate (Table 3.8)

comparisons of the dolphin species' composition at each sampling site and environmental variables showed no significant correlation. Confidence intervals around estimated r_M for each environmental variable spanned similar positive and negative correlations providing no indication of possible differences between the spatial distributions of these species.

3.4 Discussion

3.4.1 Spatial distribution

My results indicated that Irrawaddy and humpback dolphins at both study sites occurred mostly in waters less than 15 m deep that were within 10 km of the coast and 20 km from the nearest river mouth. This result fits with what is known of the distribution of both species along the Queensland coast (see Chapter 2, Corkeron et al. 1997, Parra et al. 2002), and throughout their range (Marsh et al. 1989, Ross et al. 1994, Stacey and Arnold 1999, Jefferson and Karczmarski 2001).

The randomization tests indicated that the distributions of Irrawaddy and humpback dolphins in both study areas were strongly influenced by proximity to the coast, with both species occurring closer to land than would be expected under a random scenario. In the CS site, both species also occurred in shallower waters, and Irrawaddy dolphins occurred closer to rivers than would be expected by chance. There appear to be interspecific differences in spatial distribution patterns with Irrawaddy dolphins occurring closer to rivers and in shallower waters than humpback dolphins. However, results from the two-sample randomization tests indicated that only at the FNS site were Irrawaddy dolphins found closer to rivers and in shallower waters than humpback dolphins.

The approach using Mantel tests provided clear inferences about the correlation of the species' distributions with environmental variables, while taking

into account problems with spatial autocorrelation and intercorrelation among variables. The Mantel test results indicated spatial autocorrelation in the dolphins' distribution data in the FNS and strong spatial autocorrelation in environmental data for both sites, reiterating the importance of considering spatial autocorrelation in the analysis of species-environment relationships. Allowing for the spatial autocorrelation in environmental data, the dolphins' distributions at both study sites were influenced by the environmental variables that I measured. Further, when comparing between species, Irrawaddy dolphins occurred closer to rivers than humpback dolphins in the FNS. The lack of detectable difference between the distributions of Irrawaddy and humpback dolphins at the CS site may be due to the small sample size, or may reflect a real difference between the two sites in the spatial distribution of the dolphins.

Cetacean distributions are generally determined by physical oceanographic and hydrographic features, and the effects of these features on prey distributions (Jaquet and Whitehead 1996, Davis et al. 1998, Benson et al. 2002, Davis et al. 2002, Jaquet and Gendron 2002). Nutrient inputs from rivers, the export of organic litter from mangrove forests, and the stratification and circulation patterns created in shallow coastal waters enhance productivity in tropical coastal areas, creating important nursery areas for fish (Alongi 1998, Hobbie 2000). Irrawaddy and humpback dolphins' preference for inshore, estuarine areas may be diet related, but quantitative studies on their foraging ecology are limited. As explained in Chapter 2, the available data suggest that both species are opportunistic-generalist feeders, eating a wide variety of coastal, estuarine and inshore reef-associated fishes (Stacey and Arnold 1999, Jefferson 2000, Jefferson and Karczmarski 2001).

Most delphinids are sociable animals and habitat selection by individuals may be influenced by the behaviour and distribution of conspecifics. Such attractions can

result in their distribution being spatially autocorrelated in a way that cannot be fully explained by the environmental variables measured (Legendre and Fortin 1989, Legendre 1993, Lichstein et al. 2002). As this was not the case in this study, I can conclude that environmental variables had a major influence on the spatial distribution of Irrawaddy and humpback dolphins at both sites.

From surveys of two preselected sites in one season, I cannot make robust inferences about the generality of my findings. However, this study confirms and refines the more qualitative observations made on broader scale surveys on the distribution of these species in waters of the Great Barrier Reef Marine Park (see Chapter 2, Corkeron et al. 1997, Parra et al. 2002) and agrees with my detailed studies on space and habitat use carried out in a selected area along the Queensland coast (see Chapter 5). The spatial patterns of the distribution of both species revealed here should be taken into consideration for conservation planning.

3.4.2 *Implications for conservation*

This study provides evidence that Irrawaddy and humpback dolphins mainly occur in waters close to the coast, in particular within 10 km from nearest coastline, 20 km from rivers and in waters less than 20m deep. In trying to define and provide distinct and workable boundaries for the management of the coastal area in relation to coastal dolphins, I have identified environmental features that delineate potential suitable and important areas for Irrawaddy and humpback dolphins, and that should facilitate their management and conservation.

The marked preference of Irrawaddy and humpback dolphins for coastal waters has strong implications for their long term conservation. As discussed in Chapter 2, coastal ecosystems in the Indo-Pacific region are under increasing pressure from expanding human populations and associated coastal zone development, and the

prospects of survival for both species are regarded as poor (Perrin et al. 1996, Smith and Jefferson 2002). Although most of Australia's coastline is relatively uninhabited and unindustrialized, increasing development and preference of human settlements for coastal locations, including the Queensland coast, has become an important issue affecting the sustainability of many of Australia's marine and coastal resources (Zann 1996). It has been estimated that at least half of the land area of catchments adjacent to the Great Barrier Reef has been modified for grazing, farming and mining activities (Haynes and Michalek-Wagner 2000, CRC Reef Research Center 2001). This pattern of land use has stimulated great concerns about the water quality and potential impacts these activities might have on the ecological integrity of nearshore environments and their associated fauna along the Queensland Coast (Haynes and Johnson 2000, Haynes and Michalek-Wagner 2000, Haynes et al. 2000). Significant measures have been implemented to address this issue (Great Barrier Reef Marine Park Authority 2001).

The finding that Irrawaddy dolphins occurred closer to river mouths than humpback dolphins in the FNS site may be particularly important. Drowning in inshore gillnets set across creeks, rivers and shallow estuaries represents one of the major threats to inshore dolphins along the Queensland coast (see Chapter 2, Corkeron et al. 1997, Hale 1997, Parra et al. 2002). Irrawaddy dolphins appear to be the rarest of Queensland's coastal dolphins (Parra et al. 2002). The results of this study suggest that their habitat preferences put them at greater risk of encountering river-set gillnets than other dolphins. Replication of this study at other sites along the Queensland coast is necessary to confirm whether Irrawaddy dolphins generally occur closer to river mouths than do humpback dolphins. Long-term studies in Cleveland Bay, Queensland, support this spatial pattern for Irrawaddy dolphins (see Chapter 5).

The results presented here also reveal current concerns in relation to the recent (2004) rezoning of the Great Barrier Reef Marine Park particular to the study areas. The current zoning plan for the Far Northern Section delineates a large area of Princess Charlotte Bay into a Marine National Park Zone, where gillnetting is banned. However, the remainder of Princess Charlotte Bay, including waters around Bathurst Head (Fig. 3.1a), was zoned as Habitat Protection Zone, including a Special Management Area (Great Barrier Reef Marine Park Authority 2003).

Commercial gillnetting is allowed in the Special Management Area, subject to a Great Barrier Reef Marine Park Authority permit. The entire Far Northern Section of the Great Barrier Reef Marine Park is very remote, relatively unpopulated and difficult to police (Gribble and Robertson 1998). The efficacy of acoustic alarms (Barlow and Cameron 2003) remains undemonstrated for humpback and Irrawaddy dolphins, and enforcing regulations regarding their use in this remote region is impractical. The current boundaries of the Marine National Park Zone in Princess Charlotte Bay provide limited protection to Irrawaddy and humpback dolphins and other coastal species (e.g., dugongs) as the MNPZ is situated mainly in offshore waters. Waters around Bathurst head, zoned as Special Management Area, appear to be a hotspot for aggregations of Irrawaddy and Humpback dolphins (Fig. 3.1a). Fortunately under the provisions of this Special Management Area, the number of gillnets licenced to work in this region has been limited to < 10. In addition, the fishery is closed for 3 months of the year (1st of November-1st of February) and severe restrictions on netting practice are being implemented. Whether these measures will be adequate to protect the dolphin populations is unknown.

A similar situation arises in the Cardwell region along the Central Section of the Great Barrier Reef Marine Park. The current zoning delineates only Missionary

Bay and a small portion of the Hinchinbrook Channel and Rockingham Bay (Fig. 3.1b), as a Conservation Park Zone where all netting activities are prohibited. Outside this area, where most sightings of both species took place, netting is allowed. If management goals of protected areas in Princess Charlotte Bay and the Cardwell region are to protect inshore dolphins, the areas banning netting should be increased to cover these important coastal areas.

3.5 Chapter summary

- In this chapter, I used Geographic Information Systems (GIS), randomization techniques and Mantel tests to examine the relationship between the spatial distribution of Irrawaddy and humpback dolphins and three simple, readily quantified, environmental variables: distance to land, distance to river, and water depth.
- Data on the spatial distribution of Irrawaddy and humpback dolphins were obtained in October-November 2001 during vessel-based line transect surveys in the Far Northern Section (FNS) and Central Section (CS) of the Great Barrier Reef Marine Park, northeast Queensland, Australia.
- As indicated by randomization tests, the distribution of Irrawaddy and humpback dolphins in both study areas was strongly influenced by proximity to the coast, with both species occurring closer to land than would be expected under a random scenario. This confirms and extends observations made during broad scale surveys along the Queensland coast (Corkeron et al. 1997, Parra et al. 2002).
- Regarding interspecific differences in spatial distribution, the two-sample randomization tests indicated that only at the FNS site, Irrawaddy dolphins were found closer to rivers and in shallower waters than were humpback

dolphins. The lack of interspecific differences in the CS may reflect the actual distribution patterns or may be the result of the small sample sizes obtained for both species.

- Mantel tests results suggested that all environmental data and some of the distributional data for both species were spatially autocorrelated, emphasizing the importance of accounting for autocorrelation in the interpretation of species-environment relationships. Once spatial autocorrelation was controlled for, all environmental data had a patterning effect on the spatial distribution of both species. When comparing between species, Irrawaddy dolphins occurred closer to rivers than humpback dolphins in the FNS.
- Analysis of spatial distribution suggests that existing protected areas in the FNS and CS may not include the most critical habitats for Irrawaddy and humpback dolphins.
- The techniques used here provide relationships between the spatial distribution of the dolphins and environmental features that should facilitate their management and conservation. These relationships can be used to develop spatially-explicit management strategies.

Table 3.1 Survey effort and number of sightings of Irrawaddy and humpback dolphins in the Far Northern Section (FNS) and Central Section (CS) study areas.

Study area	Search effort (km)	Number of sightings		Sightings per km		Total surface area surveyed (km ²) ^a
		Irrawaddy	Humpback	Irrawaddy	Humpback	
FNS	431.3	17	7	0.039	0.016	782
CS	242.9	5	7	0.021	0.029	413

^aThe total surface area surveyed was calculated as the area within 1 km buffer on each side of transect lines.

Table 3.2 Mean, median, and ranges of distance to land, distance to river and water depth for the study areas, and sightings of Irrawaddy, and humpback dolphins in the Far Northern Section (FNS) and Central Section (CS) study areas.

	Study area	Distance to land (km)					Distance to river (km)				Water depth (m)			
		n	Mean ± SD	95% CI Mean	Median	Range	Mean ± SD	95% CI Mean	Median	Range	Mean ± SD	95% CI Mean	Median	Range
Study area	FNS	3721	6.5±4.36	6.4-6.7	5.8	0.5-21.5	12.9±6.04	12.7-13.1	12.2	0.5-27.5	7.3±5.34	7.1-7.5	6.0	0.7-26.9
	CS	1762	3.3±2.12	3.2-3.4	2.9	0.5-8.7	8.2±4.71	8.0-8.4	7.6	0.5-22.1	6.4±4.67	6.2-6.6	5.0	0.5-23
Irrawaddy	FNS	17	3.4±2.86	2.3-5.0	2.5	0.5-10.0	12.8±3.90	10.9-14.6	13.1	5.9-19.9	8.3±6.17	5.7-11.5	6.9	0.7-22.4
	CS	5	2.7±2.59	1.3-5.2	2.0	0.5-7.2	4.3±3.31	1.9-7.2	2.5	1.4-8.9	3.7±1.92	2.2-5.2	3.0	2.0-6.0
Humpback	FNS	7	4.2±4.53	1.6-8.2	2.0	0.7-11.0	17.6±4.49	14.3-20.6	17.2	11.7-22.9	12.4±4.01	9.3-14.9	13.4	6.8-16.8
	CS	7	1.9±0.84	1.2-2.4	2.2	0.5-2.7	6.1±5.51	3.0-11.0	2.8	1.9-15.8	4.6±1.64	3.6-5.9	5.0	2.3-7.6

Table 3.3 Effect sizes (i.e., difference between the means at locations where dolphins were sighted and random locations), confidence intervals and P-values from the one-tailed randomization test to determine if Irrawaddy and humpback dolphins occurred closer to land, rivers and in shallower waters than would be expected under a random scenario in the Far Northern Section (FNS) and Central Section (CS) study areas. A negative effect size ($\mu - \mu_r$) indicates Irrawaddy (μ_i) or humpback (μ_h) dolphins were observed closer to land, rivers or in shallower water than would be expected if animals were occurring at random. Significant differences are indicated in bold italics.

	Study area	Distance to land			Distance to river			Water depth		
		$\mu - \mu_r$ (km)	95% CI (km)	P	$\mu - \mu_r$ (km)	95% CI (km)	P	$\mu - \mu_r$ (m)	95% CI (m)	P
Irrawaddy ($H_0: \mu_i - \mu_r \geq 0$)	FNS	-3.1	-4.4, -1.8	0.001	-0.1	-2.3, 1.4	0.459	1.0	-1.3, 4.4	0.778
	CS	-0.6	-2.2, 1.7	0.293	-3.9	-6.2, -0.8	0.021	-2.7	-4.1, -1.0	0.076
Humpback ($H_0: \mu_h - \mu_r \geq 0$)	FNS	-2.3	-5.2, 1.5	0.067	4.7	1.1, 7.3	0.984	5.1	2.7, 8.0	0.984
	CS	-1.4	-2.1, -0.9	0.036	-2.1	-5.1, 2.4	0.125	-1.8	-2.9, -0.5	0.140

Table 3.4 Effect sizes, confidence intervals, and P-values from two-sample randomization tests to determine differences between the spatial distribution of Irrawaddy and humpback dolphins in the Far Northern Section (FNS) and Central Section (CS) study areas. A negative effect size ($\mu_i - \mu_h$) indicates Irrawaddy dolphins occurred closer to land, rivers or in shallower water than humpback dolphins. Significant differences are indicated in bold italics.

	Study area	Distance to land			Distance to river			Water depth		
		$\mu_i - \mu_h$ (km)	95% CI (km)	P	$\mu_i - \mu_h$ (km)	95% CI (km)	P	$\mu_i - \mu_h$ (m)	95% CI (m)	P
Irrawaddy-Humpback ($H_0: \mu_i - \mu_h = 0$)	FNS	-0.8	-4.6, 2.1	0.622	<i>-4.8</i>	<i>-8.3, -1.4</i>	<i>0.013</i>	-4.1	-7.7, 0.1	0.120
	CS	0.8	-0.7, 3.8	0.565	-1.9	-7.6, 2.2	0.514	-0.9	-2.8, 0.9	0.3876

Table 3.5 Simple and partial Mantel coefficients (r_M), confidence intervals, and P-values for the correlation between dolphin occurrence (Dolphin occ., i.e., presence/absence of dolphins of either species), environmental variables, and geographic distance (Space) in the Far Northern Section (FNS) and Central Section (CS) study areas. Elements in the upper triangle of the matrix are simple correlations, while the lower triangle holds partial correlations. Significant differences are indicated in bold italics.

$H_0: r_M \leq 0$	Study area	Dolphin occurrence			Environmental variables			Space		
		r_M	95 % CI	P	r_M	95 % CI	P	r_M	95% CI	P
Dolphin occurrence	FNS				<i>0.128</i>	<i>0.075, 0.199</i>	<i>0.003</i>	<i>0.066</i>	<i>0.014, 0.123</i>	<i>0.023</i>
	CS				<i>0.178</i>	<i>0.094, 0.300</i>	<i>0.024</i>	-0.001	-0.031, 0.048	0.367
Environmental variables	FNS	<i>0.114</i>	<i>0.064, 0.172</i>	<i>0.006</i>				<i>0.301</i>	<i>0.264, 0.342</i>	<i>0.000</i>
	CS	<i>0.194</i>	<i>0.114, 0.317</i>	<i>0.015</i>				<i>0.390</i>	<i>0.304, 0.513</i>	<i>0.003</i>
Space	FNS	0.029	-0.012, 0.087	0.126	<i>0.296</i>	<i>0.258, 0.334</i>	<i>0.001</i>			
	CS	-0.078	-0.141, -0.027	0.991	<i>0.397</i>	<i>0.305, 0.507</i>	<i>0.003</i>			

Table 3.6 Simple and partial Mantel coefficients, confidence intervals, and P-values for the correlation between dolphin occurrence (Dolphin occ., i.e., presence/absence of dolphins of either species), individual environmental variables, and geographic distance in the Far Northern Section (FNS) and Central Section (CS) study areas. Significant differences are indicated in bold italics.

H ₀ : r _M ≤ 0	Study Area	Dolphin occurrence ^a			Space ^b			Dolphin occ. Space ^c			Dolphin occ. All ^d		
		r _M	95 % CI	P	r _M	95 % CI	P	r _M	95 % CI	P	r _M	95 % CI	P
Dolphin occ.	FNS				0.066	0.014, 0.123	0.031				0.026	-0.016, 0.073	0.131
	CS				-0.001	-0.031, 0.048	0.367				-0.089	-0.144, -0.034	0.993
Distance to land	FNS	0.113	0.059, 0.181	0.021	0.245	0.201, 0.293	0.004	0.101	0.047, 0.169	0.025	0.109	0.058, 0.177	0.023
	CS	0.223	0.125, 0.384	0.032	0.136	0.072, 0.221	0.091	0.225	0.124, 0.385	0.026	0.241	0.138, 0.413	0.041
Distance to river	FNS	0.066	0.023, 0.128	0.034	0.191	0.149, 0.245	0.005	0.054	0.011, 0.110	0.048	0.050	0.009, 0.108	0.069
	CS	0.099	0.018, 0.220	0.088	0.332	0.249, 0.448	0.009	0.105	0.025, 0.233	0.078	0.143	0.070, 0.276	0.060
Water depth	FNS	0.074	0.024, 0.138	0.031	0.015	-0.050, 0.083	0.381	0.073	0.021, 0.137	0.031	0.071	0.021, 0.140	0.041
	CS	0.012	-0.036, 0.065	0.203	0.523	0.020, 0.634	0.027	0.014	-0.029, 0.066	0.269	0.044	-0.001, 0.089	0.105

^aFirst column indicates simple Mantel correlations of dolphins occurrence with individual environmental variables

^bSecond column indicates simple Mantel correlations of dolphin occurrence and each environmental variable with space (autocorrelation)

^cThird column represent partial Mantel correlation of dolphin occurrence with individual environmental variables controlling for space

^dFirst two rows of fourth indicates partial Mantel correlation of dolphin occurrence with space controlling for all environmental variables. The rest of the column indicates partial Mantel correlations of dolphin occurrence with individual environmental variables controlling for all other variables.

Table 3.7 Simple and partial Mantel coefficients, confidence intervals, and P-values for the correlation between dolphin species' composition (Dolphin species comp., i.e., presence/absence of Irrawaddy and/or humpback dolphins), environmental variables, and geographic distance in the Far Northern Section (FNS) and Central Section (CS) study areas. Elements in the upper triangle of the matrix are simple correlations, while the lower triangle holds partial correlations. Significant differences are indicated in bold italics.

$H_0: r_M \leq 0$	Study area	Dolphin species comp.			Environmental variables			Space		
		r_M	95 % CI	P	r_M	95 % CI	P	r_M	95% CI	P
Dolphin species comp.	FNS				<i>0.215</i>	<i>0.134, 0.320</i>	<i>0.024</i>	-0.024	-0.084, 0.025	0.500
	CS				-0.036	-0.099, 0.081	0.750	-0.092	-0.186, 0.019	0.813
Environmental Variables	FNS	<i>0.230</i>	<i>0.140, 0.340</i>	<i>0.014</i>				<i>0.271</i>	<i>0.190, 0.372</i>	<i>0.017</i>
	CS	0.011	-0.037, 0.079	0.523				<i>0.498</i>	<i>0.385, 0.691</i>	<i>0.069</i>
Space	FNS	-0.088	-0.149, -0.018	0.803	<i>0.283</i>	<i>0.189, 0.386</i>	<i>0.014</i>			
	CS	-0.085	-0.177, 0.006	0.805	<i>0.497</i>	<i>0.369, 0.627</i>	<i>0.087</i>			

Table 3.8 Simple and partial Mantel coefficients, confidence intervals, and P-values for the correlation between dolphin species' composition (Dolphin species comp., i.e., presence/absence of Irrawaddy and/or humpback dolphins), individual environmental variables, and geographic distance. Significant differences are indicated in bold italics.

$H_0: r_M \leq 0$	Study Area	Dolphin species comp.			Space			Dolphin species comp. Space			Dolphin species comp. All		
		r_M	95 % CI	P	r_M	95 % CI	P	r_M	95 % CI	P	r_M	95 % CI	P
Dolphin species comp.	FNS				-0.024	-0.084, 0.025	0.500				-0.077	-0.145, -0.009	0.735
	CS				-0.092	-0.186, 0.019	0.813				-0.072	-0.180, 0.030	0.749
Distance to land	FNS	0.067	-0.016, 0.163	0.278	0.143	0.067, 0.295	0.284	0.071	-0.004, 0.165	0.259	0.081	-0.006, 0.182	0.308
	CS	0.055	-0.114, 0.238	0.561	0.006	-0.121, 0.246	0.393	0.055	-0.090, 0.220	0.534	0.047	-0.148, 0.228	0.737
Distance to river	FNS	0.183	0.077, 0.303	0.114	0.216	0.110, 0.293	0.222	<i>0.193</i>	<i>0.078, 0.333</i>	<i>0.080</i>	<i>0.197</i>	<i>0.084, 0.331</i>	<i>0.096</i>
	CS	-0.083	-0.171, 0.035	0.724	0.490	0.369, 0.695	0.098	-0.044	-0.113, 0.062	0.537	-0.046	-0.118, 0.087	0.737
Water depth	FNS	0.004	-0.082, 0.131	0.423	0.078	-0.059, 0.201	0.284	0.006	-0.083, 0.130	0.410	-0.013	-0.100, 0.103	0.677
	CS	0.024	-0.078, 0.169	0.561	0.345	-0.115, 0.504	0.111	0.060	-0.069, 0.241	0.534	0.051	-0.084, 0.191	0.737

Chapter 4

Occurrence patterns and school dynamics of sympatric Irrawaddy and Indo-Pacific humpback dolphins in northeast Queensland, Australia

In this chapter, I use information collected in Cleveland Bay between 1999 and 2002, to identify patterns in the occurrence and school dynamics (i.e., school size and age composition) of Irrawaddy and Indo-Pacific humpback dolphins and their relation to seasonal changes in the environment. Comparisons are made to determine interspecific differences or similarities in occurrence and school dynamics. This chapter also outlines the main methodology used for the boat-based surveys in Cleveland Bay.

Chapter 4. Occurrence patterns and school dynamics of sympatric Irrawaddy and Indo-Pacific humpback dolphins in northeast Queensland, Australia

4.1 Introduction

The science base underpinning the management efforts to conserve viable populations of Irrawaddy dolphins, *Orcaella brevirostris*, and Indo-Pacific humpback dolphins (hereafter humpback dolphins), *Sousa chinensis* in Australian waters is extremely limited. As summarized in Chapter 2, there is a general lack of species-specific information on the ecology of these species, which has consequently hampered conservation and management efforts.

The co-occurrence of Irrawaddy and humpback dolphins in the northern coastal waters of Australia has long been recognized (Heinsohn 1979). However, the distribution and threats to the conservation of these species were systematically reviewed only recently (Corkeron et al. 1997, see Chapter 2, Parra et al. 2002, Parra et al. 2004, see Chapter 2). The sparse data indicate that both species are susceptible to anthropogenic activities in and adjacent to the coast (e.g., incidental captures in gill nets) as a result of their coastal and estuarine distribution and apparently small populations.

The patterns of occurrence, as well as school size and age composition (i.e., number of adults, juveniles and calves per school) of dolphin species, are influenced by the habitats and movements of their prey, predation pressure, interspecific competition, and social behaviour (Connor et al. 2000b, Mann et al. 2000, Heithaus and Dill 2002). All of these factors are ultimately linked to changes in the physical and biological environment, and can have broad consequences for individual behaviour, population dynamics, and community structure. Consequently, an

understanding of the occurrence patterns and school dynamics of Irrawaddy and humpback dolphins provides important information that can be used to refine conservation and management efforts.

In this chapter, I assess the occurrence patterns and school dynamics of Irrawaddy and humpback dolphins in Cleveland Bay, northeast Queensland (Objective 3 of this thesis, see Chapter 1) with the purpose of: 1) providing important information that is lacking on the ecology of both species in Queensland coastal waters, 2) determining if their patterns of occurrence, school size and age composition are related to seasonal changes in the environment, and 3) comparing these sympatric species with respect to species-specific similarities and differences.

4.2 Methods

4.2.1 Study Area

Cleveland Bay is a tropical embayment located in northeast Queensland, Australia (Fig. 4.1). Cleveland Bay extends from Cape Cleveland in the southeast to Cape Pallarenda in the northwest. The bay is partially enclosed on its northwest side by Magnetic Island which is separated from the mainland by West Channel. Waters in Cleveland Bay are relatively shallow, reaching a maximum depth of 15 m at its outermost limit. A shallow bottom gradient of less than 1 m/km extends out to a depth of 10m (Anderson and Roche 2002).

Small creeks and rivers flow into the bay; Ross River and Alligator Creek to its south are the largest freshwater inputs. Large seagrass meadows extend from the intertidal zone into adjacent subtidal areas along the northern and southern coast of Cleveland Bay (Lanyon and Marsh 1995, Lee Long et al. 1998). Fringing reef seagrass communities are also found along the southwestern coast of Magnetic Island

(Lee Long et al. 1998). Coral reefs occur southeast of West Channel at Middle Reef and as fringing reefs adjacent to the southern shore of Magnetic Island.

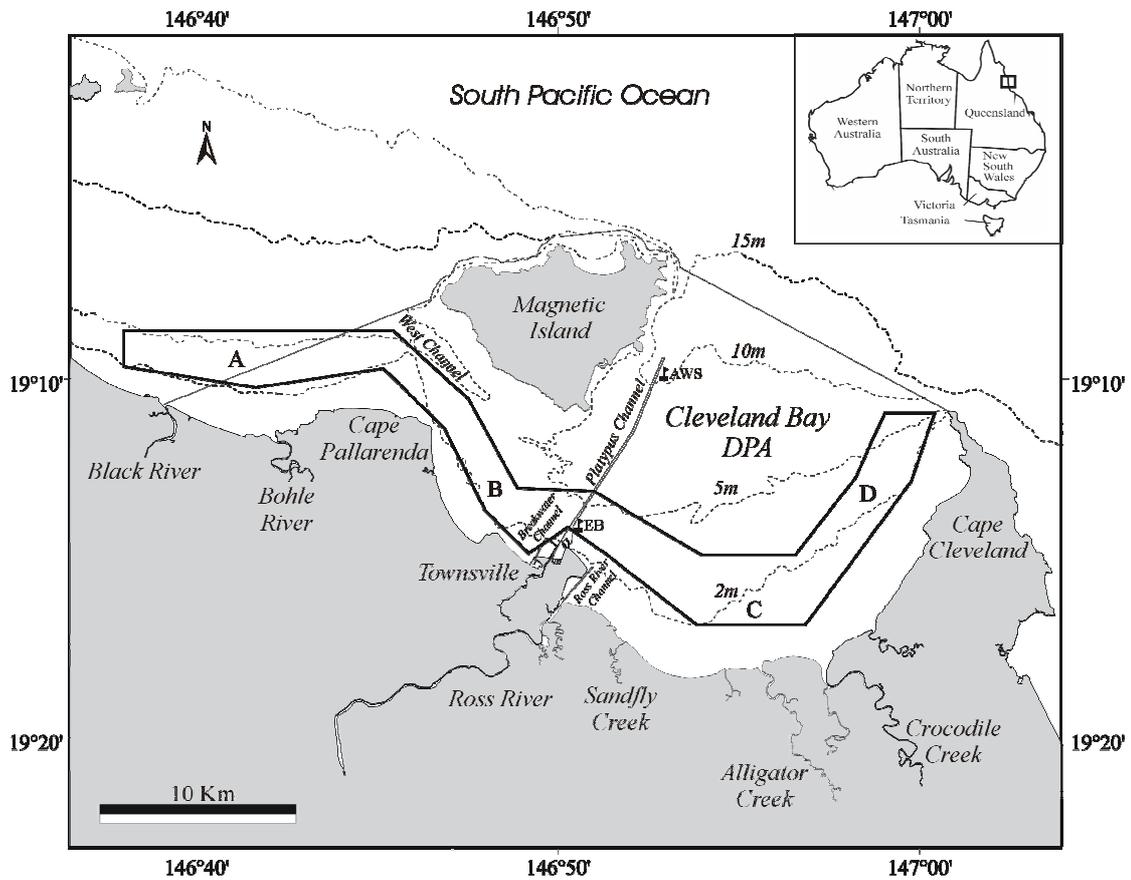


Figure 4.1 Map of Cleveland Bay indicating boat survey route (—), weather stations (▲), limits of the Dugong Protected Area (—), and principal places mentioned in the text.

The Cleveland Bay region experiences a seasonally wet (December-March) and dry (April-November) tropical climate, with 80% of the annual rainfall and maximum sea surface temperature (29°C) occurring between December and March inclusive (Walker 1981a, Walker 1981b).

Cleveland Bay is also the entrance to the Port of Townsville, the third largest commercial port in Queensland. The main shipping channel, Platypus Channel, provides access to the port and is regularly dredged to maintain depths of 10-15 m. Additional access is provided via the Breakwater Marina Channel (dredged to 2-5 m) and the Ross River Channel (dredged to 2-5 m). Cleveland Bay was declared a

Dugong Protected Area in 1997 (DPA) in recognition of its importance as habitat for the dugong (*Dugong dugon*) (Marsh 2000). Cleveland Bay DPA extends from Cape Cleveland in the southeast to the mouth of the Black River in the northwest covering an area of approximately 410 km².

4.2.2 *Survey procedures*

Boat-based surveys were conducted in the coastal waters of Cleveland Bay DPA (hereafter referred to as Cleveland Bay) from January 1999 to October 2002. Surveys were conducted at a steady speed of 10-12 km/h from a 4.7m rigid-hulled inflatable boat, powered by a 50-hp outboard engine. While on search effort, a team of three observers scanned continuously 180 degrees on each side of the boat with naked eye and 7 x 50 binoculars. All surveys took place between 06:00-07:00 hours and 12:00-14:00 hours, depending on weather conditions. For survey purposes the study area was divided into 4 sections (A, B, C, D) of similar length (Fig. 4.1). Surveys followed a predetermined route from Townsville Harbour to Black River mouth (covering sections A and B) or to Cape Cleveland and back (Covering sections C and D). The outward and return legs of the survey were spaced at least 1 km apart to 1) avoid resampling the same area, 2) minimize repeated sightings of the same dolphin school within a single survey, and 3) sample all major coastal habitat types. Most surveys were carried out on non-consecutive days, depending on weather conditions, to increase the likelihood of independence of data. Search effort and direction of travel were limited primarily by sea conditions, attempting to remain in areas with calm sea conditions \leq Beaufort 3 and swell \leq 1 m. Within these constraints, efforts were made to give equal coverage to all sections within the study area.

A school was defined as dolphins with relatively close spatial cohesion (i.e., each member within 100m of any other member). Once a dolphin school was sighted,

it was approached slowly to within 10m to record its location, identify the species, estimate school size, assess the school age composition, and obtain behavioural data.

Dolphin school position was recorded using a handheld 12-channel Global Positioning System (GPS, position accuracy = ± 15 m). School sizes were estimated independently by 2-3 observers on board the research vessel and the mean number of individual dolphins was recorded. For school composition, three age classes were distinguished based on behavioural cues and visual assessment using the average adult size for each species as a reference: 1) adults: individuals about 2-3 m long; 2) juveniles: individuals approximately 2/3 the length of an adult, usually swimming in association with an adult, but sometimes swimming independently; 3) calves: individuals with light brown (Irrawaddy dolphins) or light grey (humpback dolphins) skin colour, $\leq 1/2$ the length of an adult, in close association with an adult, and swimming regularly besides or slightly behind an adult. To ensure independence of data, dolphin schools suspected to have been seen previously within the same survey (i.e., sightings close in time and same school size and composition) were recorded but excluded from analyses.

Because the sex of most delphinids is not easily identified from surface observation, the sex of some identified animals was inferred from social interactions. An adult seen in constant association with a calf was assumed to be a female. Adult individuals that were never seen with a calf and frequently involved in socio-sexual interactions (i.e. animals in close physical contact, including swimming belly to belly) with known females were assumed to be males.

As dolphin schools were approached during surveys, I scanned the school from front to back and the predominant behaviour of $\geq 50\%$ of the individuals at the surface was recorded. After this initial behavioural sample, school behaviour was

recorded every 5 minutes for the duration of the sighting. Dolphin schools were classified into different behavioural states according to the following criteria:

- Foraging (F): Individuals moving in various directions without an obvious pattern. Dolphins diving frequently and steeply downwards (often preceded by fluke up or peduncle arches), with extended submersion times. Rapid accelerations and erratic movement at the surface, indicative of animals chasing fish. Animals seen directly pursuing a fish (e.g., fish jumping at surface) or with fish in their mouth.
- Foraging behind trawler (FBT): Repeated dived in varying directions around the side or behind the stern of a trawler boat while the boat is fishing for prawns.
- Travelling (T): Movement persistent and directional with a regular pattern of surfacing and diving. Dive angles are shallow. Animals are not underwater for extended lengths of time.
- Socializing (S): Localised movement. Dive direction is unpredictable. Dolphins in close proximity showing high levels of interaction (animals touching each other, rubbing their bodies). Fins and flukes often break the surface of the water. Frequent aerial behaviour such as leaps and summersaults.
- Milling (M): Movement slow and with no apparent direction. Dolphins swim in close proximity, but without interaction. No aerial behaviour, activity levels are low. Dolphins surface in a synchronised manner and most of the time is spent at the water's surface. Dive angles are shallow.

To avoid pseudoreplication of behaviours within a school and to minimize dependence of data, only the first behavioural samples recorded for each school were used for analysis. Any apparent indication of animals interacting with the research boat as they were approached (e.g., animals being attracted to the boat or actively avoiding it) were recorded, but not used in the analysis, as these were not indicative of natural behaviour of the school. Schools for which behaviour could not be determined were also excluded from analysis.

Sea surface temperature (SST) for 1999 was obtained from recordings made at Eastern Breakwater (EB, Fig.4.1) during the boat surveys. For the remainder of the study, sea surface temperature data were obtained from the Australian Institute of Marine Science automatic weather station (AWS, Fig. 4.1). Monthly rainfall data were obtained from the Australian Bureau of Meteorology weather station located in Townsville.

4.2.3 Data Analysis

I conducted a two sample randomization test (Manly 1997) to assess if Beaufort sea state had an effect on sighting frequencies of Irrawaddy and humpback dolphin schools. The test consisted of comparing the difference in mean sea state at which both species were observed, with the difference obtained by randomly allocating the observed values between species. The Spearman's rank correlation (rS) test (Zar 1999) was used to assess if the school sizes observed for each species were affected by sea state conditions.

As survey effort was not uniform across the study period (Table 4.1, all tables have been placed at the end of this chapter to minimize interruption to the flow of the text, and printed on yellow colour paper for ease of location), the monthly numbers of

Irrawaddy and humpback dolphin schools sighted per hour of survey (i.e., sighting rates) were used to assess the occurrence and behavioural patterns of both species. School size and age composition could not be estimated for all dolphin schools encountered, because not all animals were available. Therefore, only dolphin schools with which I was able to maintain close contact were included in the analysis of school sizes and age composition. Dolphin schools suspected to have been sighted previously within the same survey (i.e., sightings close in time and same school size and composition) were excluded from the analysis.

Kruskall-Wallis rank-sum tests (Zar 1999) were used to test for evidence of inter-annual variation in sighting rates, school sizes, school age composition, seasonal variation in the behaviour of each species, and differences in the size of dolphin schools engaged in different behaviours. Following a significant Kruskal-Wallis test a multiple pairwise t-test with corrections for multiple testing (Benjamini and Hochberg 1995) was conducted to determine significant differences between the variables tested. The type and significance of correlations between sighting rates, school sizes, school age composition, and behaviour with sea surface temperature and rainfall were tested with the Spearman rank correlation (Zar 1999).

I also used two sample randomization tests to determine if there were any general or seasonal differences in sighting rates, school sizes, and school age compositions between Irrawaddy and humpback dolphins (i.e., interspecific differences). For general interspecific differences, I compared the observed difference between the means with the difference obtained by randomly allocating the observed values between species. To test for seasonal interspecific differences, I pooled the data collected during the wet (January-March) and dry (April-November) seasons over all years. I then compared the observed differences between the means of each

species within each season with the differences obtained by randomly allocating the observed values among the two species.

To test for intraspecific (i.e., within each species) differences in sighting rates, school size and school age composition between seasons, the two sample randomization test compared the observed difference between the means with the difference obtained by randomly allocating the observed values between the two seasons for each species.

Randomization procedures were repeated 5000 times and the significance of the test evaluated by recording the number of times the differences obtained from randomization was greater than the observed value (Manly 1997). All tests were two-tailed and evaluated at $\alpha = 0.05$. To avoid an uncontrolled inflation of overall Type-I error rates in the multiple pairwise comparisons, the False Discovery Rate (FDR) correction procedure for multiple testing was used to adjust P-values (Benjamini and Hochberg 1995). Confidence intervals around the effect sizes (i.e., differences between means, correlation coefficients) were obtained by non-parametric bootstrapping using the bias corrected and accelerated method (BCa) (Efron and Tibshirani 1993).

The Kruskal Wallis rank sum tests, Spearman rank correlations, and confidence intervals were calculated with the R software version 1.7.0 for statistical computing and graphics (Ihaka and Gentleman 1996). Randomization tests were carried out with the POPTOOLS version 2.5 Excel add-in (Hood 2003). As in Chapter 3, interpretations of results are based on the examination of P-values together with confidence intervals around effect sizes, when appropriate. Confidence intervals are more informative than P-values in hypothesis testing as they describe the possible effect sizes, that could reasonably be expected in the population based on the data,

and can assist in the distinction between statistical significance and biological significance (Yoccoz 1991, Thomas 1997).

4.3 Results

4.3.1 Survey effort and sea state

Between 1999 and 2002, a total of 124.9 (wet season) and 504.7 (dry season) hours were spent in Cleveland Bay searching for Irrawaddy and humpback dolphins (Table 4.1). Because of environmental constraints during the study period, survey effort was not uniformly distributed across the study area. Survey effort across sections A (201 hrs), B (191 hrs), and C (179 hrs) was similar, however section D (59 hrs) was surveyed considerably less because of its exposure to strong south easterly winds (i.e., Beaufort > 3).

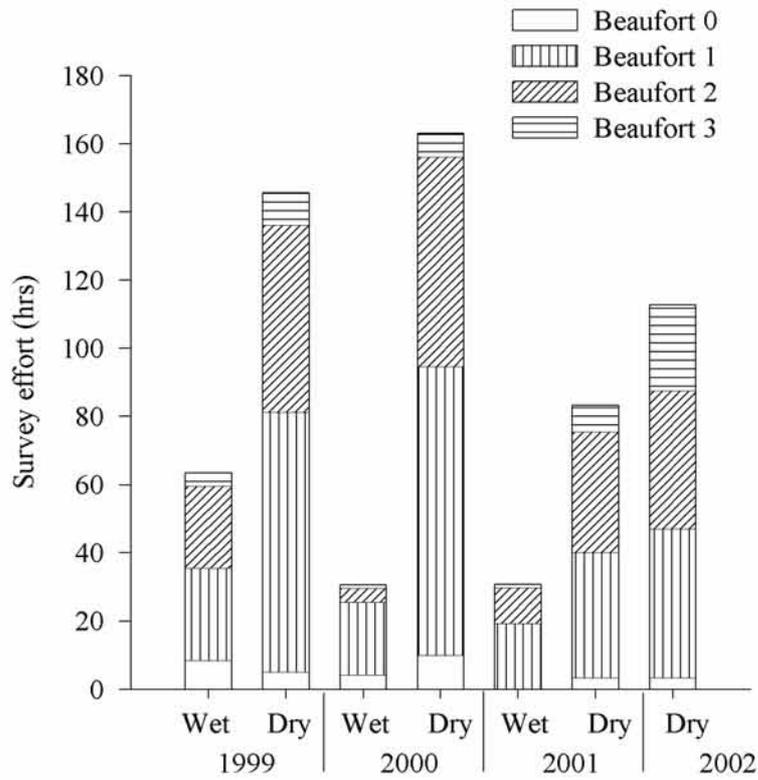
Survey effort throughout the study period took place mainly in Beaufort sea states 1 (49.2%) and 2 (36.5%) (Fig. 4.2a). During each year less than 10% of the effort was carried out in Beaufort sea states 0 and 3, with the exception of 2002 when 22.4% of the effort took place in Beaufort sea state 3. Over 60% of the survey effort in each Beaufort sea state took place during the dry season.

4.3.2 Effect of sea state on number of dolphin schools sighted and group size

A total of 117 schools of Irrawaddy dolphins and 143 schools of humpback dolphins were sighted in Cleveland Bay between 1999 and 2002 (Table 4.1). Irrawaddy and humpback dolphins were mainly sighted in Beaufort sea states 1 and 2 (Fig.4.2b). Sighting frequencies of both species were similar in Beaufort sea states 0 and 1, however humpback dolphins were sighted more frequently in Beaufort sea states 2 and 3 than Irrawaddy dolphins.

The randomization test on the difference between the mean Beaufort sea state at which Irrawaddy (Mean \pm SE = 1.4 ± 0.07) and humpback dolphins (1.6 ± 0.07) were observed indicated that humpback dolphins tended to be sighted at higher Beaufort sea states (2 and 3) than Irrawaddy dolphins (Difference = -0.23 , 95% CI = $-0.42, -0.04$, P = 0.02). Sea state did not affect the school sizes observed for Irrawaddy ($r_s = 0.06$, 95% CI = $-0.14, 0.28$ P = 0.534) or humpback dolphins ($r_s = 0.00$, 95% CI = $-0.16, 0.18$, P = 0.986).

a)



b)

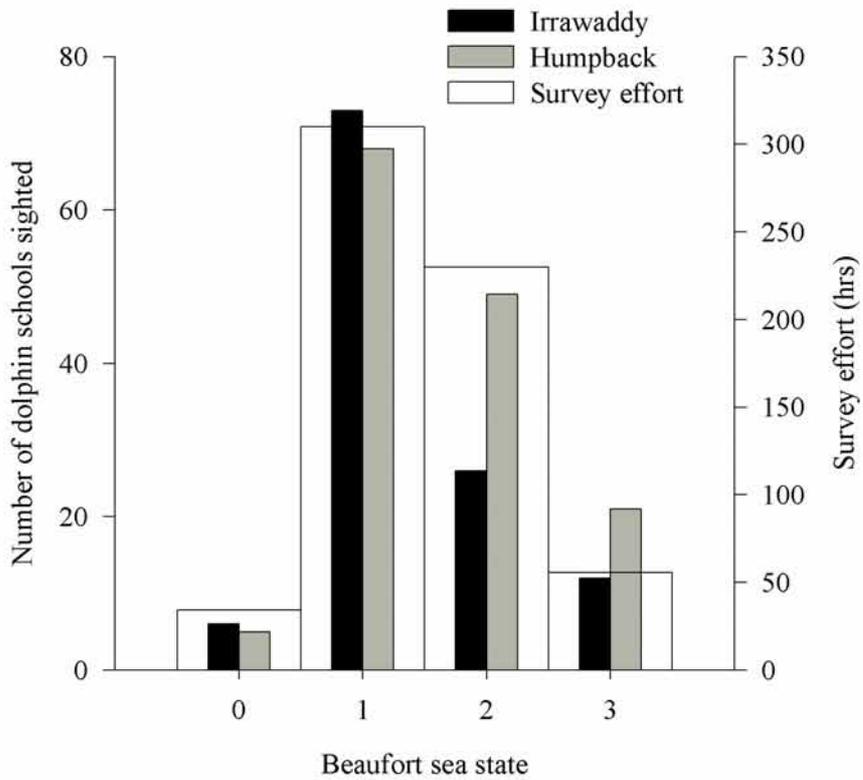


Figure 4.2 a) Distribution of survey effort by Beaufort sea state, b) Number of Irrawaddy and humpback dolphin schools sighted per sea state in Cleveland Bay.

4.3.3 *Interannual and seasonal sighting rates*

Overall, sighting rates of Irrawaddy and humpback dolphin schools showed no significant interannual variation (Fig. 4.3a, Table 4.2). The sighting rates of both species were similar during 1999, 2000, and 2001. However, sighting rates of humpback dolphins were higher than those of Irrawaddy dolphins in 2002. The low sighting rate of Irrawaddy dolphins in 2002 is likely a result from the greater survey effort carried out in Beaufort sea state 3 during this year (Fig. 4.2a).

During my study period, the climate in Cleveland Bay followed the typical tropical pattern with maximum SST (29°C) and rainfall (500 mm) during the wet season months of January through March (Fig 4.4a). Both Irrawaddy and humpback dolphins were seen throughout the study period (Fig. 4.4b, Table 4.3). The only month that Irrawaddy dolphins were not seen was February, but this is probably a result of the low survey effort carried out during this month in comparison with other months across the sampling period (Fig. 4.4b). Overall, there was no significant interspecific difference in the mean sighting rates (Table 4.4 first column). Neither species was sighted more frequently than the other during the wet or dry season (Table 4.4, second and third column). There were no seasonal intraspecific differences in sighting rates (Table 4.4, fourth and fifth column), and no correlation with SST or rainfall (Table 4.5).

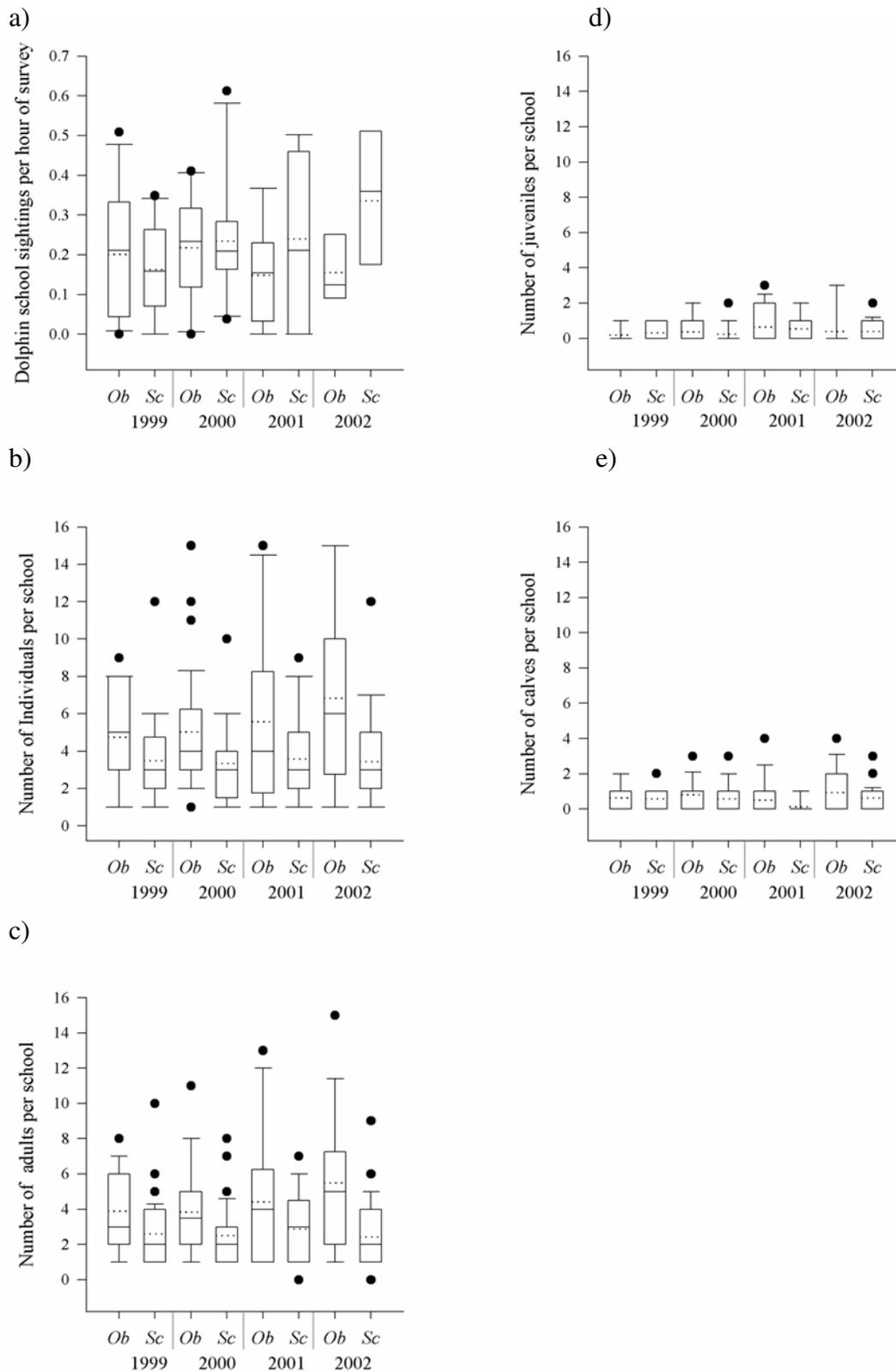


Figure 4.3 Boxplots indicating yearly variations in Irrawaddy (*Ob*) and humpback dolphins (*Sc*) sighting rates, school size and school composition: (a) sighting rates, (b) school size, and (c) number of adults, (d) juveniles and (e) calves observed per school. The box represents the interquartile range which contains the 50% of values. The solid line across the boxes represents the median, and the dotted line represents the mean. Vertical lines represent the data range excluding outliers (solid circles).

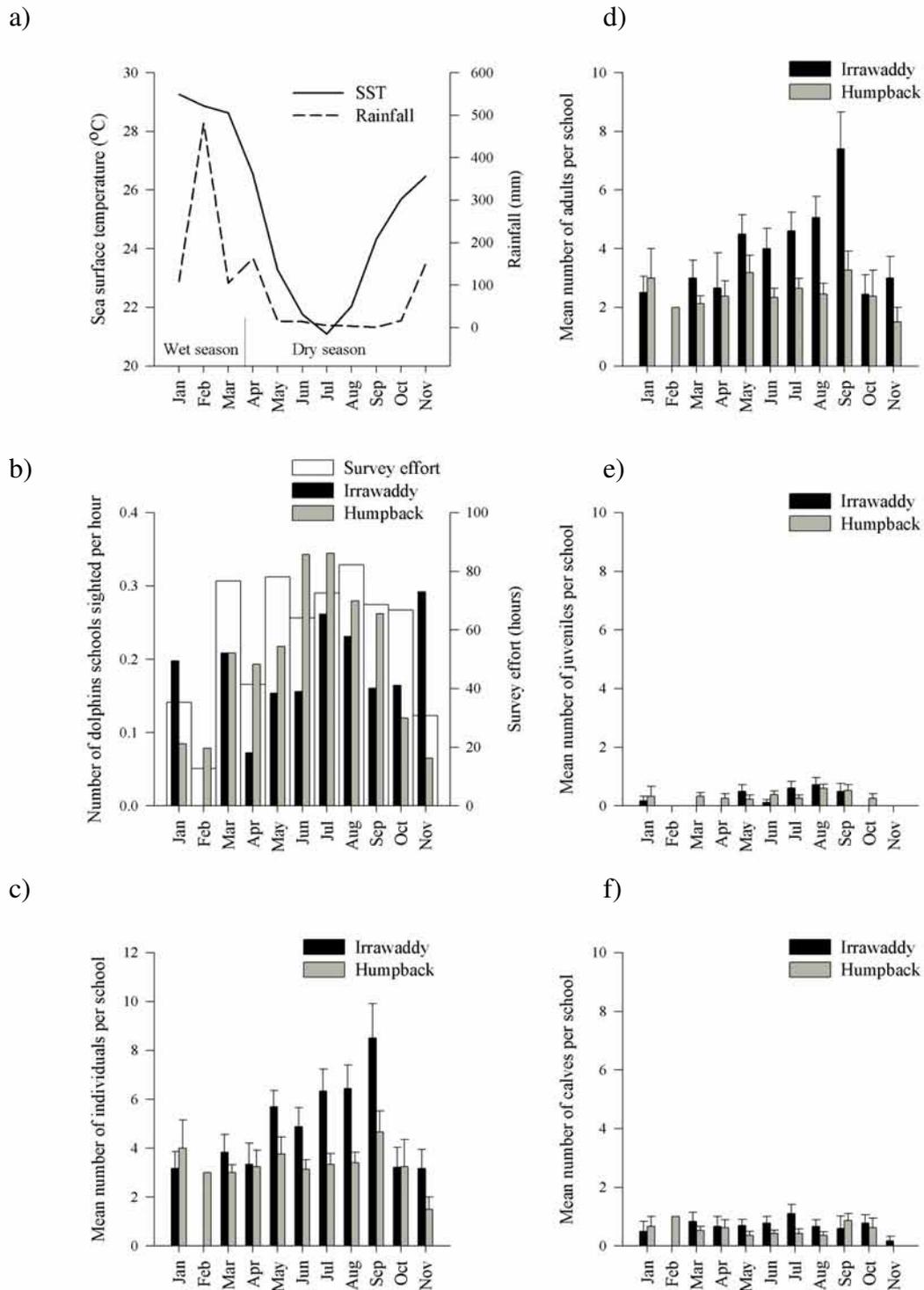


Figure 4.4 Seasonal variation in sighting rates, school size, and school composition of Irrawaddy and humpback dolphins across study period: a) mean sea surface temperature (SST) and rainfall, b) monthly number of dolphins school sighted per hour of survey, c) mean \pm SE school size, d) mean \pm SE number of adults per school, e) mean \pm SE number of juveniles per school, and f) mean \pm SE number of calves per school. There was only one sighting of humpback dolphins during the month of February, therefore school size and school age composition for this month does not represent the mean, but the value observed.

4.3.4 Behaviour Patterns

Foraging and travelling were the most frequently observed behaviours for both Irrawaddy (Foraging: 48%, Travelling: 44%) and humpback dolphins (Foraging: 44%, Travelling: 23%) (Fig. 4.5a). Humpback dolphins also foraged frequently behind trawlers (12%), a behaviour that was never seen for Irrawaddy dolphins. Both species appeared to show a seasonal variation in their behavioural activities, with predominant behaviours peaking during the dry season months (Fig. 4.5b, c). However, the peaks in the predominant behaviours of both species showed no strong seasonal differences at the intraspecific level (Table 4.6). There was a weak indication that humpback dolphins spent more time socializing than Irrawaddy dolphins, particularly during the dry season (Table 4.6).

4.3.5 School sizes

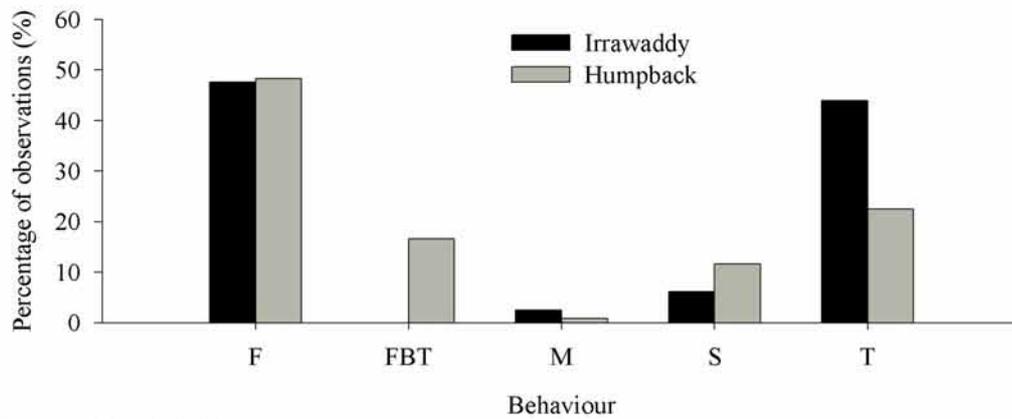
I was able to estimate the size and age composition of 101 out of 117 schools of Irrawaddy dolphins, and of 135 out of 143 schools of humpback dolphins. Schools of Irrawaddy dolphins varied in size from 1 to 15 animals, with an overall mean of 5.3 (SE = ± 0.35) (Fig. 4.6a). The modal school size for Irrawaddy dolphins was 8 animals (15.8%), followed by schools of 5 (12.9 %), 3 (12.9 %) and single animals (12.9 %). The school size of humpback dolphins ranged from 1 to 12 animals, with a mean of 3.5 (SE = ± 0.19) and a mode of 2 (26.7 %) (Fig. 4.6a).

There was no significant interannual variation in the sizes of Irrawaddy and humpback dolphin schools (Fig. 4.3). Overall, Irrawaddy dolphins formed larger schools than humpback dolphins (Table 4.4). During the wet season, both species were encountered in schools of similar size (Table 4.4). Irrawaddy dolphins formed larger schools in the dry season than in the wet season, and thus school size of

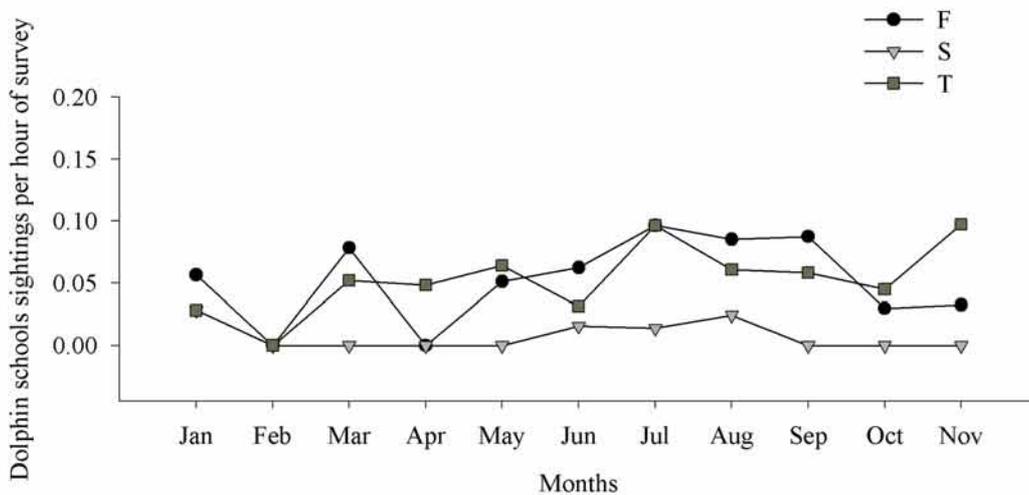
Irrawaddy dolphins was greater than humpback dolphins during the dry season (Table 4.4). The size of Irrawaddy dolphin schools was negatively correlated with SST and rainfall (Table 4.5).

The school size of Irrawaddy dolphins did not vary with behaviour (Kruskal-Wallis test: $H = 2.5$, $df = 2$, $P = 0.284$, Fig. 4.7). Irrespective of their behavioural activity, schools of Irrawaddy dolphins typically consisted of approximately 5 to 6 animals. In contrast, the size of humpback dolphin schools showed significant variations with behaviour (Kruskal-Wallis test: $H = 23.5$, $df = 3$, $P < 0.001$, Fig. 4.7). Schools of humpback dolphins were considerably larger in size when socializing than foraging (Pairwise t test: $t = -5.03$, $df = 70$, $P < 0.001$), foraging behind trawlers (Pairwise t test: $t = -2.46$, $df = 32$, $P = 0.008$), or travelling (Pairwise t test: $t = 4.66$, $df = 39$, $P < 0.001$). Additionally, schools foraging behind trawlers were larger than schools foraging independently of trawlers (Pairwise t test: $t = -2.41$, $df = 76$, $P = 0.035$), or travelling (Pairwise t test: $t = 2.53$, $df = 45$, $P = 0.038$).

a)



b) Irrawaddy dolphins



c) Humpback dolphins

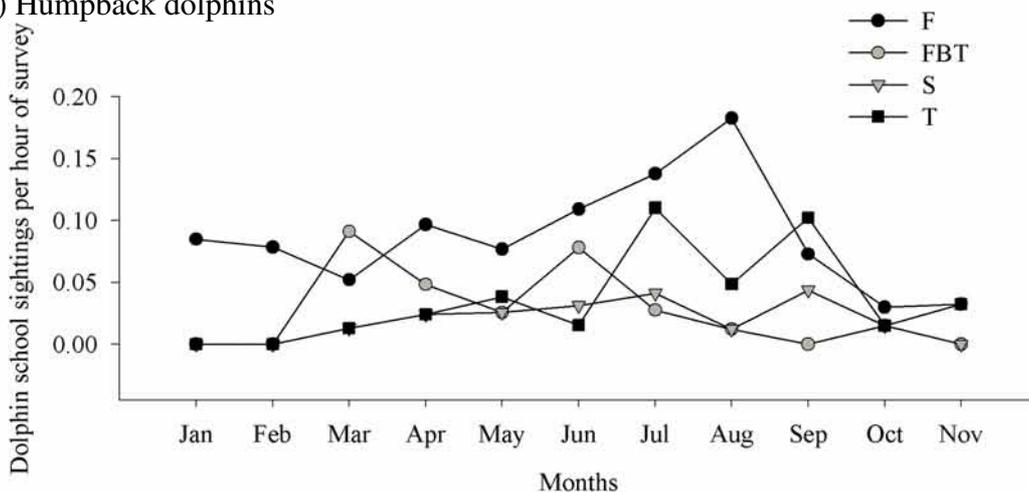


Figure 4.5 General and seasonal variation in the behaviour (F= Foraging, FBT = Foraging Behind Trawler, M= Milling, S = Socializing, T = Travelling) of Irrawaddy and humpback dolphins in Cleveland Bay: a) percentage of schools of each species observed in each behavioural category; b) seasonal variation in the sighting rates of the predominant behaviours observed for Irrawaddy dolphins; and c) seasonal variation in the sighting rates of the predominant behaviours observed for humpback dolphins.

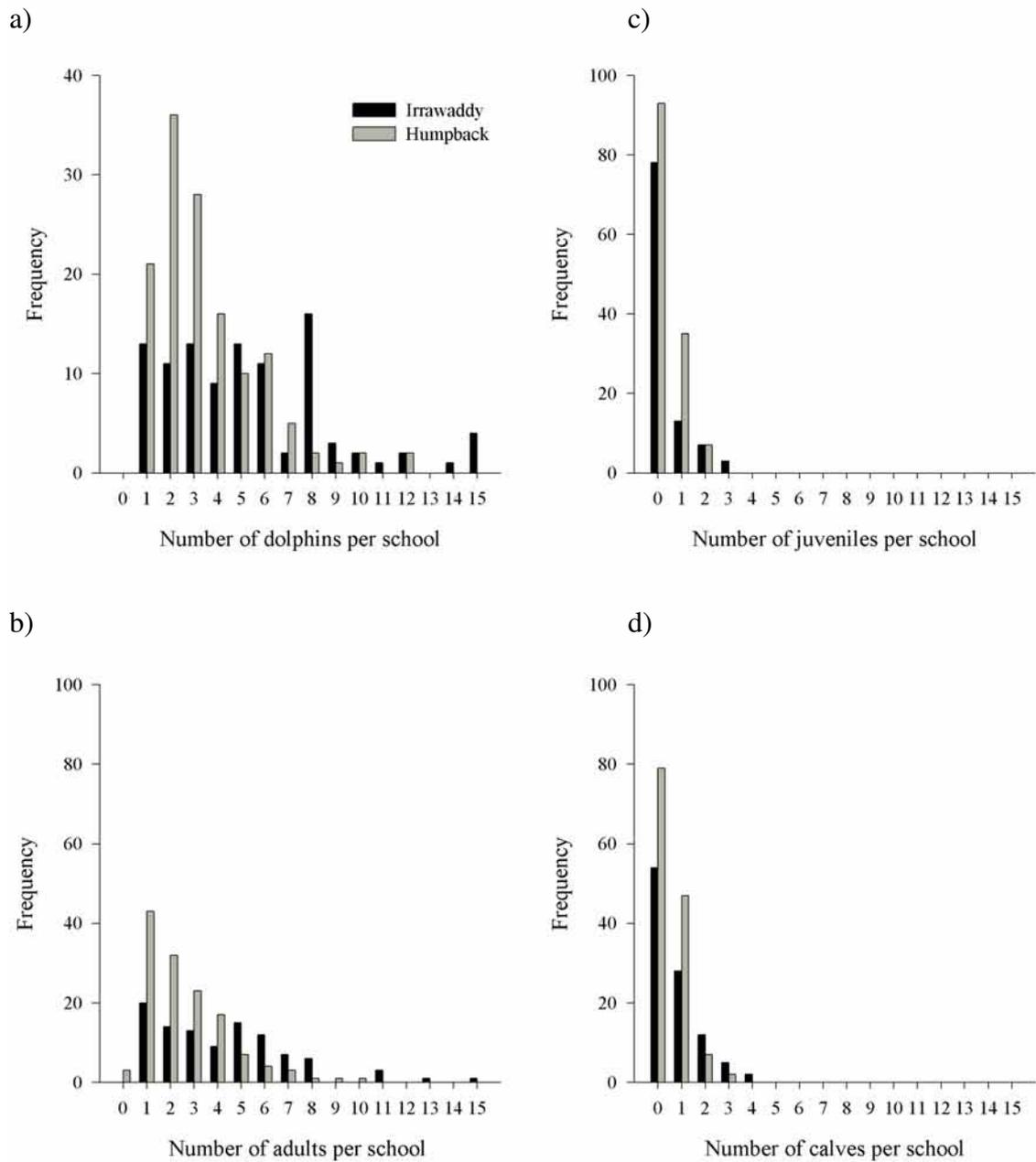


Figure 4.6 Frequency distribution of school size and school age composition of Irrawaddy and humpback dolphins in Cleveland Bay: a) school size and (b) number of adults, (c) juveniles and (d) calves observed per school.

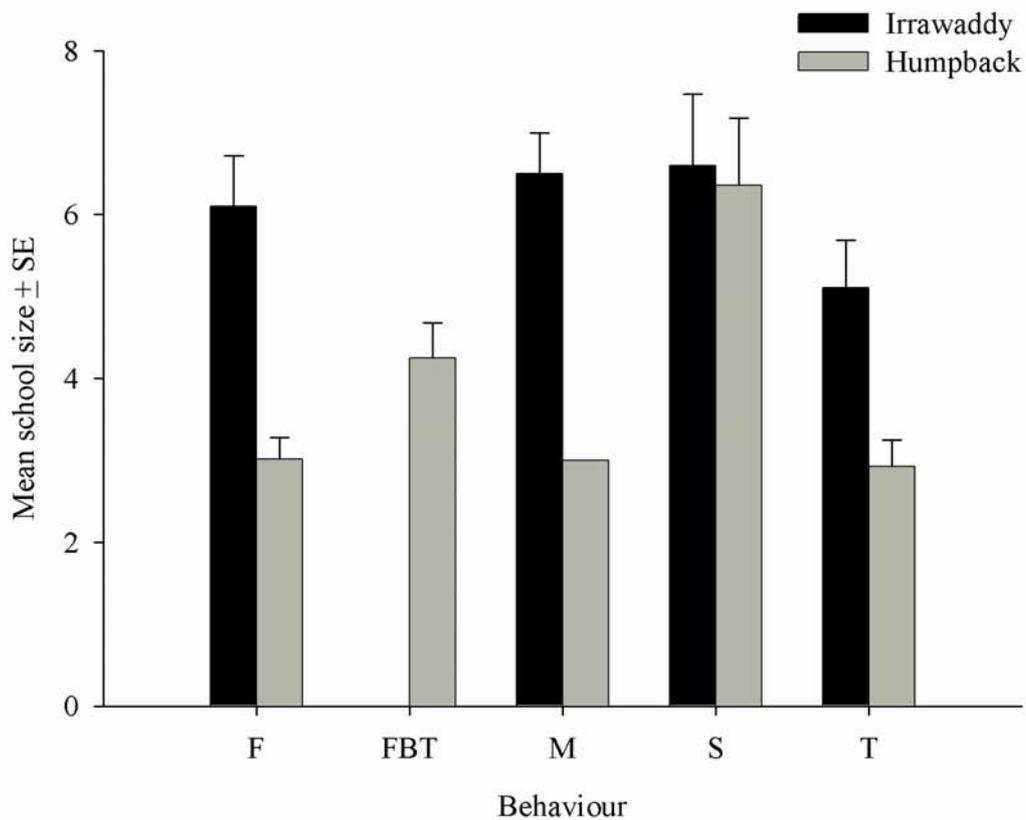


Figure 4.7 Variation in the mean school size of Irrawaddy and humpback dolphins engaged in different behavioural activities (F = Foraging, FBT = Foraging Behind Trawler, M = Milling, S = Socializing, T= Travelling).

4.3.6 School age composition

Schools containing adults, calves, and juveniles were seen throughout most of the study period (Fig. 4.4d, e, f). Overall, the number of adults, juveniles and calves of Irrawaddy dolphins tended to peak during the dry season, while humpback dolphins showed a more uniform pattern (Fig. 4.4d, e, f).

While the number of adults and juvenile humpback dolphins per school showed no variation between 1999 and 2002, the number of calves per school showed a significant interannual difference (Fig. 4.3e, Table 4.2). Fewer humpback dolphin calves per school were observed during 2001 than any other year (1999-2001: $t =$

3.49, $df = 13$, $P = 0.024$, 2000-2001: $t = 2.33$, $df = 14$, $P = 0.070$, 2001-2002: $t = 3.21$, $df = 9$, $P = 0.033$).

Irrawaddy and humpback dolphin schools were mainly composed of adults (Irrawaddy, Mean \pm SE: adults = 81 % \pm 1.8%, juveniles = 5 % \pm 1.1 %, calves = 13 % \pm 1.7 %; Humpback: adults = 75 % \pm 1.9% , juveniles = 11 % \pm 1.8 %, calves = 13 % \pm 1.5 %). The number of adult Irrawaddy dolphins per school ranged from one to 15, with an overall mean of 4.2 (SE = \pm 0.28) (Fig. 4.6b, Table 4.3). The number of adult humpback dolphins per school ranged between zero to 10 animals, with an overall mean of 2.6 (SE = \pm 0.16) (Fig. 4.6b, Table 4.3). Schools of Irrawaddy dolphins containing one (19.8 %) or five adults (14.9 %) were the most frequently encountered, while schools including one (31.9 %) or two (23.7 %) adults were most common for humpback dolphins. Thirty-nine schools of Irrawaddy dolphins (38.6%) and 45 schools of humpback dolphins were composed solely of adults. All single animal sightings of Irrawaddy dolphins (Irrawaddy = 13) were adults. The majority (86 %) of sightings of single humpback dolphins were also adults. The number of juveniles per school ranged between zero and three for Irrawaddy dolphins (Mean \pm SE = 0.4 \pm 0.07) and from zero to two for humpback dolphins (Mean \pm SE = 0.4 \pm 0.05) (Fig. 4.6c, Table 4.3). Schools composed solely of juveniles were only observed for humpback dolphins and consisted of single animals ($n = 3$). The number of calves per school ranged from zero to four for Irrawaddy dolphins (Mean \pm SE = 0.7 \pm 0.10), and from zero to three for humpback dolphins (Mean \pm SE = 0.5 \pm 0.06) (Fig. 4.6d, Table 4.3).

Overall, Irrawaddy dolphin schools contained a higher number of adults and calves than humpback dolphin schools (Table 4.4). This interspecific difference appears to be particularly strong during the dry season (Table 4.4). However, in

proportion to the total number of animals within a school, Irrawaddy dolphins had a greater number of adults than humpback dolphin schools (Difference = 0.06, 95% CI = 0.03, 0.10, P = 0.025), but not a greater proportion of calves (Difference = 0.00, 95% CI = -0.03, 0.03, P = 0.990). Humpback dolphins had a greater proportion of juveniles per group than Irrawaddy dolphins (Difference = 0.06, 95% CI = -0.10, -0.03, P = 0.01).

At the intraspecific level, the number of adult Irrawaddy dolphins per school was higher in the dry season than in the wet season (Table 4.4). Although the number of juveniles showed no significant difference between seasons, confidence intervals indicated that the number of juvenile Irrawaddy dolphins per school was also likely to be higher during the dry season (Table 4.4). The number of adult and juvenile Irrawaddy dolphins per school showed strong negative correlations with mean monthly SST and rainfall (Fig. 4.4a, 4.4e, Table 4.5).

4.4 Discussion

4.4.1 Effect of sea state on sightability of Irrawaddy and humpback dolphins

Beaufort sea state can have important effects on our ability to sight cetaceans and consequently bias abundance estimates from line transect surveys (Palka 1996). The randomization test on the effect of Beaufort sea-state on sighting frequencies of Irrawaddy and humpback dolphins revealed heterogeneities in their sightability that will need to be considered in the design and analysis of studies using line-transect sampling to estimate abundance. From this study, it is clear that the sightability of Irrawaddy dolphins decreased at Beaufort sea states ≥ 2 . The effect of including data collected in Beaufort sea states ≥ 2 will negatively bias abundance estimates of Irrawaddy dolphins. Similarly, analysis of line transect data collected at different

Beaufort sea states in Hong Kong showed that sighting rates of humpback dolphins decreased in Beaufort sea state >3 (Jefferson and Leatherwood 1997).

My estimates of the occurrence patterns of Irrawaddy dolphins in Cleveland Bay are negatively biased because of the effect of Beaufort sea state on sightability of this species. However as most of our survey effort took place in Beaufort sea states ≤ 1 , I expect this bias to be minimal.

4.4.2 *Occurrence patterns*

Despite the effect of Beaufort sea state on sighting frequencies, Irrawaddy and humpback dolphins were observed throughout the year in the coastal waters of Cleveland Bay. The low survey effort along the eastern section of Cleveland Bay (section D, Fig. 4.1) in comparison with other areas could be a source of bias in the occurrence patterns of both species in the study area. If animals were in section D more often than in any other section, sighting rates are negatively biased. However, most of this section lacks river mouths, and dredge channels features that appear to influence the habitat preferences of Irrawaddy and humpback dolphins (see Chapters 3 and 5). As a result, I suspect that animals do not spend too much time in these areas.

I found no evidence of seasonal occurrence patterns for both species (Table 4.4). Accidental catches of Irrawaddy and humpback dolphins in shark nets set off Townsville between 1968-1979 during most months of the year (Heinsohn 1979) also support the apparent year-round use of Cleveland Bay by both species.

The spatial and temporal variability in the occurrence patterns of cetacean populations is determined by several biological (e.g., prey availability, predator avoidance) and physiographic (e.g., bathymetry) factors (Benson et al. 2002, Davis et al. 2002, Jaquet and Gendron 2002). Seasonal shifts in the occurrence patterns of delphinids have been most frequently related to prey dynamics and predation risk

(Nichol and Shackleton 1996, Heithaus and Dill 2002, Benoit-Bird and Au 2003, Bräger et al. 2003). In Algoa Bay and off the Natal coast, South Africa , and in Maputo Bay, Mozambique, humpback dolphins were seen more often during summer months (November-April) and this trend appears to be related to increases in prey abundance (Karczmarski et al. 1999a, Guissamulo and Cockcroft 2004).

Daylight behaviour of Irrawaddy and humpback dolphins in Cleveland Bay was dominated by foraging (Fig. 4.5a) and it is apparent that Cleveland Bay represents an important feeding habitat within the home range of both species, or that animals whose home range is Cleveland Bay need to spend most of their time foraging for food. The lack of seasonal and interannual variation in the occurrence patterns of both species indicates prey populations in Cleveland Bay are stable and sufficiently large to support both species. Irrawaddy and humpback dolphins feed on a wide variety of fish, and cephalopods associated with coastal and estuarine environments (Heinsohn 1979, Barros et al. 2004).

As mentioned in Chapter 2, the limited data on the diets of Irrawaddy and humpback dolphins suggest that both species are generalist feeders taking food from both the bottom and from the water column (see Appendices 7 and 8). The mangrove areas and seagrass beds surrounding Cleveland Bay support a highly diverse and abundant fish community composed of several fish families (e.g., Leiognathidae, Haemullidae, Clupeidae, Engraulidae) (Robertson and Duke 1987, 1990) that have been identified as prey of Irrawaddy or humpback dolphins (Heinsohn 1979, Barros et al. 2004). Recruitment and peaks in fish abundance for Cleveland Bay vary throughout the year depending on the individual species (Robertson and Duke 1987, 1990). It is probable that this complex pattern of variability in fish availability maintains a constant supply of prey resources throughout the year following both

dolphin species to occur year round in the bay. The co-occurrence of both species in Cleveland Bay also suggests that there is some level of spatial or temporal resource partitioning, permitting their coexistence. Studies on their space use and habitat preferences in Cleveland Bay have shown that although both species space utilization patterns overlap considerably, there are differences in their habitat preferences (see Chapters 3 and 5).

4.4.3 *School size and age composition*

Identifying which, and how, ecological (e.g., prey availability, predation, competition) and social factors (e.g., mating, alloparental care, learning) influence the size and composition of animal groups, and how they do so, is a principal theme of behavioural ecology (Alexander 1974, Wrangham and Rubenstein 1986, Janson and Goldsmith 1995). As a result, comparative studies of intra- and interspecific patterns have become fundamental to the development and subsequent testing of hypotheses explaining group living in animal societies (Wrangham et al. 1993, Chapman et al. 1995, Ebensperger and Cofre 2001). Comparative studies of school size and composition across different species of marine mammals are rare, and have generally relied on information from studies that differed in location, duration, and methodology (Gygax 2002a, b). Irrawaddy and humpback dolphins in Cleveland Bay offered an exceptional opportunity to examine interspecific differences in school size and composition between distantly related delphinids co-existing under similar ecological conditions. In this study, I found that Irrawaddy and humpback dolphins exhibit significantly different school dynamics, with Irrawaddy dolphins forming larger schools, with a greater number of adults and calves than humpback dolphins (Table 4.4). These differences may reflect disparity in the ecological, social, and evolutionary factors shaping the grouping patterns of each species

Variation in school sizes among delphinids has been related to food availability (Heithaus and Dill 2002), predation risk (Heithaus and Dill 2002), interspecific competition over food (Heithaus 2001b, Acevedo-Gutierrez 2002), optimal foraging (Baird and Dill 1996), social functions (Connor et al. 1992a, Baird and Dill 1996, Connor et al. 2000b), and phylogeny (Gygax 2002b). As individuals seek to maximize their fitness by pursuing strategies that optimize their current opportunities, the range of possible grouping sizes will be determined by the trade-offs in the per capita benefits (e.g., reduction in risk of predation, location of food) and costs (e.g., increase in intraspecific competition) of group living. In terrestrial mammals, it has been shown that no single factor is likely to explain grouping sizes, and ecological and social factors may strongly interact to produce the observed patterns (Packer et al. 1990, Isbell and Young 1993, Chapman et al. 1995). Using available information about the habitat use patterns, predator occurrence, and social structure of Irrawaddy and humpback dolphins, I discuss below some of the ecological and social factors that might explain the intra and interspecific differences in their school size and composition patterns.

4.4.3.1 Food availability

Several studies, especially of primates, have provided evidence that food distribution and abundance may constrain grouping sizes, with the upper size limit of groups limited by increased intragroup competition for food (Wrangham et al. 1993, Janson and Goldsmith 1995). As food availability increases, the costs of feeding in a large group decreases, and consequently the maximum possible group size increases. For example, in Shark Bay, the group size of bottlenose dolphins appears to be responsive to a trade-off between food availability and predation risk. Foraging

bottlenose dolphins formed larger group sizes in the more productive shallow habitats during months when sharks were not abundant (Heithaus and Dill 2002).

In this study, humpback dolphins formed larger schools while foraging behind trawlers than when foraging independently of trawlers. Trawlers provide a reliable, easily located, and large source of food for dolphins through the provision and concentration of prey while trawler nets are in use and while catches are being sorted. This may allow humpback dolphins to aggregate in larger numbers while reducing costs of intraspecific competition for food. The largest school sizes of humpback dolphins in Hong Kong occurred when animals were foraging behind trawlers (Parsons 1998a, Jefferson 2000). Similarly bottlenose dolphins associating with trawlers in Moreton Bay exhibited larger school sizes than non-trawler dolphins (Chilvers and Corkeron 2001). Schools of Irrawaddy dolphins did not forage behind trawlers and their school size did not change with behaviour. These behavioural traits might be indicative of different feeding habits, foraging strategies, or pressure from other selective forces (e.g., predation).

4.4.3.2 *Predation risk*

Predation risk is considered one of the major ecological determinants driving group-living, with individuals in larger groups reducing their risk of predation through shared vigilance, and reduction of chances of being captured by predators (Pulliam 1973, Alexander 1974, Elgar 1989, Roberts 1996, Lingle 2001).

Differences in habitat use and predation risk might explain the differences in school size between Irrawaddy and humpback dolphins. At least 8 species of sharks of the family Carcharhinidae and Sphyrnidae, including tiger sharks *Galeocerdo cuvier*, a regular predator of delphinids (Heithaus 2001b), use the coastal waters of Cleveland Bay as a nursery area (Simpfendorfer 1992, Simpfendorfer and Milward 1993). Tiger

sharks change their diet as they grow, and only large individuals (> 3 m in length) appear to feed on dolphins and other large bodied prey (e.g., sea turtles, dugongs) (Heithaus 2001b). Although, most of the tiger sharks caught in Cleveland Bay are < 3 m, animals up to 4.2 m have been caught in coastal waters (Simpfendorfer 1992). In Cleveland Bay, individuals of both Irrawaddy and humpback dolphins show scars resulting from interactions with sharks (personal observations) and dolphin remains were identified among the stomach contents of tiger sharks caught in Cleveland Bay (Simpfendorfer 1992). Adult and juvenile tiger sharks are present in Cleveland Bay almost year round, with catch rates of mature specimens peaking during September to October (Simpfendorfer 1992). Studies on tiger sharks and bottlenose dolphins (*Tursiops aduncus*) in Shark Bay, Western Australia, showed that tiger sharks occurred in shallow water habitats (waters < 4 m, but predominantly < 2.5 m with bottom covered with seagrass) more often than expected during both warm and cold months, and that dolphins formed larger groups in these shallow habitats as a result of increasing predation risk (Heithaus and Dill 2002).

In Cleveland Bay, Irrawaddy dolphins showed preference for shallow waters (< 2 m deep), close to river mouths, and seagrass meadows (see Chapter 5). Dugongs (*Dugong dugon*), and sea turtles (mainly green turtles: *Chelonia mydas*) which are known to be prey of tiger sharks (Simpfendorfer 1992, Heithaus 2001a, Simpfendorfer et al. 2001), also occur predominantly in the shallow areas of Cleveland Bay (Preen 1999). Although humpback dolphins overlapped greatly in space use with Irrawaddy dolphins, they preferred slightly deeper waters (>2 m), dredge channels (> 2 m and > 10 m deep), and areas with coral reefs than Irrawaddy dolphins (see Chapter 5). Because of their shallower habitat preferences, and co-occurrence with other species known to be major prey of tiger sharks, Irrawaddy

dolphins might be exposed to higher risks of predation than humpback dolphins. Their larger school sizes might act as an anti-predator strategy. The larger school sizes of Irrawaddy dolphins observed during the dry season (Table 4.4) are consistent with the hypothesis that predation risk might be higher during these months of the year, which coincides with the greater catch rates of adult tiger sharks in Cleveland Bay (Simpfendorfer 1992).

Group composition may also be affected by predation risk, as adults may possess superior abilities to detect predators than conspecific juveniles or calves (Van Schaik and Van Noordwijk 1989, Van Schaik and Hoersterman 1994, Lingle and Wilson 2001). For example, adult females of white tailed deer (*Odocoileus virginianus*) and Mule deer (*O. hemionus*) detected approaches by predators sooner than juvenile conspecifics (Lingle and Wilson 2001). In some species of primates, adult males are known to be more vigilant and better at detecting potential predators than females (Van Schaik and Van Noordwijk 1989, Van Schaik and Hoersterman 1994). The age composition of dolphin schools is likely to be affected by predation risk. For example, Corkeron (1987) observed that adult female bottlenose dolphins are more likely to avoid close proximity to sharks, while males are less evasive. Heithaus (2001c) also provided evidence that adult male bottlenose dolphins appear to be more willing to risk shark predation than adult females. The greater number and proportion of adults in Irrawaddy dolphin schools may reflect an anti-predator strategy, improving detection or defence against predators.

4.4.3.3 *Interspecific interactions*

Interactions between sharks and dolphins are not limited to predator-prey interactions, but also include competitive interactions for food (Heithaus 2001b, Acevedo-Gutierrez 2002). Studies on interspecific interactions between sharks and

bottlenose dolphins feeding on the same schooling fish in Costa Rica suggested that increases in dolphin group size during a feeding event prevent sharks from aggregating around the clump of prey and thus give advantages to the dolphins (Acevedo-Gutierrez 2002). Many of the Carcharhinid and Sphyrnid sharks in Cleveland Bay feed largely on teleost fishes (Simpfendorfer and Milward 1993), a trait in common with Irrawaddy and humpback dolphins (Heinsohn 1979, Barros et al. 2004). As many of the sharks occurring in Cleveland Bay are not considered regular, occasional, or suspected predators of delphinids (Heithaus 2001b) and all of the sharks were collected in waters less than 5 m deep (Simpfendorfer and Milward 1993), it is possible that sharks compete with dolphins for food. Differences in Irrawaddy and humpback dolphins school size might reflect specific differences in the level of dietary overlap with sharks and thus on the degree of competitive interactions each dolphin species faces with the sharks.

Behavioural interactions between Irrawaddy and humpback dolphins might also play a role in the school size patterns observed. Interactions between both species in Cleveland Bay have been mainly aggressive/sexual with humpback dolphins always initiating such interactions (see Chapter 9). Most of the aggressive/sexual interactions involved adult humpback dolphins and an Irrawaddy dolphin adult and a calf, even though the school of Irrawaddy dolphins might have been composed of up to 21 animals (see Chapter 9). Although the nature of these interactions is not fully understood, they do not seem to be reciprocal; Irrawaddy dolphins swam away or showed resistance to physical contact from humpback dolphins. It is possible that individual Irrawaddy dolphins form larger schools as a way of avoiding encounters with humpback dolphins. By forming larger schools Irrawaddy dolphin might improve detection of humpback dolphins through shared vigilance, and also reduce

the probability any individual within the school will interact with humpback dolphins, similar to an anti-predator strategy. The avoidance of conspecific attacks has been found to influence the grouping patterns and social organization of other mammal species including primates (Treves and Chapman 1996, Treves 1998, Borries et al. 1999), and lions (Packer et al. 1990, McComb et al. 1994, Grinnell and McComb 1996).

Predation risk and interspecific interactions may also offer a possible explanation for differences in school size at the intraspecific level. While the mean school size of Irrawaddy dolphins in Cleveland Bay (Mean \pm SE = 5.3 ± 0.35) is comparable to school sizes previously reported in coastal estuarine areas off the Queensland coast (Parra et al. 2002), and in Philippines waters (Dolar et al. 2002), riverine and lagoonal populations appear to have slightly smaller school sizes of 3 to 4 animals (Smith et al. 1997, Krebs 2002, Stacey and Hvenegaard 2002). However, similar school sizes to coastal populations have been observed during periods of low water levels in the Mahakam River in Indonesia (Krebs 2002). The smaller school sizes reported for riverine populations of Irrawaddy dolphins might reflect: 1) the lack of natural predators or potential competitors, in this habitat in comparison to coastal habitats; or 2) limited food resources.

School sizes of humpback dolphins in Cleveland Bay (Mean \pm SE = 3.5 ± 0.19) are similar to those reported for populations in southeast Queensland (Corkeron 1990), Hong Kong (Jefferson and Leatherwood 1997, Parsons 1998a, Jefferson 2000), and India (Parsons 1998b). On the other hand, the mean school sizes of 2-3 animals observed in these areas are considerably smaller than the mean school size of about 7 animals observed in different regions of South Africa (Saayman and Tayler 1979, Durham 1994, Karczmarski 1999, Karczmarski et al. 1999a), and the larger school

sizes averaging 11 to 14 individuals in Mozambique (Guissamulo and Cockcroft 2004), Madagascar (Razafindrakoto et al. 2004), and in the Arabian region (Baldwin et al. 2004). The larger school sizes reported for the populations in South Africa, Madagascar and in the Arabian region could reflect greater predation and competitive interactions with sharks in these regions. For example, in South Africa, humpback dolphins showed higher frequency of scarring by sharks than bottlenose dolphins (Cockcroft 1991), and moderate levels of prey overlap with sharks (Heithaus 2001b).

4.4.3.4 *Social factors and phylogeny*

Despite considerable evidence that ecological constraints influence the grouping patterns of animals, an increasing number of studies are finding that social factors may also play an important role in determining group size and composition (Chapman et al. 1995, Treves and Chapman 1996, Chapman and Pavelka *in press*). For example, in Shark, Bay, Western Australia, male bottlenose dolphins form cooperating groups of 2 to 3 animals to sequester and control the movement of individual females likely to be in estrus (Connor et al. 1992b). In my study, the largest schools of humpback dolphins were observed during socializing activities, thus the occasional formation of larger school sizes may provide increasing opportunities for mating or other social activity (e.g., playing, learning, and exchange of information).

My study on the social structure of Irrawaddy and humpback dolphins has shown that while adult Irrawaddy dolphins have strong and temporally stable association patterns, adult humpback dolphins appear to associate in schools that often change in composition as individuals join and leave resembling a “fission-fusion” society (see Chapter 7). These differences in social structure are supported by the constant observation of 5 to 6 Irrawaddy dolphins in a school irrespective of their predominant behaviour, in comparison to the more labile school sizes of three to six

humpback dolphins which vary in relation to their behavioural activity (Fig. 4.6). These striking differences in social structure might indicate specific differences in the importance of social constraints on school size and composition. The aggregation of Irrawaddy dolphins in larger school sizes than humpback dolphins, could serve important social functions such as alloparental care and social learning. These social factors are thought to play important roles in odontocetes with stable association patterns such as the killer whale, *Orcinus orca* (Baird and Dill 1996, Baird 2000), and sperm whale, *Physeter macrocephalus* (Whitehead 1996, Whitehead and Weilgart 2000). These important social functions are discussed further in Chapter 7.

Finally, although there are several socioecological factors that might explain the differences in school dynamics of Irrawaddy and humpback dolphins, there is also the possibility that the present traits resulted from evolutionary processes and common descent, rather than to adaptation. Studies on primates have shown that a species' evolutionary history can explain similarity or differentiation in behaviour and social organization among taxa (Struhsaker 1969, Di Fiore and Rendall 1994, Chan 1996, Thierry et al. 2000). Similarly, a recent comparative study on groups sizes in the superfamily Delphinoidea (Delphinidae, Phocoenidae and Monodontidae) concluded that phylogeny seemed to play an important role in the evolution of group size in Delphinoidea (Gygax 2002b). Thus closely related species are likely to share many aspects of their social and ecological adaptation due to their common evolutionary history.

As discussed in Chapter 2, the most recent classification of the family Delphinidae (LeDuc et al. 1999) placed Irrawaddy dolphins in the subfamily Orcininae together with Killer whales, *Orcinus orca*. On the other hand, humpback dolphins are grouped together with dolphins of the genus *Stenella*, *Delphinus*,

Tursiops, and *Lagenodelphis* in the subfamily Delphininae. This difference in phylogeny places Irrawaddy and humpback dolphins at two extreme points in the continuum of school dynamics and social structures in delphinids. Killer whales form stable long-term associations in matrilineal groupings with individuals rarely dispersing from maternal groups (Baird and Dill 1996, Baird 2000). This pattern appears to extend only to pilot whales within the Delphinidae (Amos et al. 1993, Ottensmeyer and Whitehead 2003). In contrast, some of the species closely related to humpback dolphins (i.e., *Stenella spp.*, *Delphinus spp.*, *Tursiops spp.*) appear to live in fluid societies with fission and fusion of groups observed frequently (Norris et al. 1994, Connor et al. 2000b, Neumann 2001).

It is clear that the pattern of differing school sizes and composition in Irrawaddy and humpback dolphins could be the result of a wide variety of ecological, social, and evolutionary factors. The relative importance that each of these factors has played in the evolution of school size and composition in both of these species remains to be studied. I have generated hypotheses that should serve as a guide to future investigations on determinants of school size and composition in Irrawaddy and humpback dolphins. Future research should be directed towards gaining a better understanding about their feeding habits, the distribution and abundance patterns of their prey and potential predators (i.e., sharks), and nature of interspecific interactions with sharks and between both dolphin species (See section 10.5 Future research directions, Chapter 10). As we gain a more detailed picture on the phylogeny of delphinids, their schooling patterns, and social structure, comparative phylogenetic methods should also reveal the importance of evolutionary history on their school dynamics.

4.5 Chapter summary

- The science base underpinning management efforts to conserve viable populations of Irrawaddy dolphins, *Orcaella brevirostris*, and humpback dolphins, *Sousa chinensis* in Australian waters is very limited. Information on some of the most basic ecological aspects for both species is lacking. As a result efforts towards their conservation and management have been held back.
- In this chapter, I have used information collected on both Irrawaddy and humpback dolphins between 1999 and 2002 in Cleveland Bay, northeast Queensland, Australia, to identify patterns in their occurrence, and school dynamics (i.e., school size and age composition).
- Results on the effect of Beaufort sea state on sighting rates of Irrawaddy and humpback dolphins indicated the sightability of Irrawaddy dolphins decreased under Beaufort sea states > 2 . This effect will produce a downwards bias in abundance estimates obtained using distance sampling techniques and will need to be considered in the design and analysis of such studies.
- Irrawaddy and humpback dolphins were present year-round in Cleveland Bay and there was no evidence of variation in their occurrence with year or season. Both species used Cleveland Bay mainly for foraging activities indicating this area represents an important feeding area within their home range. The year round presence and predominant foraging behaviour by both species suggest resources in Cleveland Bay are abundant and stable.
- Irrawaddy and humpback dolphins exhibited different school dynamics. Overall, schools of Irrawaddy dolphins were larger in size than those of humpback dolphins, and had a greater number of adults and calves. Irrespective of their behavioural activity, schools of Irrawaddy dolphins

typically consisted of approximately 5 to 6 animals. In contrast, the size of humpback dolphin schools showed significant variations with behaviour.

- Differences in school size and composition may be attributed to socioecological and phylogenetic factors. Potential explanations for the patterns and differences observed are provided in the light of food availability, predation risk, interspecific interactions, social structure and phylogeny. There is evidence that social as well as behavioural constraints may be responsible for differences in school size (see Chapters 7 and 9). The relative importance that predation risk, food availability and phylogeny might play in determining school sizes and composition in Irrawaddy and humpback dolphins remains to be tested

Table 4.1 Survey effort and number of Irrawaddy, and humpback dolphin schools sighted in Cleveland Bay between 1999 and 2002.

Year	Period covered	Searching effort (hrs)		Number of dolphin schools sighted			
		Wet season (Jan-March)	Dry season (Apr-Nov)	Irrawaddy		Humpback	
				Wet season	Dry season	Wet season	Dry season
1999	Jan-November	63.5	145.7	7	30	10	29
2000	Jan-November*	30.5	163.1	11	35	7	30
2001	Jan-October*	30.8	83.3	5	11	3	26
2002	May-October	NA	112.7	NA	18	NA	38
TOTAL		124.9	504.7	23	94	20	123

* Surveys during the month of February in both of these years were not possible due to bad weather.

Table 4.2 Yearly sighting rates (i.e., number of dolphins sighted per hour of survey) school size, and school composition of Irrawaddy and humpback dolphins in Cleveland Bay Dugong Protected Area. Significant interannual differences ($P < 0.05$) are in italics.

	1999		2000		2001		2002		Kruskal Wallis test results	
	Irrawaddy	Humpback	Irrawaddy	Humpback	Irrawaddy	Humpback	Irrawaddy	Humpback	Irrawaddy	Humpback
Sighting rates										
n	11	11	10	10	9	9	6	6		
Mean	0.20	0.16	0.22	0.24	0.15	0.24	0.16	0.34	H	2.28
SE	0.05	0.04	0.04	0.05	0.04	0.07	0.03	0.08	df	3
Range	0.00-0.51	0.00-0.35	0.00-0.41	0.04-0.61	0.00-0.37	0.00-0.50	0.08-0.27	0.00-0.57	P	0.515
School size										
n	31	36	38	33	14	29	18	37		
Mean	4.7	3.5	5.0	3.3	5.6	3.6	6.8	3.4	H	2.73
SE	0.05	0.04	0.04	0.05	0.04	0.07	0.03	0.08	df	3
Range	1-9	1-12	1-15	1-10	1-15	1-9	1-15	1-12	P	0.436
School composition										
Adults										
Mean	3.9	2.6	3.8	2.5	4.43	2.9	5.50	2.43	H	3.00
SE	0.41	0.31	0.38	0.30	1.03	0.37	0.86	0.30	df	3
Range	1-8	1-10	1-11	1-8	1-13	0-7	1-15	0-9	P	0.392
Juveniles										
Mean	0.2	0.3	0.4	0.2	0.64	0.55	0.39	0.38	H	1.55
SE	0.07	0.08	0.11	0.09	0.29	0.13	0.23	0.11	df	3
Range	0-1	0-1	0-2	0-2	0-3	0-2	0-3	0-2	P	0.670
Calves										
Mean	0.6	0.6	0.8	0.6	0.5	0.1	0.9	0.6	H	2.36
SE	0.14	0.10	0.15	0.14	0.29	0.07	0.31	0.12	df	3
Range	0-2	0-2	0-3	0-3	0-4	0-1	0-4	0-3	P	0.502

Table 4.3 General and seasonal differences in number of dolphins sighted per hour of survey (i.e., sighting rates), school size, and school age composition of Irrawaddy and humpback dolphins in Cleveland Bay over all years of study (1999-2002).

	General		Wet season		Dry season	
	Irrawaddy	Humpback	Irrawaddy	Humpback	Irrawaddy	Humpback
Sighting rates						
n	36	36	7	7	29	29
Mean	0.19	0.23	0.15	0.14	0.19	0.25
SE	0.02	0.03	0.06	0.04	0.02	0.03
Range	0-0.51	0-0.61	0-0.37	0-0.30	0-0.51	0-0.61
School size						
n	101	135	18	19	83	116
Mean	5.3	3.5	3.6	3.2	5.7	3.5
SE	0.35	0.19	0.54	0.31	0.40	0.22
Range	1-15	1-12	1-9	1-6	1-15	1-12
School composition						
Adults						
Mean	4.2	2.6	2.8	2.3	4.5	2.7
SE	0.28	0.16	0.44	0.25	0.32	0.18
Range	1-15	0-10	1-8	1-4	1-15	0-10
Juveniles						
Mean	0.4	0.4	0.1	0.3	0.4	0.4
SE	0.07	0.05	0.06	0.11	0.09	0.06
Range	0-3	0-2	0-1	0-1	0-3	0-2
Calves						
Mean	0.7	0.5	0.7	0.6	0.7	0.4
SE	0.10	0.06	0.24	0.12	0.11	0.06
Range	0-4	0-3	0-4	0-1	0-4	0-2

Table 4.4 General and seasonal interspecific and intraspecific differences in sighting rates, school size, and school age composition of Irrawaddy and humpback dolphins in Cleveland Bay over all years of study (1999-2002). Significant differences are in bold italics.

	General differences		Seasonal differences		
	Interspecific	Interspecific		Intraspecific	
	Irrawaddy-humpback	Irrawaddy-humpback (Wet)	Irrawaddy-humpback (Dry)	Irrawaddy (Wet-Dry)	Humpback (Wet-Dry)
Sighting rates					
Difference	-0.05	0.00	-0.06	-0.03	-0.09
95 % CI	-0.12, 0.02	-0.13, 0.13	-0.14, 0.02	-0.15, 0.07	-0.20, 0.02
P	0.355	0.984	0.984	0.691	0.355
School size					
Difference	1.9	0.5	2.2	-2.1	-0.4
95 % CI	1.1, 2.7	-0.58, 1.72	1.31, 3.08	-3.42, -0.78	-1.12, 0.37
P	< 0.001	0.544	< 0.001	< 0.001	0.544
School composition					
Adults					
Difference	1.638	0.6	1.9	-1.7	-0.4
95 % CI	1.0, 2.3	-0.3, 1.6	1.2, 2.6	-2.7, -0.6	-1.0, 0.2
P	< 0.001	0.363	< 0.001	0.033	0.430
Juveniles					
Difference	-0.01	-0.26	0.05	-0.37	-0.05
95 % CI	-0.2, 0.2	-0.5, 0.0	-0.1, 0.3	-0.6, -0.2	-0.3, 0.2
P	1	0.221	1	0.221	1
Calves					
Difference	0.25	0.14	0.26	-0.02	0.10
95 % CI	0.04, 0.48	-0.29, 0.75	0.04, 0.53	-0.48, 0.58	-0.17, 0.33
P	0.08	0.90	0.08	1.00	0.90

Table 4.5 Spearman correlations (r_s) of Irrawaddy and humpback dolphins sighting rates, school sizes, and school age composition with sea surface temperature and rainfall in Cleveland Bay over all years of study (1999-2002). Significant correlations are in bold italics. P-values for multiple pairwise comparisons have been adjusted with the False Discovery Rate (FDR) correction method (Benjamini and Hochberg 1995).

	Sea surface Temperature		Rainfall	
	Irrawaddy	Humpback	Irrawaddy	Humpback
Sighting Rates				
r_s	-0.19	-0.30	-0.17	-0.21
95% CI	-0.51, 0.22	-0.58, 0.01	-0.49, 0.21	-0.49, 0.15
P	0.326	0.152	0.326	0.214
School Size				
r_s	-0.48	0.06	-0.44	-0.19
95% CI	-0.67, -0.16	-0.33, 0.44	-0.68, 0.01	-0.53, 0.22
P	0.015	0.769	0.015	0.61
School Composition				
Adults				
r_s	-0.41	0.09	-0.43	-0.17
95% CI	-0.67, -0.06	-0.28, 0.46	-0.67, -0.03	-0.50, 0.18
P	0.025	0.645	0.025	0.645
Juveniles				
r_s	-0.45	0.06	-0.43	-0.31
95% CI	-0.66, -0.12	-0.37, 0.48	-0.69, -0.09	-0.60, 0.07
P	0.018	0.737	0.018	0.192
Calves				
r_s	-0.09	0.21	0.05	0.15
95% CI	-0.44, 0.29	-0.18, 0.54	-0.30, 0.40	-0.26, 0.54
P	0.773	0.416	0.773	0.416

Table 4.6 General and seasonal interspecific and intraspecific differences in the number of dolphin school sighted per hour in each of the behavioural categories most frequently observed in Cleveland Bay over all years of study (1999-2002). Significant correlations are in bold italics. P-values for multiple pairwise comparisons have been adjusted with the False Discovery Rate (FDR) correction method (Benjamini and Hochberg 1995).

Behaviour	General differences		Seasonal differences		
	Interspecific Irrawaddy-humpback	Interspecific Irrawaddy-humpback (Wet)	Interspecific Irrawaddy-humpback (Dry)	Intraspecific Irrawaddy (Wet-Dry)	Intraspecific Humpback (Wet-Dry)
Foraging					
Difference	-0.03	-0.01	-0.03	0.02	0.00
95 % CI	-0.07, 0.01	-0.06, 0.02	-0.08, 0.02	-0.03, 0.04	-0.04, 0.03
P	0.565	0.982	0.565	0.982	0.982
Foraging Behind Trawler	NA	NA	NA	NA	
Difference	NA	NA	NA	NA	0.01
95 % CI	NA	NA	NA	NA	-0.03, 0.03
P	NA	NA	NA	NA	0.935
Socializing					
Difference	-0.02	-0.01	-0.02	0.00	-0.01
95 % CI	-0.03, 0.00	-0.04, 0.01	-0.04, 0.00	-0.01, 0.00	-0.03, 0.00
P	0.080	0.669	0.080	0.908	0.669
Travelling					
Difference	0.01	0.02	0.01	-0.05	-0.06
95 % CI	-0.04, 0.05	-0.01, 0.05	-0.03, 0.06	-0.09, -0.02	-0.10, -0.03
P	0.633	0.633	0.633	0.400	0.400

Chapter 5

Space use and habitat preferences of sympatric Irrawaddy and Indo-Pacific humpback dolphins

In this chapter, I provide a quantitative assessment of the relative use of space and habitat preferences of Irrawaddy and Indo-Pacific humpback dolphins in Cleveland Bay. I identify areas of high and representative use, the behavioural activities associated with these areas, and the degree of interspecific overlap and concordance in space use. I also assess interspecific differences in habitat preferences

Chapter 5. Space use and habitat preferences of sympatric

Irrawaddy and Indo-Pacific humpback dolphins

5.1 Introduction

Conservation and management of wildlife requires an understanding of the space use and habitat preferences of target species. As discussed in Chapter 1, coastal dolphins are among the most threatened species of cetaceans because of their close proximity to anthropogenic activities (Thompson et al. 2000, DeMaster et al. 2001). However, we know little about the relationships between the space use, resource selection, and the underlying behavioural mechanisms of most species of coastal dolphins. Additionally, and as discussed in Chapter 1, very little is known of the mechanisms that allow sympatric coastal dolphins to coexist because studies have mainly focused on single species communities. Knowledge of the spatial dynamics and habitat preferences of coexisting species is important to understanding species-specific requirements, and thus provides valuable information on how we can manage areas effectively to meet their needs (Durant 1998, Johnson et al. 2000, Sachot et al. 2003).

As described in Chapter 2, Irrawaddy dolphins and Indo-Pacific humpback dolphins (hereafter humpback dolphins) are commonly found in shallow, coastal, and estuarine waters of the Indian and west Pacific Oceans (Stacey and Arnold 1999, Jefferson and Karczmarski 2001). There is great deal of concern about the long-term survival of both genera, as a result of increasing human populations in coastal zones throughout their range and associated human impacts (e.g., gillnetting, pollution, habitat loss) (Perrin et al. 1996, Smith and Jefferson 2002). Despite these concerns, our current understanding of their space use and habitat preferences is limited. Previous studies on the habitat use of Irrawaddy dolphins have focused on the

Mekong River population (Stacey and Hvenegaard 2002). Studies on humpback dolphins have been carried out only in the waters off South Africa (Karczmarski et al. 2000a) and around Hong Kong (Jefferson 2000).

In Australia, Irrawaddy and humpback dolphins occur in sympatry along most of the northern tropical coast (see Chapter 2). Recent taxonomic studies indicate Australian populations of Irrawaddy and humpback dolphins represent different species/subspecies from populations elsewhere (Beasley et al. 2002a, Rosenbaum et al. 2003). However, little is known of their ecology and their population status is uncertain (see Chapter 2, Parra et al. 2002, Parra et al. 2004). Reviews of aerial survey sightings throughout the region indicated both species occur mainly in coastal shallow waters (see Chapters 2 and 3, Corkeron et al. 1997, Parra et al. 2002). Boat-based line transect surveys in selected areas along the Queensland coast of Australia, confirm this distribution pattern (see Chapter 3). Nonetheless, the preference of Irrawaddy and humpback dolphins for certain environmental conditions or resource patches within these areas has not been quantified.

When the most productive habitats are also the most dangerous, habitat selection should reflect a trade off between the conflicting demands of food and risk of predation (Lima and Dill 1990, Grand 2002). Habitat selection by delphinids has been mainly studied by relating their spatial distribution to physical/chemical environmental factors that may influence the animals directly (e.g., thermoregulatory and energy demands) or indirectly (e.g., prey distribution, predator avoidance) (Bräger et al. 2003). Most studies have shown that coastal dolphins are not randomly distributed within their ranges, reflecting the spatial and temporal arrangement of resource patches (e.g., habitat, prey) and/or predators. For example, areas favoured by coastal bottlenose dolphins (*Tursiops truncatus*) in the Shannon estuary, Ireland,

Moray Firth, Scotland, and Clearwater, Florida occur over deep water areas with a steep seabed gradient (Wilson et al. 1997, Allen et al. 2001, Ingram and Rogan 2002, Hastie et al. 2003). In New Zealand, Hector's dolphins (*Cephalorhynchus hectori*) prefer shallower and more turbid waters in summer than in winter (Bräger et al. 2003). The behavioural mechanisms underlying these distinctive patterns in habitat use appear to be strongly related to foraging activities (Benoit-Bird and Au 2003, Hastie et al. 2004).

Resource partitioning between coexisting populations of coastal dolphins has not received much attention. All communities of animals show niche differentiation at some niche dimension, principally along the axes of space, time, and diet. Quantitative differences along these axes have been suggested as the possible mechanisms by which coexistence of sympatric species is mediated and competition avoided (Pimm and Rosenzweig 1981, Rosenzweig 1981, Schoener 1986, Rosenzweig 1991). A first step in investigating the ecological factors that might be promoting the coexistence of broadly sympatric species is to measure the level of overlap in resource use, as this may provide indirect evidence of the interactions and influences species can have on one another (Mac Nally 1983).

In this Chapter, I expanded the approach used in Chapter 3, by using data collected during boat based surveys in Cleveland Bay (discussed in Chapter 4) to: 1) determine the space use patterns of Irrawaddy and humpback dolphins in Cleveland Bay, 2) assess whether their space use patterns relate to behaviour, 3) measure the spatial overlap and concordance in space use between both species, and 4) determine their habitat preferences (Objective 4 of this thesis, see Chapter 1).

This study is the first comprehensive assessment of space use and habitat preferences of Irrawaddy and humpback dolphins in Australian waters. As we

continue to alter coastal habitats, identifying which particular areas and habitats are important for Irrawaddy and humpback dolphins will play a key role in their conservation and management.

5.2 Methods

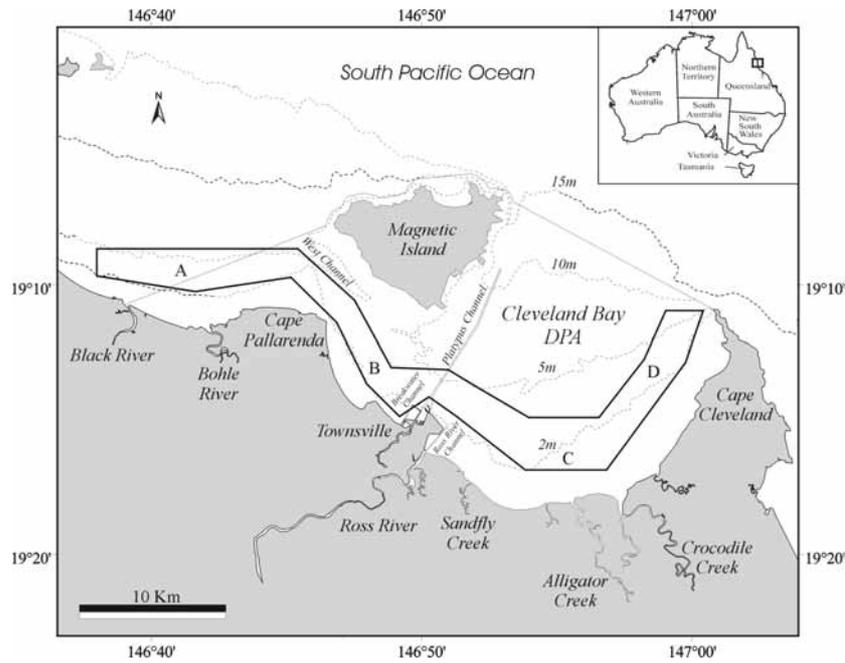
5.2.1 *Study Area*

Fig. 5.1a. As described in Chapter 4.

5.2.2 *Data collection*

As outlined in Chapter 4.

a)



b)

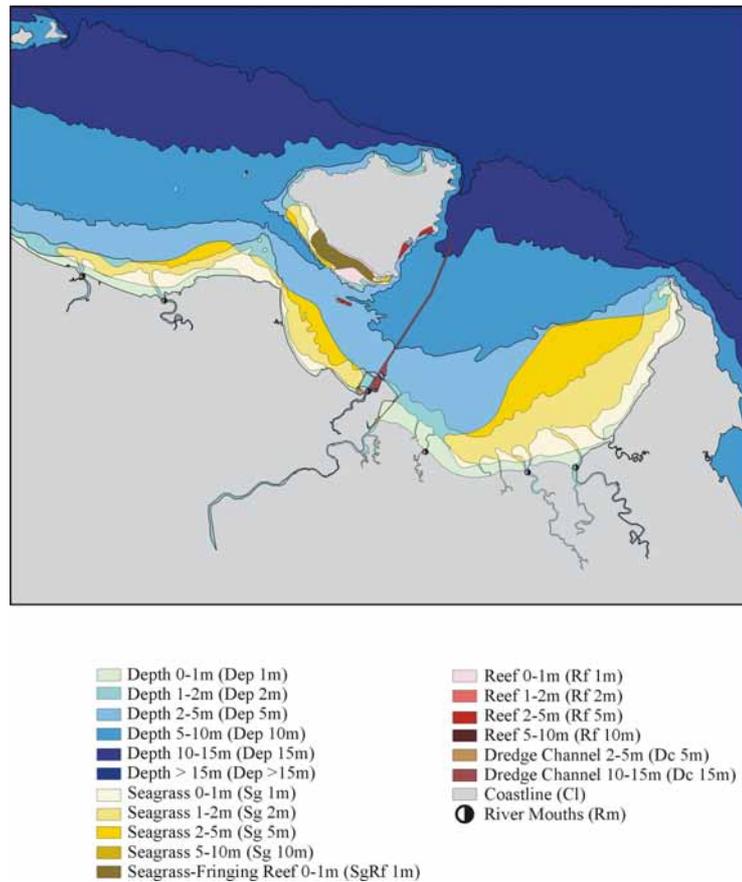


Figure 5.1 Study area: a) Map of the Cleveland Bay indicating survey route (—), limits of Dugong Protected Area (—), and principal locations named in text, b) ArcView GIS coverage of the different habitat types found in the Cleveland Bay region. See Table 5.1 for description of habitat types and abbreviations used in figures and tables.

5.2.3 *Data analysis*

5.2.3.1 *Space use patterns and behaviour*

The Utilization Distribution (UD) is a probability density function that describes the relative use of space by an animal, within a defined area based on a sample of animal locations (Van Winkle 1975). To estimate the UD of Irrawaddy and humpback dolphins, I converted all school sightings into an ArcView GIS point coverage and used the ArcView-Animal Movement Analyst extension to estimate a fixed kernel UD for each species (Hooge and Eichenlaub 2000). Preliminary analysis of kernel ranges in relation to season indicated no significant temporal variation in space use for both species, and therefore data from both seasons were combined for analysis. Kernel ranges of 50% (core area) and 95% (representative range) probability of occurrence were calculated using smoothing parameters calculated via the least squares cross validation procedure (Seaman et al. 1999).

Generally, a UD is calculated for individual animals from locations through some form of remote tracking technique (e.g., radio or satellite telemetry) in combination with a home range estimator (Kernohan et al. 2001). Although individual animals were tracked by means of photo-identification (e.g., Parra and Corkeron 2001), the number of relocations for most animals was insufficient to use true probabilistic methods (i.e., kernel methods) to estimate UDs reliably for each individual. Therefore, I have calculated UDs for Irrawaddy and humpback dolphins using locations of schools of animals rather than of individuals, an approach similar to Wilson (1997) and Ingram (2002). In this regard, the space use and habitat preference analysis presented here follows the “Design I” of Thomas and Taylor (1990) for the study of resource use and selection and inferences on space use and habitat preferences are made at the population level.

The kernel method was chosen to determine the UD of both species in preference to other methods (e.g., Minimum Convex Polygon, Harmonic Mean), because it: 1) requires no assumptions about the underlying distribution of the data, 2) is not influenced by effects of grid size and placement, and 3) provides a true probabilistic model of the UD (Worton 1989, 1995). The 50% and 95% kernel ranges were selected as they are generally considered the most robust estimators of an animal's core area and home range, respectively (Worton 1989). Because my data were restricted to inshore waters of the Cleveland Bay DPA area (hereafter Cleveland Bay), and dolphin schools instead of individual animals were used for analysis, I considered the 50% and the 95% kernel ranges as the core area and representative range of both species at the population level within the study area (e.g., dolphin schools recorded in the study area). The 95% kernel range of each species also defined the area for the analysis of habitat preferences.

To investigate whether behavioural states varied spatially and with time of day, I used Chi-square homogeneity tests (Zar 1999) to compare the behaviours observed per time of day within the 50% core areas to behavioural states per time of day occurring outside this range. As some behaviours were observed only a few times (e.g., milling) comparisons were made only across the predominant behavioural states. This comparison was done for each species separately.

5.2.3.2 *Spatial overlap and concordance in space use*

To measure the level of space sharing between Irrawaddy and humpback dolphins, I computed the percent area overlap (PAO) between the representative ranges (i.e., 95% kernel range) (Atwood and Weeks 2003) of both species as:

$$PAO = \left(\frac{A_{Ob,Sc}}{A_{Ob}} \times \frac{A_{Ob,Sc}}{A_{Sc}} \right)^{0.5},$$

where $A_{Ob,Sc}$ is the area of overlap between the two species, A_{Ob} is the area of Irrawaddy dolphins 95% kernel range, and A_{Sc} the area of humpback dolphins 95% kernel range. Although this index provides a first approximation of the space use sharing by both species, it does not take into account the UD (i.e., probability of use) within these shared parts (Doncaster 1990). For example, the ranges of two species may overlap by over 50% but contain the least utilized parts of both ranges.

Alternatively, a shared area may contain a region used intensively by one species and less by the other. To account for this problem and measure the concordance in relative use of shared areas, I tested for correlation (Spearman's coefficient of rank correlation r_s) between the UDs of Irrawaddy and humpback dolphins. A Spearman's coefficient was calculated on the pairs of probability of use estimates obtained from all grid-cells (100 x 100 m) frequented by one or both species. Species with perfectly matched utilization distributions will show a r_s of 1, while species with complete discordance will have a r_s of -1 (Doncaster 1990).

5.2.3.3 *Habitat delineation and analyses of habitat use*

A habitat map of Cleveland Bay including areal (e.g., seagrass, reefs), linear (i.e., coastline) and point features (i.e., river mouths) was developed for analysis of habitat use (Fig. 5.1b, Table 5.1; as before all tables have been placed at the end of this chapter to minimize interruption to the flow of the text, and printed on yellow colour paper for ease of location). Areal habitat types were defined based on water depth, presence of seagrass, coral reefs, and dredge channels. Bathymetry, coral reefs, dredge channels, and coastline were digitized into ArcView Geographic Information System (ESRI 1996a) from a 1:50000 scale navigation chart of Cleveland Bay provided by the Australian Hydrographic Service.

The bathymetry of the study area was digitized using the isobaths (i.e., 1 m, 2 m, 5 m, 10 m, and 15 m) in the navigation chart which represent the lowest level of Astronomical tide. As a result, all areal habitats (i.e., coral reefs, dredge channels, and seagrass) are represented at the minimum depth they are found.

The seagrass coverage for the region was provided by the Seagrass Ecology Group, Queensland Department of Primary Industries (Lee Long et al. 1998). Point locations of major river mouths were obtained from the Australian National Mapping Agency. All spatial layers were sampled at a cell resolution of 100 x 100m, and projected into Universal Transverse Mercator (UTM) Zone 55 for distance and area calculations. Only the habitat types that fell within the representative range of each species were considered available to the animals and included in subsequent analyses of habitat use.

To assess habitat selection, I used a distance-based analytical approach which has several advantages over classification-based methods (Conner et al. 2003). This method has been used for habitat selection at the individual level; however I have modified it to be used with locations of groups of animals (i.e., dolphin schools). The distance-based approach I used compares the average Euclidean distance (e.g. the shortest straight distance between two features) between the locations of dolphin schools and the nearest representative of each habitat type to expected distances obtained from random dolphin school locations. Random locations, equalling the number of schools observed for each species, were generated within the respective representative ranges. The vectors of distances from observed locations and random locations to habitat types were then used to derive a habitat use/habitat availability ratio (following Conner et al. 2003). This procedure was repeated 2000 times and an average habitat use ratio ρ calculated for each habitat type. Under the null hypothesis

of no habitat selection the expected value of ρ is 1 (i.e., mean dolphin distance to habitat = mean random distance to habitat). If ρ is < 1 the corresponding habitat was preferred (i.e., mean dolphin distance to habitat $<$ mean random distance to habitat) and the opposite if ρ is > 1 . To determine which habitat types were used more frequently in relation to their availability, I used a randomization test (Manly 1997) to evaluate the number of times the ratio obtained from 2000 randomizations exceeded or was equal to the expected ratio of 1.

The habitat use/habitat availability ratio ρ provides a ranking matrix of habitat use relative to habitat availability (which habitat type animals occurred closer to relative to random points), but it does not assess which habitat types were selected significantly more than others (Conner et al. 2003). To determine if there were preferences in habitat selection, I carried out a pairwise t-test among the different habitats and adjusted P-values with the False Discovery Rate (FDR) method (Benjamini and Hochberg 1995).

To evaluate if there were any significant interspecific differences in habitat use, I carried out a two sample randomization test between the distances to habitat types that were common to both species (i.e., found within the representative ranges of both species). The test compared the observed difference between mean distances to a habitat type with the difference obtained by randomly allocating the observed values between the two species multiple times (i.e., 2000). The significance of the test was evaluated by recording the number of times the differences obtained from randomization were greater than the observed difference.

As in Chapters 3 and 4, randomization tests were carried out with the POPTOOLS version 2.5 Excel add-in (Hood 2003). The Spearman rank correlations, pairwise t-test, and confidence intervals around effect sizes (e.g., differences between

means, correlation coefficients) were calculated with the R software version 1.7.0 for statistical computing and graphics (Ihaka and Gentleman 1996). Confidence intervals around the effect sizes were obtained by non-parametric bootstrapping using the bias corrected and accelerated method (BCa) (Efron and Tibshirani 1993). Interpretations of results are based on the examination of P-values (evaluated at $\alpha = 0.05$) together with confidence intervals around effect sizes when appropriate.

5.3 Results

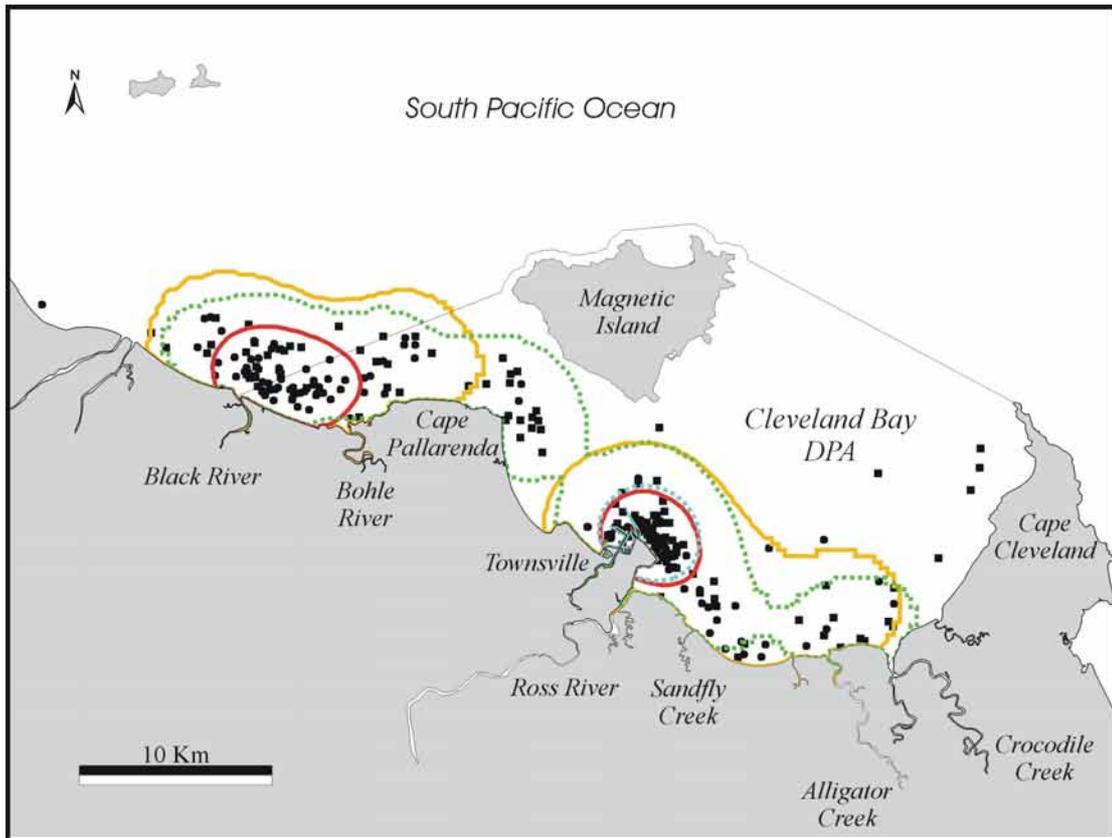
5.3.1 *Survey effort*

As explained in Chapter 4, a total of 630 hours were spent in Cleveland Bay searching for Irrawaddy and humpback dolphins. In total, 117 schools of Irrawaddy dolphins and 143 schools of humpback dolphins were sighted in Cleveland Bay during the study period. Survey effort was not uniformly distributed across the study area because of environmental constraints. Survey effort was similar across sections A (201 hrs), B (191 hrs), and C (179 hrs), however section D (59 hrs) was surveyed less than the other sections because of its exposure to strong south easterly winds (Fig. 5.1a).

5.3.2 *Space use patterns and behaviour*

The kernel UD analysis revealed that Irrawaddy and humpback dolphins do not use Cleveland Bay uniformly (Fig. 5.2). The representative ranges (95% kernel range) of Irrawaddy and humpback dolphins were similar in size covering a total area of about 197 km² and 190 km², respectively. The representative range of Irrawaddy dolphins concentrated in two areas: northwest of Cape Pallarenda (93 km²), and south (104 km²) towards Townsville's Port. Within these two areas there were also two core areas (50% kernel range): 16 km² around the Port of Townsville, and 27 km² between

the mouths of the Bohle and Black rivers. Humpback dolphins showed a continuous representative range extending from Crocodile Creek in the southeast to Black River in the northwest. Inside this range, a core area of approximately 17 km² was located around the Port of Townsville.



- Irrawaddy dolphin sightings
- Irrawaddy dolphin 50% kernel range (Core area)
- Irrawaddy dolphin 95% kernel range (Representative range)
- Humpback dolphin sightings
- Humpback dolphin 50% kernel range (Core area)
- Humpback dolphin 95% kernel range (Representative range)
- Limits of Cleveland Bay Dugong Protected Area (DPA)

Figure 5.2 Core areas (50% kernel range) and representative ranges (95% kernel range) of Irrawaddy and humpback dolphins in Cleveland Bay.

The discontinuity in the representative range of Irrawaddy dolphins does not demonstrate the presence of two distinct populations. Photo-identification data show that animals do move between these two areas (see Chapter 6). Rather this is likely to be an artefact of the sampling scheme with animals: 1) moving between these two areas at time periods and/or over sections of the bay that were not surveyed, or 2) spending little time in this area. Hence, these data were pooled for analysis of behaviour and habitat use.

As discussed in Chapter 4, overall, Irrawaddy dolphins were mainly seen foraging and travelling. In combination, these behaviours contributed over 50% of the behaviours observed at any time (Fig. 5.3a). No differences in the incidence of foraging and travelling activities were detected between core and non-core areas according to time (Foraging: $\chi^2_{0.05, 3} = 2.4$, $P = 0.501$, Travelling: $\chi^2_{0.05, 3} = 1.7$, $P = 0.642$). Irrawaddy dolphins were never seen foraging behind trawlers. Milling was observed only outside the core areas.

The behaviour of humpback dolphins within and outside their core areas was dominated by foraging (Fig. 5.3b). The frequency of foraging, and foraging behind trawler behaviours varied according to time and location (Foraging: $\chi^2_{0.05, 3} = 23.5$, $P < 0.001$, Foraging Behind Trawlers: $\chi^2_{0.05, 3} = 10.1$, $P = 0.018$). Foraging in the early morning hours (i.e., 6:00-8:00) took place mainly inside the core area. Between 8:00-10:00 foraging activities appeared to shift to locations outside the core area (Fig. 5.3b). Foraging behind trawlers occurred mainly inside the core area in the morning hours (Fig. 5.3b).

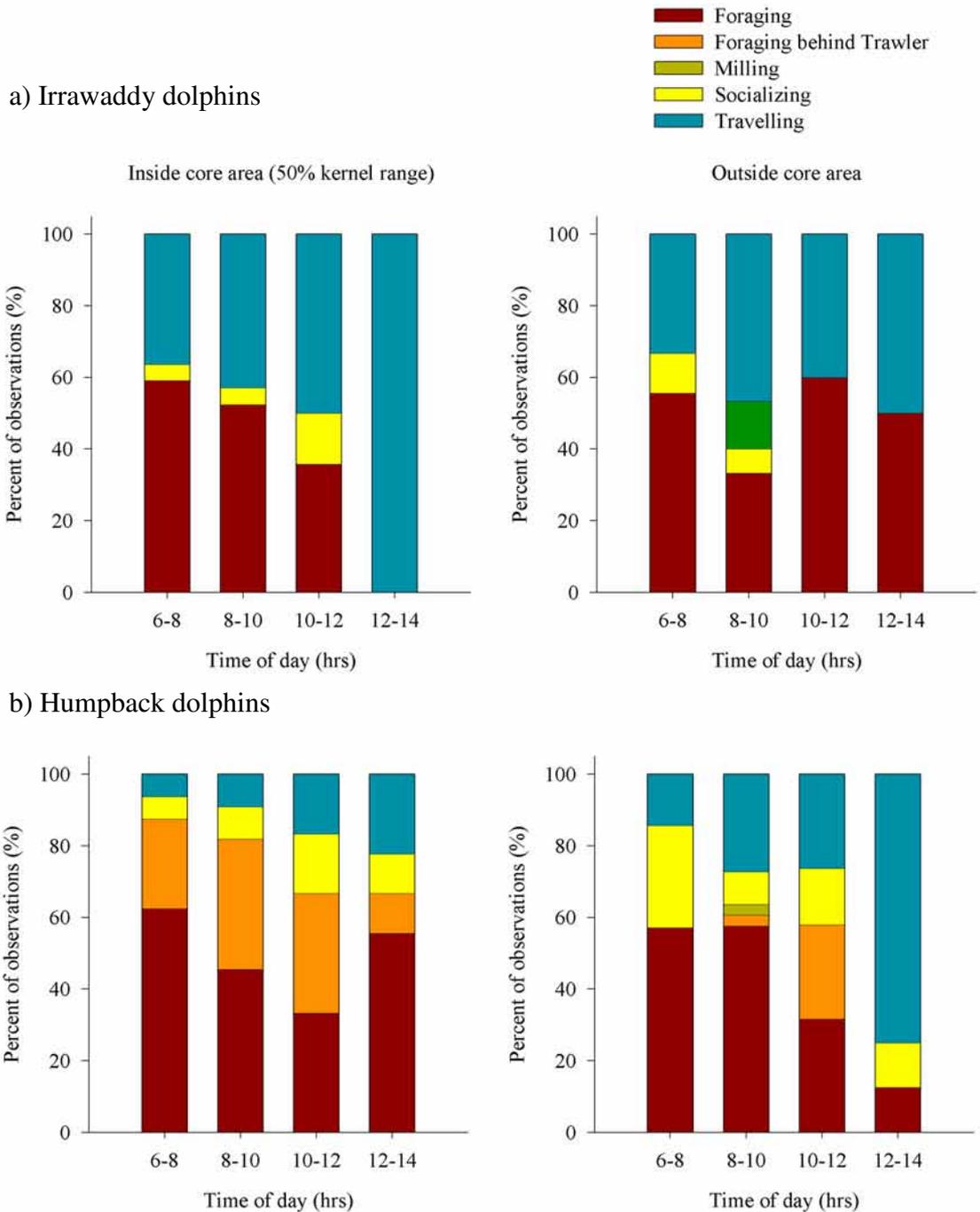


Figure 5.3 Differences in the frequency of various behavioural states observed within and outside core areas (50% kernel range) of (a) Irrawaddy and (b) humpback dolphins. Values inside columns indicate corresponding sample size of each behaviour by time of day.

5.3.3 *Spatial overlap and concordance in space use patterns*

The 95% representative ranges of Irrawaddy and humpback dolphins showed considerable spatial overlap (Fig. 5.2). The area shared between both species was 156 km² with a percent area overlap of 81%. Almost all of the two core areas of Irrawaddy dolphins (99%) and all of the humpback dolphin's core area were contained within this shared area. The Spearman rank correlation between the UD_s of Irrawaddy and humpback dolphins ($r_s = 0.55$, $P < 0.05$) indicated strong concordance in the utilization patterns of these shared areas by both species.

5.3.4 *Habitat preferences*

Overall, the representative ranges of Irrawaddy and humpback dolphins comprised the same habitat types in similar proportions (Figure 5.4). However, coral reefs and fringing reefs with seagrass occurred within the representative range of humpback dolphins only (between Cape Pallarenda and southern coast of Magnetic Island).

The analysis of distance ratios (ρ) indicated that habitat use within the representative range of each species was not random (Table 5.2). Irrawaddy dolphins occurred closer to most habitat types than would be expected under the null hypothesis of no habitat selection. The only habitats showing no selection were dredged channels and waters 5-10m deep. Humpback dolphins selected most habitat types including dredged channels, except: 1) areas with seagrass present, 2) reefs at 0-1 m depth, and 3) waters 5-10m deep. The ranking of habitats based on pairwise comparisons of ρ indicated that Irrawaddy dolphins used waters 1-2 m deep, followed by waters close to the coast, and waters 0-1 m deep and 1-2 m deep with seagrass, proportionally more than any other habitats (Table 5.3). Humpback dolphins preferred

waters 2-5 m deep, followed by waters close to the coast, and waters 1-2 m deep over all other habitat types (Table 5.4).

Examination of the difference between the mean distances to habitat types common to both species (Table 5.5) revealed that Irrawaddy dolphins occurred closer to waters 0-1 m deep, closer to waters 0-2 m deep with seagrass, and closer to river mouths than humpback dolphins. Humpback dolphins occurred closer to the dredge channels than Irrawaddy dolphins. Both species occurred at similar distances to waters 5-10m deep, and waters close to the coast.

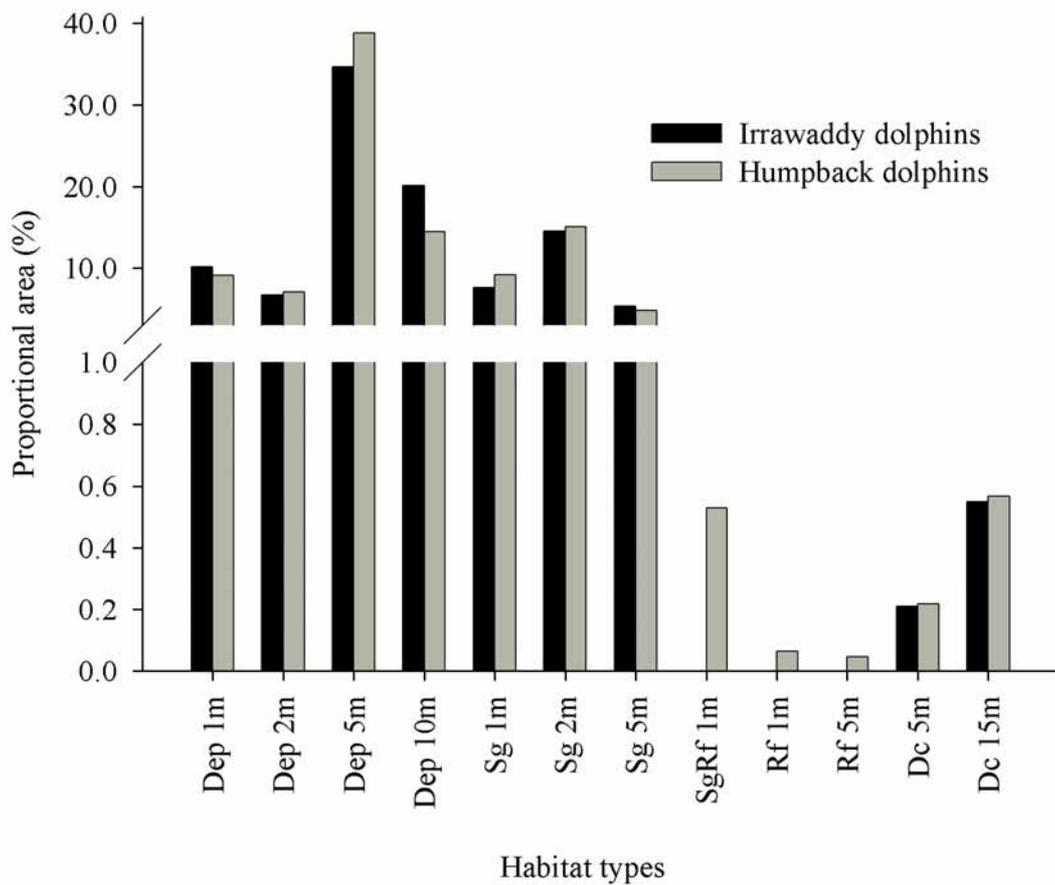


Figure 5.4 Relative proportion of various habitat types within the representative range (95% kernel range) of Irrawaddy and humpback dolphins in Cleveland Bay. See Table 5.1 for descriptions of habitat types and abbreviations..

5.4 Discussion

5.4.1 Limitations

5.4.1.1 Uneven survey effort

As discussed in Chapter 4, the low survey effort along the eastern section of Cleveland Bay (section D, Fig. 5.1a) in comparison with other areas in response to weather constraints is a potential source of bias in my analysis. If both species spent considerable time in this area, my estimates of the UD are negatively biased as their representative ranges would extend further into these areas, and/or additional core areas would have been identified. Thus, my interpretation of the of space use and habitat preferences of Irrawaddy and humpback dolphins is biased towards the use animals made of sections A-C (Fig. 5.1 a), the areas that were subject to intensive sampling. Nonetheless, the eastern section of Cleveland Bay (i.e., section D) lacks river mouths and I suspect neither species spends considerable time in this area. Irrawaddy dolphins are known to occur close to river mouths in Australian waters (see Chapters 2 and 3, Parra et al. 2002) and elsewhere where coastal populations have been recorded (Stacey and Arnold 1999). Humpback dolphins exhibit a similar pattern with most populations studied been associated with areas receiving freshwater inputs (see Chapters 2 and 3, Jefferson and Karczmarski 2001).

5.4.1.2 Schools versus individual behaviour

Animals typically show individual variation in their behaviour and habitat preferences, however pooling data across individuals (e.g., using schools of dolphins instead of individuals) is justifiable if this variation is not considerable (Aebischer et al. 1993). The behaviour and habitat selection of individuals in many social species is highly influenced by the presence of their conspecifics (Beauchamp et al. 1997).

Presence of conspecifics may act as cues of habitat quality and reproductive success resulting in aggregations of animals in selected areas within their habitat (Stamps 1988, Reed and Dobson 1993, Muller et al. 1997, Danchin et al. 1998) . Most delphinids are very sociable animals with complex group and social dynamics, spending a great proportion of their time in the presence of conspecifics (Bräger et al. 1994, Bräger 1999, Baird and Whitehead 2000). Thus, the individual patterns of movement and habitat selection by individuals are influenced by the behaviour and distribution of conspecifics. Such attraction among conspecifics results in the distribution of individuals within a school being spatially autocorrelated. Thus, though individual variation in behaviour is likely, the use of schools rather than individual location data in analysis of habitat preferences should indicate the general patterns found in a population.

5.4.2 *Space use, spatial overlap and concordance in space use patterns*

Despite the co-occurrence of several species of delphinids in similar habitats, studies of space use patterns and habitat preferences have been mainly directed at single species (Wilson et al. 1997, Allen and Read 2000, Heithaus and Dill 2002, Bräger et al. 2003, Hastie et al. 2004). Thus, the ecological interactions and mechanisms promoting the coexistence of sympatric delphinids remain largely unknown. In terms of biodiversity, the coastal zone represents the most naturally diverse and productive marine environment of the sea, supporting the majority of the world's living marine resources (Ray 1991, Clark 1998). Like other large marine vertebrates operating in high trophic levels, coastal dolphins are ecologically important and can profoundly affect food-web interactions and community structure to the point of collapse (Estes et al. 1998, Jackson et al. 2001). Thus, understanding

how dolphin species coexist in such a diverse environment is important to identifying mechanisms that may threaten the biodiversity of the coastal zone.

In this study, I found that sympatric Irrawaddy and humpback dolphins have a high degree of interspecific spatial overlap, with shared areas used heavily and similarly by both species. The use of space by delphinids is likely to match the distribution of the resources they use, while ideally avoiding areas of high predation risk (Heithaus and Dill 2002). The considerable overlap and concordance in space use between Irrawaddy and humpback dolphins might be a result of abundance in critical resources for both species, or convergence in the areas safest from shared predators such as sharks.

The predominance of foraging activity throughout the core areas and representative ranges of both species indicates that coastal waters of Cleveland Bay represent an important feeding area. Thus, the high degree of spatial overlap between the representative ranges of Irrawaddy and humpback dolphins, may be indicative of a patchy distribution of prey, with both species foraging in areas where prey are abundant.

Cleveland Bay is an important nursery area for a wide variety of fishes including several fish families (Ariidae, Carangidae, Clupeidae, Engraulidae, Haemulidae, Hemiramphidae, Leiognathidae, Mugilidae, Pomadasyidae, Sillaginidae, Terapontidae) (Robertson and Duke 1987, 1990, Sheaves 1992) that are known to be part of the diet of Irrawaddy and humpback dolphins (Heinsohn 1979, Barros et al. 2004). The location of core areas of use for both species around river mouths (i.e., Bohle River and Ross River, Fig. 5.2) and near modified habitats such as dredge channels and breakwaters around Townsville's Port (Fig. 5.2) might reflect important aggregation areas for prey.

Freshwater inflow is thought to be one of the most important factors encouraging biological productivity in estuaries (Mallin et al. 1993), and studies in Ross River estuary, Cleveland Bay reflect this attribute (Davis 2001). Artificial structures such as breakwaters and jetty pillars appear to encourage species richness and fish abundance, as they offer a variety of niches for adult and juvenile fish (Rilov and Benayahu 1998, Guidetti 2004). Alternatively, dredge channels offer fewer refuges from predators for fishes, and structural features such as channel walls might act as barriers facilitating the ambush and herding of prey, as it has been suggested for coastal bottlenose dolphins (Wilson et al. 1997, Allen et al. 2001, Ingram and Rogan 2002). On the other hand, humpback dolphins might also be attracted to these areas because of the frequent presence of trawlers which provide a reliable, easily located and large source of food for dolphins through the provision and concentration of prey while trawler nets are in use and while catches are being sorted.

As discussed in Chapter 4, in Cleveland Bay, individuals of both Irrawaddy and humpback dolphins show scars resulting from interactions with sharks (personal observations) and dolphin remains have been identified among the stomach contents of tiger sharks caught in Cleveland Bay (Simpfendorfer 1992). Thus it is likely that predation risk influences habitat selection by both species. Adult tiger sharks, *Galeocerdo cuvier*, which are regular predators of delphinids (Heithaus 2001b) are present almost year round in Cleveland Bay (Simpfendorfer 1992, Simpfendorfer and Milward 1993). However, we do not know their space use patterns and thus their relationship with the habitat preferences of Irrawaddy and humpback dolphins.

Home range has been traditionally defined as the area traversed by an animal while engaging in its daily activities (Burt 1943). I did not estimate home range size *per se* because: 1) Irrawaddy and humpback dolphins are known to occur in areas

adjacent to my study area which I did not sample, and 2) photoidentification data shows that some individuals do move between Cleveland Bay and these areas. Thus the actual home range size for both species is likely larger than the representative ranges (i.e., 95% kernel ranges) estimated here. However, the occurrence of both species year round (see Chapter 4), the predominance of foraging activities, and the high interannual site fidelity detected for identified individuals (see Chapter 6), indicates Cleveland Bay is an important part of their actual home range.

5.4.3 *Habitat preferences and resource partitioning*

Despite the high spatial overlap and concordance in space use, there were differences in the habitats selected by both species and their preferences. Irrawaddy dolphins selected almost all habitat types within their representative ranges, except dredged channels and waters 5-10 m deep. Humpback dolphins selected almost all habitat types (including dredged channels and reefs in waters 5 m deep), but showed no selection for areas with seagrass. Among the different habitats found in each species representative ranges, Irrawaddy dolphin preferred mainly shallow (1-2 m) waters, while humpback dolphins preferred deeper (2-5 m) waters. Areas with seagrass ranked high in the habitat preferences of Irrawaddy dolphins, while dredged channels ranked high in the preference of humpback dolphins.

Analysis of interspecific differences in selection among habitats common to both species corroborated these differences. While Irrawaddy dolphins occurred closer to waters 0-1 m deep, closer to waters 0-2 m deep with seagrass, and closer to river mouths than humpback dolphins, humpback dolphins occurred closer to the dredged channels than Irrawaddy dolphins. Overall, these habitat preferences correspond well with the almost exclusive coastal and estuarine distribution of both species throughout their range (Jefferson *et al.*, 2001; Stacey *et al.*, 1999).

The predominance of foraging behaviour by both species indicates that prey distribution is one of the main factors driving both species habitat preference in Cleveland Bay. Throughout their range, foraging humpback dolphins are usually associated with coastal estuarine areas (Parsons 2004). Irrawaddy dolphins in Malampaya Sound, Philippines, are mainly found in highly productive shallow waters (< 6 m), close to the coast, and close to major river mouths (Dolar et al. 2002).

Differences in the habitat preferences of Irrawaddy and humpback dolphins in Cleveland Bay may partly relate to different feeding habits, or may also be a result of niche differentiation at sympatric localities to alleviate or avoid interspecific competition. Available information on the diet of Australian Irrawaddy dolphins and humpback dolphins from Hong Kong indicates that both species consume prey from the same families and genera of fish (Appendices 3 and 4). On the other hand, while fish appear to be common in the diet of both species, the stomach contents of Irrawaddy dolphins from Australia included cephalopod remains (Heinsohn 1979), which do not seem to form part of the main diet of humpback dolphins in Hong Kong (Barros et al. 2004). These differences in diet composition might reflect some of the morphological differences between both species.

The shape of the odontocete skull, jaw, and the type and number of teeth is closely related to the diet and method of food capture (Evans 1987, Berta and Sumich 1999). Irrawaddy dolphins have a short-blunt rostrum (43-45% of condylobasal length), their teeth have an expanded crown but are not compressed and vary in number from 13-20 (upper jaw) and from 12-19 (lower) in each tooth row (Stacey and Arnold 1999). In contrast, humpback dolphins have a long-narrow rostrum (57-67% of condylobasal length); their teeth are conical, pointed and vary from 27-38 in each tooth row. The short-blunt rostrum and the reduced tooth count in Irrawaddy dolphins

resemble characteristics of squid-eating odontocetes like pilot whales (*Globicephala melas*) and finless porpoises (*Neophocaena phocaenoides*). In addition, the practice of spitting water recorded for riverine populations (Stacey and Arnold 1999, Stacey and Hvenegaard 2002) and marine populations (personal observations) of Irrawaddy dolphins has been associated with a suction feeding strategy in pilot whales (Stacey and Arnold 1999, Werth 2000). This strategy helps pilot whales capture and hold small and presumably less manageable slippery-bodied prey (e.g., cephalopods) (Heyning and Mead 1996, Werth 2000). The long rostrum with many teeth of humpback dolphins resembles the typical morphology of other delphinids which are known to feed mainly on fish but may also include significant numbers of cephalopods in their diet (e.g., Common dolphin, *Delphinus delphis*; Spotted dolphin, *Stenella attenuata*; and spinner dolphin; *S. longirostris*). Quantitative studies on the diet preferences of Irrawaddy and humpback dolphins are needed to elucidate levels of dietary overlap between both species.

Niche differentiation through differential uses of resources in space or time is often the basis for the coexistence of species (Schoener 1974, Chesson 2000). Several studies have shown that mammals often partition resources through differential use of space (Johnson and Franklin 1994, Palomares et al. 1996, Johnson et al. 2000), different activity patterns (Fedriani et al. 1999, Neale and Sacks 2001), different prey preferences (Medina 1997, Neale and Sacks 2001, Loveridge and Macdonald 2003), or different habitat use patterns (Jones and Barmuta 2000, Loveridge and MacDonald 2002). The use by Irrawaddy dolphins of two spatially separated core areas, both within the area shared by both species, but only one overlapping the humpback dolphin's core area (i.e., the area around Townsville's Port, Fig. 5.2), might represent some local avoidance behaviour in space. Irrawaddy dolphins might reduce their

exposure to aggressive/sexual interactions from humpback dolphins (see Chapter 9) by distributing their foraging activities across two areas. Additionally, humpback dolphins foraged behind trawlers more frequently inside their core area around the Townsville's Port than outside this area. Irrawaddy dolphins were never seen foraging behind trawlers, and thus this difference in behaviour might promote the sharing of space by both species while alleviating interspecific interactions.

Temporal separation in space use might be contributing to space sharing between the two species. This question was not addressed in this study as simultaneous tracking of school of both species was not feasible. Nonetheless, the similarity in space use patterns and behavioural activities with time and location, observations of interactions between both species (see Chapter 9), and their year round occurrence (see Chapter 4), all indicate that both species use similar areas at similar times in Cleveland Bay.

The results presented here suggest that difference in habitat preferences, which may also reflect some food partitioning, is one of the principal factors promoting the coexistence of Irrawaddy and humpback dolphins. Although information on the level of resource partitioning among coexisting delphinids is limited, differences in habitat use and prey resources appear to be the major mechanisms allowing sympatric species to coexist. For example, humpback dolphins and finless porpoises in Hong Kong waters, though sharing similar areas, appear to show niche separation through temporal segregation in habitat use (Parsons 1998a). Although both species show dietary overlap to some extent, humpback dolphins feed primarily on estuarine fish whereas finless porpoises consume mainly cephalopods (Barros et al. 2002, Barros et al. 2004). Bottlenose and humpback dolphins co-occurring in coastal waters off South Africa also show substantial diet overlap, however humpback dolphins prefer shallow,

turbid waters of estuaries, while bottlenose dolphins are seen often in clear deeper waters (Barros and Cockcroft 1999, Barros et al. 2004).

Competition theory predicts that for potential competitors to coexist, they should exhibit niche differentiation or resource partitioning in space or time (Begon et al. 1996). If coexisting species fail to differentiate their niche or partition their resources this may lead to the eventual exclusion of one species, or to the restriction of one species to competition refuges (Begon et al. 1996, Durant 1998). Irrawaddy and humpback dolphins are similar in size, show considerable overlap in their space use patterns, select similar habitats, appear to have at least some prey in common, and show interspecific interactions, thus there is potential for interspecific competition. Interspecific competition is difficult to demonstrate without experimental manipulation (Mac Nally 1983). High degrees of spatial overlap need not mean that ecological processes such as competition are taking place (Wiens 1977). However, low levels of overlap do not reveal much about current or past relationships between species (Wiens 1977, Rosenzweig 1981). An indirect approach as the one taken in this study, concurrent with data on overlap at other niche axes (e.g., diet, time), may prove useful in elucidating the potential importance interspecific interactions might play in structuring coastal dolphin communities.

5.5 Chapter summary

- Knowledge about the space use patterns and habitat preferences of sympatric Irrawaddy and humpback dolphins in Australian waters is lacking. Identifying which particular areas and habitats are important for Irrawaddy and humpback dolphins will play a key role in their conservation and management.

Additionally, the level of overlap in space use and habitat preferences between

these two sympatric species can provide indirect evidence into the ecological factors that might be promoting their coexistence.

- I used ArcView Geographic Information System, kernel methods, and a distance-based analytical approach to estimate the relative use of space, the spatial overlap, and habitat preferences of Irrawaddy and humpback dolphins within Cleveland Bay, northeast Queensland.
- The kernel analysis showed that Irrawaddy and humpback dolphins do not use Cleveland Bay uniformly. The representative ranges (95% kernel range) of Irrawaddy and humpback dolphins were similar in size and location covering mainly the area between Townsville's Port and the Black river mouth. The area around the Port of Townsville was a core area (50% kernel range) for both Irrawaddy and humpback dolphins. I identified an additional core area for Irrawaddy dolphins between the mouths of the Bohle and Black rivers.
- The behaviour of Irrawaddy and humpback dolphins within and outside their core areas was dominated by foraging and travelling activities. The incidence of foraging and travelling behaviour of Irrawaddy dolphins showed no difference between core and non-core areas according to time. Humpback dolphins foraged during the early morning hours (i.e., 6:00-8:00) inside their core area, and between 8:00-10:00 they shift their foraging activities to locations outside their core area. Humpback dolphins foraging behind trawlers were mainly observed inside their core area in the morning hours.
- The 95% representative ranges of Irrawaddy and humpback dolphins showed considerable spatial overlap (81%), and shared areas showed strong concordance in the utilization patterns by both species.

- I found that habitat use within the representative range of each species was not random. Irrawaddy dolphins occurred closer to most habitat types than would be expected under a random scenario except for dredge channels and waters 5-10m in depth. Humpback dolphins showed preference for all habitats including dredge channels except: 1) areas with seagrass present, 2) reefs at 0-1 m depth, and 3) waters 5-10m deep. Irrawaddy dolphins preferred waters 1-2 m deep, followed by waters close to the coast, and waters 0-1 m deep and 1-2 m deep with seagrass, proportionally more than any other habitats. Humpback dolphins showed preference for deeper waters (2-5 m deep), followed by waters close to the coast, shallow waters(1-2 m deep) with no seagrass, and dredge channels (5-15 m deep). Difference between the mean distances to habitat types common to both species indicated that:1) Irrawaddy dolphins occurred closer to waters 0-1 m deep, closer to waters 0-2 m deep with seagrass, and closer to river mouths than humpback dolphins, and 2) humpback dolphins occurred closer to the dredge channels than Irrawaddy dolphins.
- I suggest that the high degree of spatial overlap between the representative ranges of both dolphin species might be a result of abundance in critical resources for both species, or convergence in the areas safest from shared predators such as sharks.
- The predominance of foraging behaviour by both species indicates that prey distribution is one of the main factors driving both species habitat preference in Cleveland Bay. Differences in the habitat preferences of Irrawaddy and humpback dolphins in Cleveland Bay may partly relate to different feeding habits, or may also be a result of niche differentiation at sympatric localities to

alleviate or avoid interspecific competition. I propose that the difference in habitat preferences is one of the principal factors promoting the coexistence of Irrawaddy and humpback dolphins.

Table 5.1 Descriptions of the different habitat types and abbreviations used in figures and tables.

Water depth (m)	Seagrass present?	Reef present?	Dredge Channel Present?	Habitat type
0-1	No	No	No	Dep 1m
1-2	No	No	No	Dep 2m
2-5	No	No	No	Dep 5m
5-10	No	No	No	Dep 10m
0-1	Yes	No	No	Sg 1m
1-2	Yes	No	No	Sg 2m
2-5	Yes	No	No	Sg 5m
0-1	Yes	Yes	No	SgrRf 1m
0-1	No	Yes	No	Rf 1m
2-5	No	Yes	No	Rf 5m
2-5	No	No	Yes	Dc 5m
10-15	No	No	Yes	Dc 15m
Na ^a	Na	Na	Na	Cl ^b
Na	Na	Na	Na	Rm ^b

^a Na = Not applicable

^b Cl = Coastline

^c Rm = River mouths

Table 5.2 Mean ratios (ρ) of the distance between dolphin school locations and habitat types to the distance between random locations and habitat types after 2000 randomizations. Associated P-values of randomization test are shown in parenthesis. Values for $\rho < 1$ indicate that animal locations were closer to habitat than expected by chance. Significant values are indicated in bold italics. P-values for multiple pairwise comparisons have been adjusted with the False Discovery Rate (FDR) correction method (Benjamini and Hochberg 1995). See Table 5.1 for description of habitat types and abbreviations.

	Irrawaddy dolphins	Humpback dolphins
Habitat ^a	ρ (P-value)	ρ (P-value)
Dep 1m	<i>0.60</i> (<i>< 0.0001</i>)	<i>0.87</i> (<i>0.033</i>)
Dep 2m	<i>0.47</i> (<i>< 0.0001</i>)	<i>0.66</i> (<i>< 0.0001</i>)
Dep 5m	<i>0.64</i> (<i>0.001</i>)	<i>0.65</i> (<i>0.002</i>)
Dep 10m	1.11 (0.890)	0.99 (0.557)
Sg 1m	<i>0.66</i> (<i>< 0.0001</i>)	1.06 (0.799)
Sg 2m	<i>0.60</i> (<i>< 0.0001</i>)	1.03 (0.706)
Sg 5m	<i>0.77</i> (<i>< 0.0001</i>)	1.02 (0.706)
SgrRf 1m	Na ^b	0.96 (0.274)
Rf 1m	Na	0.95 (0.184)
Rf 5m	Na	<i>0.89</i> (<i>0.014</i>)
Dc 5m	1.02 (0.664)	<i>0.72</i> (<i>< 0.0001</i>)
Dc 15m	1.02 (0.664)	<i>0.69</i> (<i>< 0.0001</i>)
Cl	<i>0.58</i> (<i>< 0.0001</i>)	<i>0.65</i> (<i>< 0.0001</i>)
Rm	<i>0.68</i> (<i>< 0.0001</i>)	<i>0.81</i> (<i>< 0.0001</i>)

^a Habitat types available within 95% kernel range of each species

^b Habitat types not available (Na) within 95% kernel range of Irrawaddy dolphins

Table 5.3 Ranking matrix of the habitat preferences of Irrawaddy dolphins (most preferred {Ranking =1} to least preferred {Ranking = 9}). Numbers indicate differences associated with pairwise comparison of mean ratios (ρ) to habitat types. Negative differences indicate preference of habitat above over habitat to the left, positive differences indicate underutilization of habitat above over habitat to the left. Significant differences (Pairwise t-test, $P < 0.05$) are indicated in bold italics. Habitats with the same ranking did not differ significantly in relative preference. P-values for multiple pairwise comparisons have been adjusted with the False Discovery Rate (FDR) correction method (Benjamini and Hochberg 1995). See Table 5.1 for description of habitat types and abbreviations.

Habitat	Habitat ranking										
	3	1	4	9	5	3	7	8	8	2	6
	Dep 1m	Dep2m	Dep5m	Dep 10m	Sg 1m	Sg 2m	Sg 5m	Dc 5m	Dc 15m	Cl	Rm
Dep 1m	-										-
Dep 2m	<i>0.128</i>	-	-	-	-	-	-	-	-	-	-
Dep 5m	<i>-0.043</i>	<i>-0.171</i>	-	-	-	-	-	-	-	-	-
Dep 10m	<i>-0.509</i>	<i>-0.636</i>	<i>-0.466</i>	-	-	-	-	-	-	-	-
Sg 1m	<i>-0.055</i>	<i>-0.182</i>	<i>-0.012</i>	<i>0.454</i>	-	-	-	-	-	-	-
Sg 2m	0.000	<i>-0.127</i>	<i>0.043</i>	<i>0.509</i>	<i>0.055</i>	-	-	-	-	-	-
Sg 5m	<i>-0.168</i>	<i>-0.296</i>	<i>-0.125</i>	<i>0.341</i>	<i>-0.113</i>	<i>-0.168</i>	-	-	-	-	-
Dc 5m	<i>-0.414</i>	<i>-0.542</i>	<i>-0.371</i>	<i>0.095</i>	<i>-0.359</i>	<i>-0.414</i>	<i>-0.246</i>	-	-	-	-
Dc 15m	<i>-0.415</i>	<i>-0.542</i>	<i>-0.371</i>	<i>0.094</i>	<i>-0.360</i>	<i>-0.415</i>	<i>-0.246</i>	0.000	-	-	-
Cl	<i>0.019</i>	<i>-0.109</i>	<i>0.062</i>	<i>0.528</i>	<i>0.074</i>	<i>0.019</i>	<i>0.187</i>	<i>0.433</i>	<i>0.433</i>	-	-
Rm	<i>-0.078</i>	<i>-0.205</i>	<i>-0.035</i>	<i>0.431</i>	<i>-0.023</i>	<i>-0.078</i>	<i>0.090</i>	<i>0.336</i>	<i>0.337</i>	<i>-0.097</i>	-

Table 5.4 Ranking matrix of the habitat preferences of humpback dolphins (most preferred {Ranking =1} to least preferred {Ranking = 14}). Numbers indicate differences associated with pairwise comparison of mean ratios (ρ) to habitat types. Negative differences indicate preference of habitat above over habitat to the left, positive differences indicate underutilization of habitat above over habitat to the left. Significant differences (Pairwise t-test, $P < 0.05$) are indicated in bold italics. Habitats with the same ranking did not differ significantly in relative preference. P-values for multiple pairwise comparisons have been adjusted with the False Discovery Rate (FDR) correction method (Benjamini and Hochberg 1995). See Table 5.1 for description of habitat types and abbreviations.

Habitat	Habitat Ranking													
	7	3	1	11	14	13	12	10	9	8	5	4	2	6
	Dep 1m	Dep 2m	Dep 5m	Dep 10m	Sg 1m	Sg 2m	Sg 5m	SgRf 1m	Rf 1m	Rf 5m	Dc 5m	Dc 15m	Cl	Rm
Habitat	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dep 1m	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Dep2m	<i>0.209</i>	-	-	-	-	-	-	-	-	-	-	-	-	-
Dep5m	<i>0.227</i>	<i>0.018</i>	-	-	-	-	-	-	-	-	-	-	-	-
Dep 10m	<i>-0.118</i>	<i>-0.327</i>	<i>-0.345</i>	-	-	-	-	-	-	-	-	-	-	-
Sg 1m	<i>-0.184</i>	<i>-0.393</i>	<i>-0.411</i>	<i>-0.066</i>	-	-	-	-	-	-	-	-	-	-
Sg 2m	<i>-0.155</i>	<i>-0.364</i>	<i>-0.382</i>	<i>-0.037</i>	<i>0.029</i>	-	-	-	-	-	-	-	-	-
Sg 5m	<i>-0.144</i>	<i>-0.353</i>	<i>-0.371</i>	<i>-0.026</i>	<i>0.040</i>	<i>0.011</i>	-	-	-	-	-	-	-	-
SgRf 1m	<i>-0.086</i>	<i>-0.296</i>	<i>-0.314</i>	<i>0.031</i>	<i>0.097</i>	<i>0.069</i>	<i>0.057</i>	-	-	-	-	-	-	-
Rf 1m	<i>-0.073</i>	<i>-0.282</i>	<i>-0.300</i>	<i>0.045</i>	<i>0.111</i>	<i>0.082</i>	<i>0.071</i>	<i>0.013</i>	-	-	-	-	-	-
Rf 5m	<i>-0.012</i>	<i>-0.222</i>	<i>-0.240</i>	<i>0.105</i>	<i>0.171</i>	<i>0.143</i>	<i>0.131</i>	<i>0.074</i>	<i>0.061</i>	-	-	-	-	-
Dc 5m	<i>0.157</i>	<i>-0.052</i>	<i>-0.070</i>	<i>0.275</i>	<i>0.341</i>	<i>0.312</i>	<i>0.301</i>	<i>0.244</i>	<i>0.230</i>	<i>0.170</i>	-	-	-	-
Dc 15m	<i>0.179</i>	<i>-0.031</i>	<i>-0.049</i>	<i>0.296</i>	<i>0.362</i>	<i>0.334</i>	<i>0.322</i>	<i>0.265</i>	<i>0.252</i>	<i>0.191</i>	<i>0.021</i>	-	-	-
Cl	<i>0.224</i>	<i>0.015</i>	<i>-0.003</i>	<i>0.342</i>	<i>0.408</i>	<i>0.379</i>	<i>0.368</i>	<i>0.311</i>	<i>0.297</i>	<i>0.237</i>	<i>0.067</i>	<i>0.046</i>	-	-
Rm	<i>0.066</i>	<i>-0.143</i>	<i>-0.161</i>	<i>0.184</i>	<i>0.250</i>	<i>0.221</i>	<i>0.210</i>	<i>0.153</i>	<i>0.139</i>	<i>0.079</i>	<i>-0.091</i>	<i>-0.112</i>	<i>-0.158</i>	-

Table 5.5 Differences in mean distance to habitat types between Irrawaddy and humpback dolphins. A negative difference indicates Irrawaddy dolphins occurred closer to this habitat than humpback dolphins, a positive difference indicates humpback dolphins occurred closer to this habitat than Irrawaddy dolphins. Significant differences in mean distances are indicated in bold italics. See Table 5.1 for description of habitat types and abbreviations.

Habitat	Difference (m)	95%CI (m)	P
Dep 1m	<i>-331.5</i>	<i>-598.7, -95.0</i>	<i>0.017</i>
Dep2m	-116.7	-324.4, 85.4	0.339
Dep5m	55.6	-215.36, 291.6	0.682
Dep 10m	350.6	-70.1, 784.5	0.120
Sg 1m	<i>-549.0</i>	<i>-854.5, -202.7</i>	<i>0.004</i>
Sg 2m	<i>-412.3</i>	<i>-664.3, -115.3</i>	<i>0.015</i>
Sg 5m	-269.5	-540.8, 48.5	0.091
Dc 5m	<i>3865.2</i>	<i>2017, 5802.0</i>	<i>< 0.0001</i>
Dc 15m	<i>4297.3</i>	<i>2321, 6213.0</i>	<i>< 0.0001</i>
Cl	85.4	-154.52, 325.3	0.405
Rm	<i>-771.5</i>	<i>-1282.8, -352.5</i>	<i>0.006</i>

Chapter 6

Site fidelity and ranging patterns of Irrawaddy and Indo-Pacific humpback dolphins

In this chapter, I use sighting data of identified individuals of both species to compare their sighting patterns, residence times, and range sizes. I determine annual and monthly sighting patterns for each identified individual, and their fidelity towards specific areas within Cleveland Bay. I use exponential mathematical models and the sighting data to assess the temporal patterns of residence, and residence times inside and outside Cleveland Bay. I assess range sizes and intra and interspecific overlap using minimum convex polygon techniques. This chapter also outlines the photo-identification methodology used during the boat-based surveys carried out in Cleveland Bay.

Chapter 6. Site fidelity and ranging patterns of Irrawaddy and Indo-Pacific humpback dolphins

6.1 Introduction

Animals live in spatially and temporally heterogeneous environments. As a response to this heterogeneity, individuals have developed a range of movement strategies to acquire the resources required for key activities (e.g., feeding, breeding). Within heterogeneous environments, animals may use a variety of cues to assess habitat suitability or quality (i.e., the habitat yielding the highest fitness) and use this information to make decisions about their dispersal and/or settlement in a particular habitat (Hoover 2003). Site fidelity or philopatry is the tendency of animals to remain in, or return to, and re-use a previously occupied location (Switzer 1993). The decision to remain faithful to a particular area can convey several ecological benefits as it reduces the costs and risks involved in relocating to new sites and provides familiarity with resources and predators (Greenwood 1980). This strategy has been observed in many taxa including various territorial and non-territorial mammals (Greenwood 1980, Switzer 1993).

The ranging patterns exhibited by individuals are important attributes linked to site fidelity. The extent of site fidelity and ranging patterns displayed by an organism can have profound effects on the dynamics, demography, and persistence of local populations (Hestbeck and Nichols 1991, Schmidt 2004). Additionally, information on the ranging patterns of a species provides insights into its space use (South 1999, Chamberlain et al. 2000), resource partitioning (Johnson and Franklin 1994, Juarez and Marinho 2002), social organization and mating systems (Ribble and Stanley 1998, Geffen et al. 1999), and energetics (McNab 1963, Kelt and Van Vuren 1999). A basic understanding of site fidelity and ranging patterns is important for conservation and

management efforts (Joshi et al. 1995, Warkentin and Hernandez 1996, Schultz 1998, Linnell et al. 2001).

Within the delphinids, most studies of site fidelity and ranging patterns have focused on a single genus, the bottlenose dolphin *Tursiops sp.* (Ballance 1990, Ballance 1992, Bearzi et al. 1997, Corkeron 1997, Wilson et al. 1997, Defran and Weller 1999, Defran et al. 1999, Maze and Wursig 1999, Bristow and Rees 2001, Campbell et al. 2002, Gubbins 2002, Ingram and Rogan 2002, Owen et al. 2002, Zolman 2002, Corkeron and Martin 2004). Overall, the results from these studies indicate that populations of bottlenose dolphins are typically composed of a mixture of resident and transient-migratory individuals. Studies on site fidelity or ranging patterns of other delphinids include Atlantic white sided dolphins, *Lagenorhynchus acutus* (Weinrich et al. 2001), humpback dolphins, *Sousa chinensis* (Karczmarski 1999, Jefferson 2000, Karczmarski et al. 2000a, Hung and Jefferson 2004); Hector's dolphins, *Cephalorhynchus hectori* (Bräger et al. 2002), common dolphins *Delphinus delphis* (Neumann et al. 2002), and tucuxi dolphins, *Sotalia fluviatilis* (Santos et al. 2001). These studies show that there can be considerable interspecific differences among delphinids. For example while Hector's dolphins in the Banks Peninsula, New Zealand, show strong site fidelity to small localized coastal areas (Bräger et al. 2002), most humpback dolphins in Algoa Bay appear to be infrequent visitors with long-range movements (Karczmarski 1999).

As discussed in Chapters 1 and 2, Irrawaddy dolphins, *Orcaella brevirostris*, and Indo-Pacific humpback dolphins (hereafter humpback dolphins), *Sousa chinensis*, are two of the least known coastal dolphins occurring in tropical subtropical waters of the Indo - west Pacific region. Nothing is known about the site fidelity and ranging patterns exhibited by individual animals. Studies on site fidelity and ranging patterns

of Irrawaddy and humpback dolphins are of interest for their conservation; as such studies can provide valuable information about their relative use of space, dispersal behaviour, and movements.

In this study, I present data on sightings of individual Irrawaddy and Indo-Pacific humpback dolphins collected over a four year (1999-2002) photo-identification study in coastal waters of Cleveland Bay, northeast Queensland, Australia. A primary focus is to examine and compare their patterns of site fidelity, residence times, range size, and range overlap (Objective 5 of this thesis, see Chapter 1). I also discuss some of the potential biases in using photo-identification data to estimate these ecological parameters.

6.2 Methods

6.2.1 Photo-identification surveys

As outlined in Chapter 4, boat-based surveys were conducted in the coastal waters of Cleveland Bay Dugong Protected Area (hereafter Cleveland Bay), northeast Queensland, between January 1999 and October 2002 (see Figure 4.1 in Chapter 4). Previous studies have shown that Irrawaddy and humpback dolphins are reliably identified from marks and white pigmentation patterns on their dorsal fins (Corkeron 1990, Parra and Corkeron 2001). Photographs of Irrawaddy and humpback dolphins were taken using a 35-mm camera with a 70-300-mm zoom lens, shooting Kodak Ektachrome 100 ASA colour slide film (pushed to 200 ASA) at shutter speeds of 1/500-1/1000 of a second. Photographs were taken as perpendicular to the dolphin's body axis as possible and concentrated mainly on the dorsal fin. All photographs taken on surveys were examined and classified into three grades (excellent, good, poor) according to focus, contrast between dorsal fin and background, relative angle to the animal, and the size of dorsal fin relative to the frame. Photographs classified as

excellent and good were used to identify individuals and develop identification catalogues for each species (Würsig and Jefferson 1990).

6.2.2 Data analysis

6.2.2.1 Site fidelity

Although some animals were identified more than once during the same day, only sightings separated at least a day apart were used in the analysis to minimize likelihood of dependence in the data. The first sighting of the day for each identified individual was used for analysis. Four measures were used to define site fidelity patterns. To investigate the presence of identified individuals in the study area over time, I calculated: 1) the number of months a dolphin was identified as a proportion of the total number of months in which at least one survey was conducted (i.e., monthly sighting rate), and 2) the number of calendar years a dolphin was identified as a proportion of the total surveyed (i.e., yearly sighting rate). Potential, monthly sighting rates range between 0.02 (i.e., animals sighted in only one month out of 36) and one for an individual sighted in all months. Similarly, potential yearly sighting rates range between 0.25 (i.e., animals sighted in only one year out of four) and one for an individual sighted in all years of study.

To assess if sightings of individuals showed a consistent interannual seasonal pattern, I examined the number of times dolphins identified in more than one year were reidentified (i.e., subsequent times an animal is identified after first identification) in the particular month they were first identified. As survey effort was not even throughout the study period (Table 6.1, all tables have been placed at the end of this chapter to minimize interruption to the flow of the text, and printed on yellow colour paper for ease of location), I used survey effort data (i.e., hours of survey per

month) to estimate monthly resighting rates (i.e., number of times dolphins identified in more than one year were reidentified in the particular month they were first identified per hour of survey for that month).

Finally, to investigate if individual dolphins displayed fidelity towards specific areas within Cleveland Bay, I used the CrimeStat spatial statistics software to measure the standard distance deviation (S_{XY}). The standard distance deviation is the spatial equivalent to the standard deviation (Levine 2002). The S_{XY} measures the standard deviation of the distance of each individual dolphin location from their mean center:

$$S_{xy} = \sqrt{\frac{\sum (X_i - \bar{X})^2 + \sum (Y_i - \bar{Y})^2}{N - 2}}$$

where X_i and Y_i are the coordinates of individual dolphin locations (projected into Universal Transverse Mercator Zone 55), \bar{X} and \bar{Y} are the means of each coordinate, and N is the total number of times an individual animal was sighted. Since there are two constants (\bar{X} and \bar{Y}) from which S_{XY} is calculated, two is subtracted from the number of points to produce an unbiased estimate of standard distance (Levine 2002). To provide a balance between the representativeness of the data (e.g., include the maximum number of individuals) and its reliability (e.g., include individuals with maximum sighting frequencies, Chilvers and Corkeron 2002), S_{XY} was calculated only for individuals that were seen on \geq eight occasions throughout the study period, separated at least a day apart, and with at least one of those occasions separated a year apart. The more dispersed individual locations are, the larger the standard distance deviation and the less faithful an individual was to a specific area within Cleveland Bay. Interpecific differences in monthly sighting rates, yearly sighting rates, and standard distances were evaluated with two sample randomization tests. All

randomization test were carried out 2000 times with the POPTOOLS Excel add-in software (Hood 2003), and P-values evaluated at $\alpha = 0.05$.

6.2.3 *Residence times*

To estimate the amount of time identified individuals reside inside Cleveland Bay, I calculated the probability that if an individual is identified in the study area at any time, it is identified during any single identification made in the area some time lag later (i.e., lagged identification rate, Whitehead 2001). Lagged identification rates can be estimated from the number of identifications and reidentifications of a particular individual for any time lag (Whitehead 2001). Plots of lagged identification rates against time lag were produced for all individual dolphins identified of each species as these plots provide indications of the temporal use of the area by individual animals. A plot of lagged identification rates that drops after a certain time lag and then levels off above zero at a larger time lag indicates that many animals leave the study area (i.e., emigration and/or mortality) after residing in the area for a certain time lag, but that: 1) there are either animals that remain resident, and/or 2) others that reimmigrate back into the study area (Whitehead 2001).

After estimating lagged identification rates for each species, I compared the observed rates to expected lagged identification rates from exponential mathematical models of emigration/mortality and emigration + reimmigration (Whitehead 2001):

Emigration/mortality:

$$R(\tau) = 1/a1 \times \exp(-\tau/a2)$$

Emigration + reimmigration:

$$R(\tau) = (1/a1) \times ((1/a3) + (1/a2) \times \exp(-(1/a3 + 1/a2) \times \tau)) / (1/a3 + 1/a2)$$

where $R(\tau)$ is the lagged identification rate, a_1 = mean population size in study area, a_2 = mean residence time inside the study area before leaving, a_3 = mean residence time outside study area before entering, and t_d = time lag. The model minimizing the adjusted Akaike Information Criterion for small-sample bias (AIC_c) was chosen as the best fit model (Burnham and Anderson 1998). Estimates of mean residence time inside the study area and mean residence time outside the study area were obtained from the best fitting model. Computation of lagged identification rates and model fitting was carried out using the computer software SOCPROG 2.1 (Whitehead 2004). It is important to note that these methods give relatively imprecise estimates compared with methods based on continuous tracking data (i.e., radio or satellite tracking) (Whitehead 2001). However, they provide a first approximation of residence times for both species and a basis for future studies using radio or satellite telemetry.

6.2.4 Ranging patterns

The range size of identified individuals was estimated by the Minimum Convex Polygon (MCP) method (Hayne 1949). Because surveys were limited to the inshore waters of Cleveland Bay, and previous data indicated that identified animals range outside this area (Parra and Corkeron 2001), my use of the term “range” simply defines the area where an individual was sighted during this study, rather than their home range *per se*. Although probabilistic methods (i.e., kernel range) provide more reliable estimates of range size and intensity of use of different areas, they require large sample sizes, and often produce disjunct ranges because of small number of locations between sampling areas even though animals may actually use these areas (Powell 2000). I was mainly interested in defining the area where an individual was sighted and data locations of individual dolphins were limited. Accordingly, I decided to use the MCP method to estimate range size.

Unrestricted (100%) minimum convex polygon areas were calculated using the ArcView-Animal Movement Analyst extension (Hooge and Eichenlaub 2000). MCPs were estimated for each dolphin of both species identified on \geq eight occasions, separated at least a day apart. To investigate if each individual's range size reached an asymptote, I constructed area observation curves of MCP range size with an increasing number of sightings for each individual, starting with three sightings (Laundre and Keller 1985). I considered that an individual's range reached an asymptote when at least 90% of the estimated range size of the individual was reached. The length of the range was estimated as the shortest distance between the two most extreme sightings without crossing land. Interspecific differences in range size and length were estimated with two sample randomization tests (Manly 1997).

Finally, to assess the degree of overlap between the ranges of both species, I calculated the percent area overlap (PAO) between the MCP ranges of each pair of individuals as:

$$PAO = \left(\frac{A_{Ob-i, Sc-i}}{A_{Ob-i}} \times \frac{A_{Ob-i, Sc-i}}{A_{Sc-i}} \right)^{0.5},$$

where $A_{Ob-i, Sc-i}$ is the area of overlap between the two individual MCP ranges been compared, A_{Ob-i} the area of the Irrawaddy dolphin MCP range, and A_{Sc-i} is the area of the humpback dolphin MCP range (Atwood and Weeks 2003). The degree of overlap between individuals of the same species was estimated in the same way.

6.2.5 Potential biases

Dolphins spent most of their lives in an underwater environment. This poses formidable obstacles in estimating their movement, space use patterns and ranging behaviour. Because the results presented here are based on 1) the analysis of photo-identification data, 2) survey effort could not be evenly distributed across all sections

of the study area, and 3) surveys were limited to an area of finite size, there are important systematic biases that might affect the estimates of site fidelity, residence times and ranging patterns.

6.2.5.1 Sampling bias

Surveys were limited to coastal waters (i.e., waters within 6 km from the coast) and weather conditions (Beaufort sea states 0-3). Because of weather limitations surveys were carried out only between 6:00-14:00 hours because of increasing winds in the afternoon. Additionally, the eastern section of Cleveland Bay (section D, see Figure 4.1 in Chapter 4) was surveyed less in comparison with other areas. Thus, if animals spend considerable time in offshore waters, and/or in the study area during the late afternoon hours or in section D, my estimates of site fidelity and residence times may be negatively biased.

Although I expect both species to also occur in offshore waters of Cleveland Bay there is evidence that indicates animals occur mainly in waters close to the coast. Most sightings of Irrawaddy and humpback dolphins that were made in aerial surveys (see Chapter 2) and boat-based line transect surveys (see Chapter 3), which included offshore waters (waters > 6 km from the coast) of different areas along the Queensland coast, occurred in waters within 6 km from the nearest coastline (see Chapters 2 and 3, Corkeron et al. 1997, Parra et al. 2002). Pilot studies in Cleveland Bay totalling 14 hours and 163 km of line transect that covered waters up to 10 km from the coast yielded no sightings beyond 5 km from the coast (Parra unpublished data). Therefore, I expect the patterns presented here to be representative of most animals making use of Cleveland Bay.

Schools of both species were seen in section D of the study area (see Chapter 5) thus MCP ranges of individual animals are likely to extend into this area. This

section, however, lacks river mouths, a feature that appears to influence the habitat preferences of Irrawaddy and humpback dolphins throughout their range (see discussion Chapter 5). As a result, I suspect animals do not spend much time in this section of the study area.

6.2.5.2 *Availability bias*

Although photo-identification provides several benefits as a non-invasive tracking technique, it is also relatively limited. Photo-identification is dependant on good weather, daylight hours, locating the animals, animals having distinctive marks, and a researcher's ability to take good quality pictures. For an individual dolphin to be photographically identified, the dolphin must be first sighted. However, schools of dolphins may be unavailable to observers because of the sea state. The probability of sighting a dolphin or school of dolphins is likely to decrease with Beaufort sea state (Palka 1996).

I showed that Irrawaddy dolphins are sighted less frequently in Beaufort sea states ≥ 2 , while humpback dolphins showed no heterogeneity in their sightability up to Beaufort sea state 3 (see Chapter 4). As explained in Chapter 4, survey effort throughout the study period took place mainly in Beaufort sea states 1 (49.2%) and 2 (36.5%), thus humpback dolphins were likely to be sighted more often than Irrawaddy dolphins. This difference in sighting probabilities might explain the higher lagged identification rates and higher residence times of humpback dolphins in Cleveland Bay compared with Irrawaddy dolphins (Fig. 6.5b).

6.2.5.3 *Identification bias*

Positive identification of all dolphins encountered could not be obtained, because: 1) good or high quality photographs of all individuals in a school were not

obtained; 2) some animals within a school did not come close enough to the boat (i.e., heterogeneity in behaviour); and 3) not all animals in the population develop distinctive marks.

Identified animals were not tracked continuously in space and time and sighting probabilities were likely to be affected by Beaufort sea state, heterogeneity in individual behaviour, and unsuccessful attempts to photograph individuals. Therefore, the sighting rates, standard distance deviations, residence times, and range sizes and lengths estimated for Irrawaddy and humpback dolphins in this study are minimum estimates. Additionally, the analysis presented here is based on adult animals, and site fidelity, residence times and ranging patterns of other age classes may show different patterns.

The only realistic method to gain accurate estimates of site fidelity and ranging patterns of Irrawaddy and humpback dolphins is radio- or satellite telemetry. Telemetry provides an almost continuous collection of movement data across different spatial and temporal scales allowing precise and accurate descriptions of movement and space use patterns (Koenig et al. 1996). As discussed in Chapter 10, future studies should be directed at assessing the feasibility of using such technology on Irrawaddy and humpback dolphins.

6.2.5.4 *Lack of independence*

Most analysis of ranging patterns requires independence of observations to obtain unbiased estimates (Kernohan et al. 2001). Although I have minimized dependence in the location data of each individual by only using animals identified at least a day apart, total independence in the data is unlikely. Dolphins are social animals and the movement patterns of an individual are likely to be influenced by the movements of their conspecifics. Analyses of the social structure of Irrawaddy and

humpback dolphins in Cleveland Bay (see Chapter 7) indicated that out of the 15 Irrawaddy dolphins sighted on \geq eight occasions, 14 had at least one strong associate among the individuals in the analysis. Out of the nine humpback dolphins sighted on \geq eight occasions, four had at least one strong associate among the individuals in the analysis. In this context, the range sizes and lengths estimated in this study cannot be viewed as independent samples, as biological interactions between individuals are likely. This situation explains the similarity in standard distance deviations, range locations, range sizes, and range length among individuals of each species. Thus, the ranging patterns presented here may not represent the full range of individual variability present in the population.

Despite these limitations, the results presented here provide insights into the site fidelity, ranging patterns, and spatial interactions among coexisting delphinids—a topic that has received little attention in marine mammal studies. This information is fundamental towards our understanding of species specific requirements and improving our ability to effectively manage peoples' interactions with these dolphins .

6.3 Results

6.3.1 Survey effort and identified animals

As discussed in Chapter 4, I spent a total of 630 hours in Cleveland Bay searching for Irrawaddy and humpback dolphins (Table 6.1). Most survey effort took place during the dry season (May–November). Because of bad weather survey effort was not uniformly distributed across the study area. Survey efforts were similar across sections A (201 hrs), B (191 hrs), and C (179 hrs), however section D (59 hrs) was surveyed considerably less because of its exposure to strong south easterly winds.

I identified 63 Irrawaddy dolphins and 54 humpback dolphins during the study period. Only one juvenile Irrawaddy dolphin was identified, the remainder of the dolphins identified were adults. Sex was determined (see Chapter 4 for methodology) for eight Irrawaddy dolphins (i.e., eight females), and eight humpback dolphins (i.e., four females and four males).

6.3.2 Site fidelity

Individual dolphins of both species exhibited varying degrees of site fidelity. Twelve Irrawaddy dolphins (19%) and 22 (41%) humpback dolphins were identified only once throughout the study period (Fig. 6.1a). Forty-three Irrawaddy (68%) and 28 (52%) humpback dolphins were identified in more than one calendar year (Fig. 6.1b).

Relative to the total number of months surveyed, most Irrawaddy dolphins identified were sighted relatively seldom (Mean \pm SE = 0.12 ± 0.01 sightings per month) (Fig 6.1c). However, yearly sighting rates (0.54 ± 0.03 sightings per year) indicated that many of the Irrawaddy dolphins identified were seen in more than one calendar year. Humpback dolphins showed a similar pattern, with low monthly sighting rates (0.10 ± 0.02 sightings per month), and relatively high sightings across years (0.46 ± 0.03 sightings per year) (Fig. 6.1c). Six out of the eight female Irrawaddy dolphins, all four humpback males, and two out of the four humpback females identified were among the animals with high yearly sighting rates (i.e., 0.75 to 1 sighting per year). No differences in monthly sighting rates were found between the two species (Difference = 0.01, 95% CI = -0.03, 0.05, P = 0.47). Yearly sighting rates were higher in Irrawaddy dolphins than in humpback dolphins although the effect was not substantial (Difference = 0.09, 95% CI = -0.01, 0.17, P = 0.087).

Irrawaddy and humpback dolphins identified in more than one year were mainly identified and reidentified during the dry season between May and September when greater survey effort was carried out (Fig. 6.2). However, the difference in mean resighting rates of identified individuals between the wet and dry seasons was small for both species (Irrawaddy dolphins: Difference = -0.25, 95% CI = -0.42, -0.09 P = 0.08; humpback dolphins: Difference = -0.17, 95% CI = -0.34, 0.02, P = 0.108).

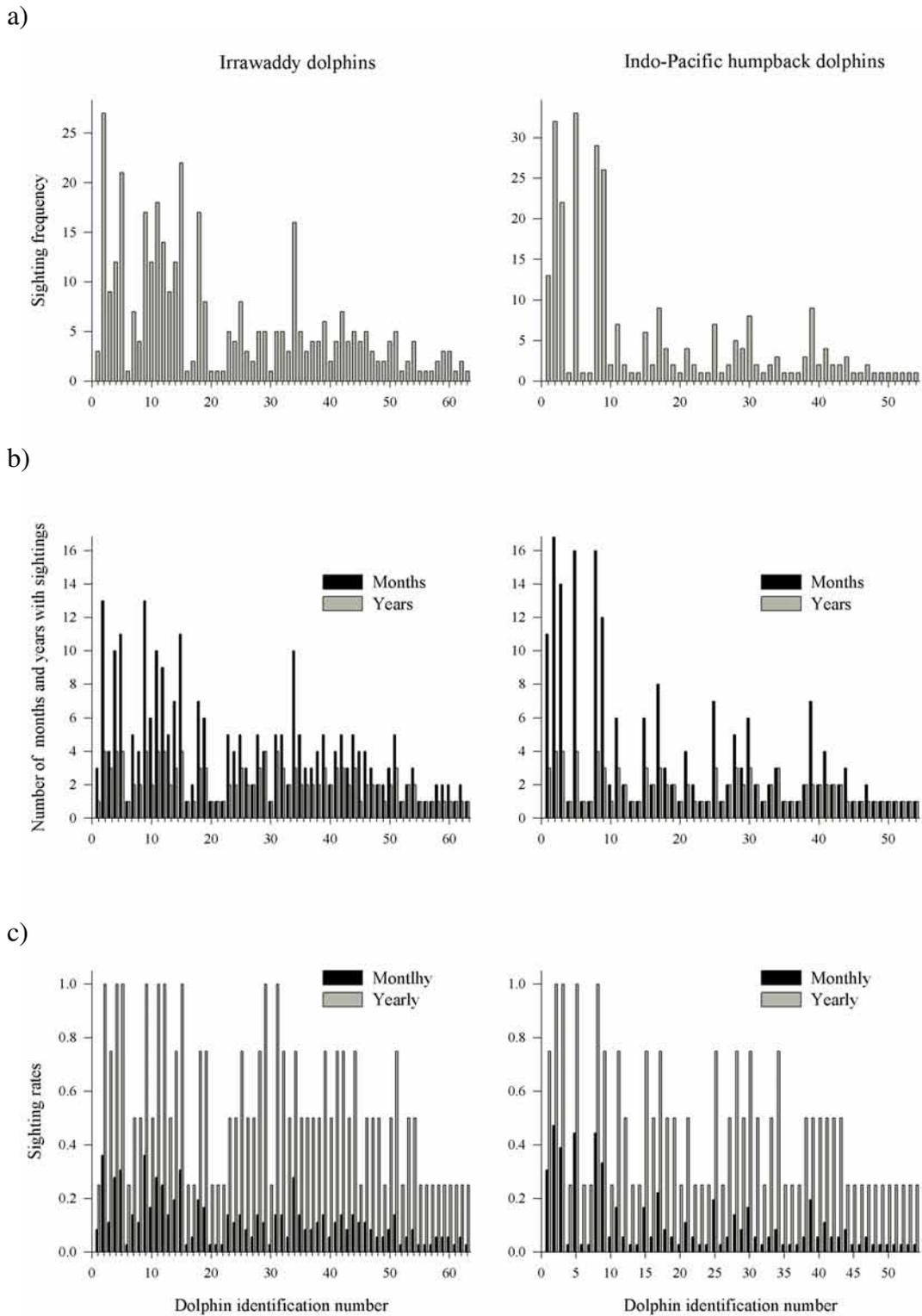


Figure 6.1 Sightings of 63 and 54 Irrawaddy and humpback dolphins identified in Cleveland Bay between 1999-2001: a) total number of sightings of all identified individuals; b) number of months and years in which each individual dolphin was sighted; c) number of months and years a dolphin was identified as the proportion of the total number of months and years surveyed.

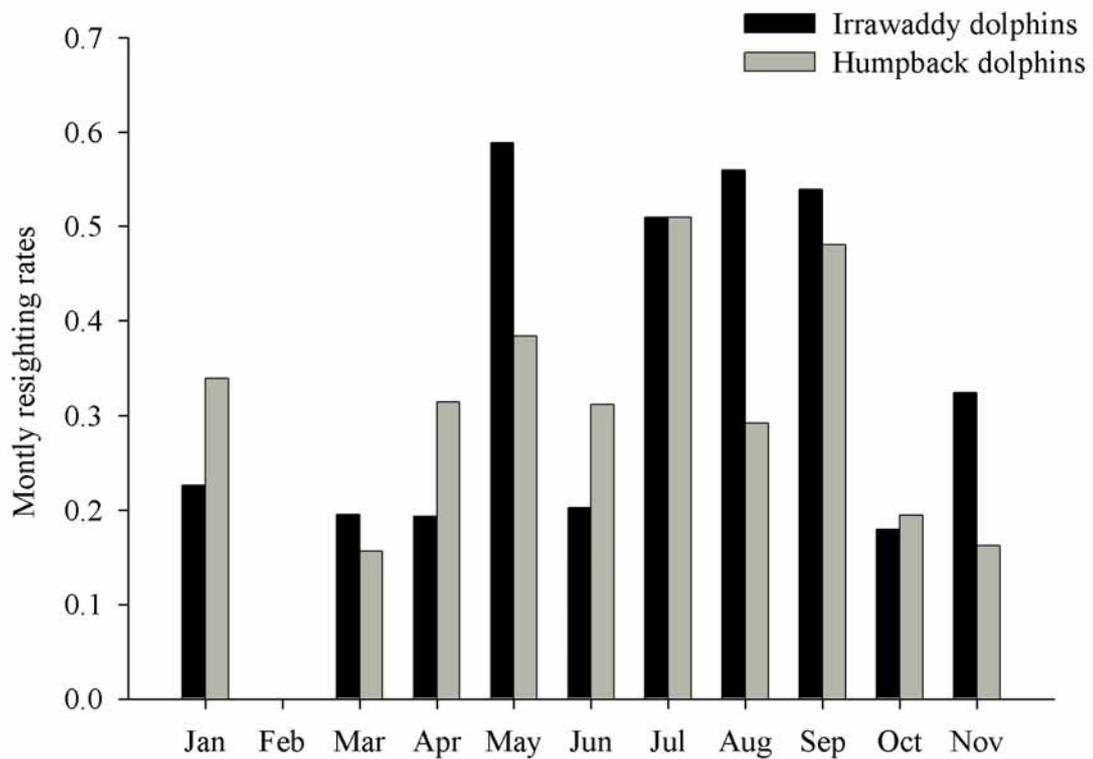


Figure 6.2 Number of times dolphins identified in more than one calendar year were reidentified in the particular month they were first identified per hour of survey for that month (i.e., Monthly resighting rates).

The standard deviation of the distance of each individual dolphin location from their mean centre indicated that over 50% of the Irrawaddy and humpback dolphins sighted on \geq eight occasions were found within less than 10 km of their mean centre (Fig. 6.3). Although on average Irrawaddy dolphins (Mean \pm SE = 8.7 ± 0.87 km) showed a more dispersed pattern with larger standard distances than humpback dolphins (6.3 ± 1.01 km), the interspecific difference was not significant (Difference = 2.4 km, 95% CI = -0.59, 4.49, $P = 0.09$).

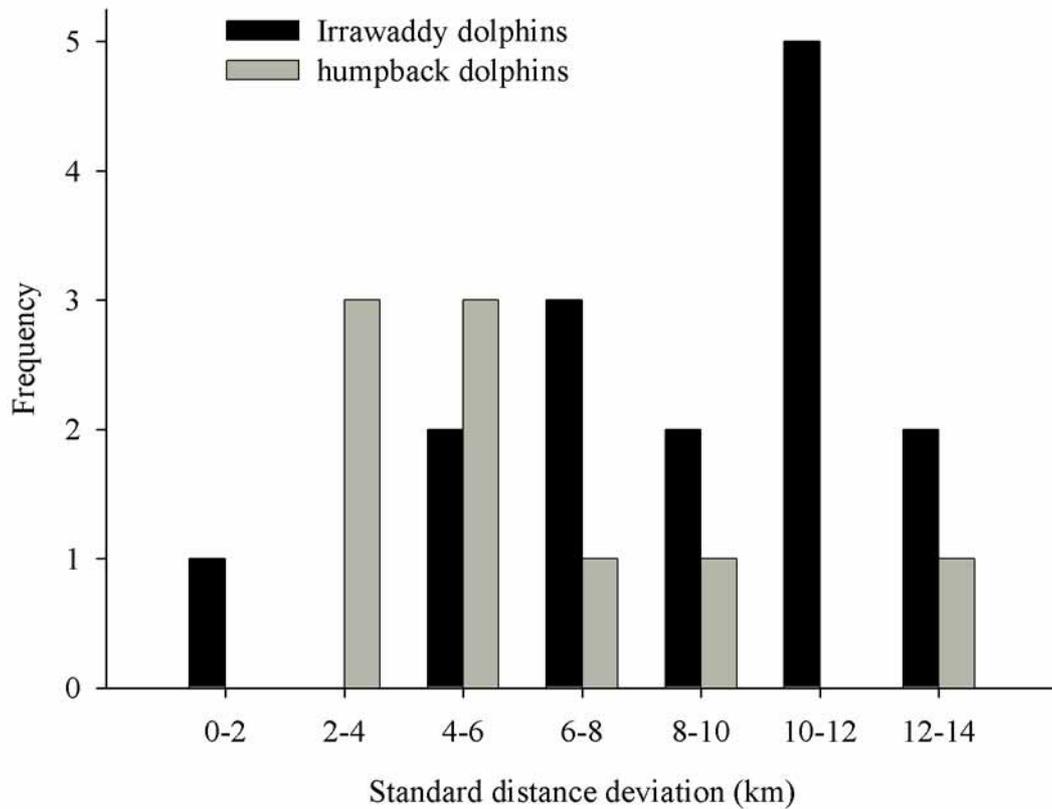


Figure 6.3 Frequency distribution of the standard deviation of the distance of each individual dolphin location from their mean center (i.e., standard distance deviation) for all Irrawaddy dolphins (n = 15) and humpback dolphins (n = 9) identified ≥ 8 times in Cleveland Bay between 1999-2002.

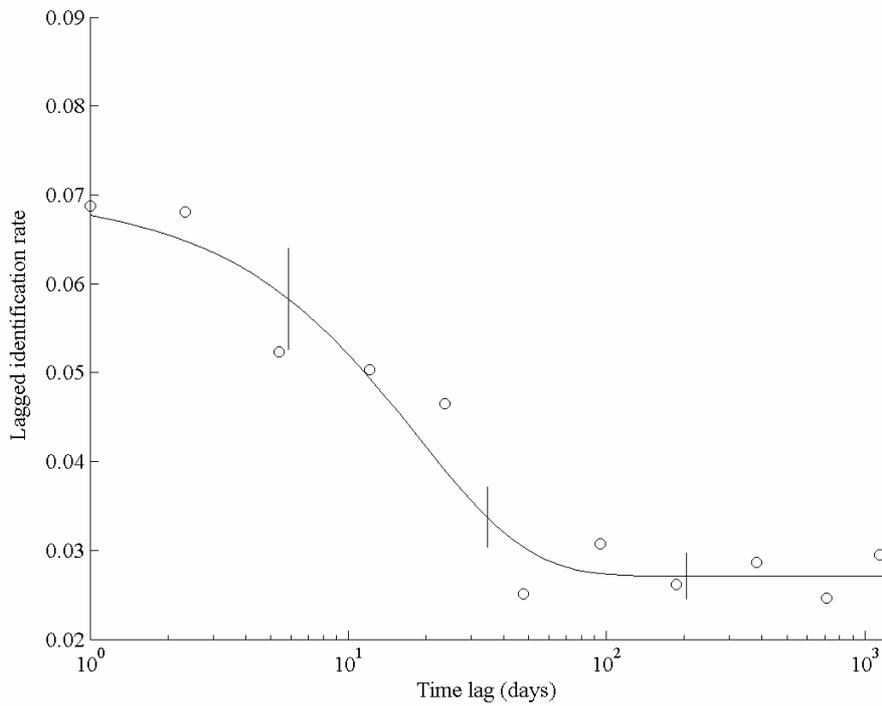
6.3.3 *Residence times*

The lagged identification rate of Irrawaddy dolphins fall after lags of approximately 3 to 30 days and then leveled off above zero at longer time lags (Fig.6.4a). This pattern suggests that animals may spend periods of up to 30 days in the bay before leaving the study area. The lagged identification rate of humpback dolphins showed a similar pattern but with different residence times. For humpback dolphins it appears that animals left the study area after periods of 10 to 140 days (Fig. 6.4b). For both species the lagged identification rate levelled off above zero,

suggesting that some animals are permanent residents and/or others reimmigrate into the study area after longer time lags.

Of the two models applied to the data, the model curve of emigration and reimmigration into the study area fitted the data best for both species (Fig 6.4). This model also showed the lowest AIC_c values (Irrawaddy: 17841; humpback:17146) in comparison to emigration/mortality models (Irrawaddy: 17913; humpback: 17183). Estimates of mean population size and residence times from this model indicate that about 14.3 (\pm SE = 1.7729, 95% CI =11.6, 18.5) Irrawaddy dolphins and 10.1 (\pm SE = 1.87, 95% CI = 7.7, 14.1) humpback dolphins were in the study area at any one time, and that animals could spend from a few days to over a month inside the study area before leaving. Irrawaddy dolphins appeared to reside inside the study area for periods of 30.3 days (\pm SE =24.70, 95% CI =17.2-56.2), and spend periods of 47.8 days (\pm SE = 29.7, 95% CI = 27.5, 85.3) outside the study area before entering back into it. Humpback dolphins had considerably longer residence times inside the study area of 141 days (\pm SE = 110.3, 95% CI =88.7, 281.1), and periods of 109 days (\pm SE = 47.7, 95% CI = 68.1, 212.7) outside the study area.

a) Irrawaddy dolphins



b) Humpback dolphins

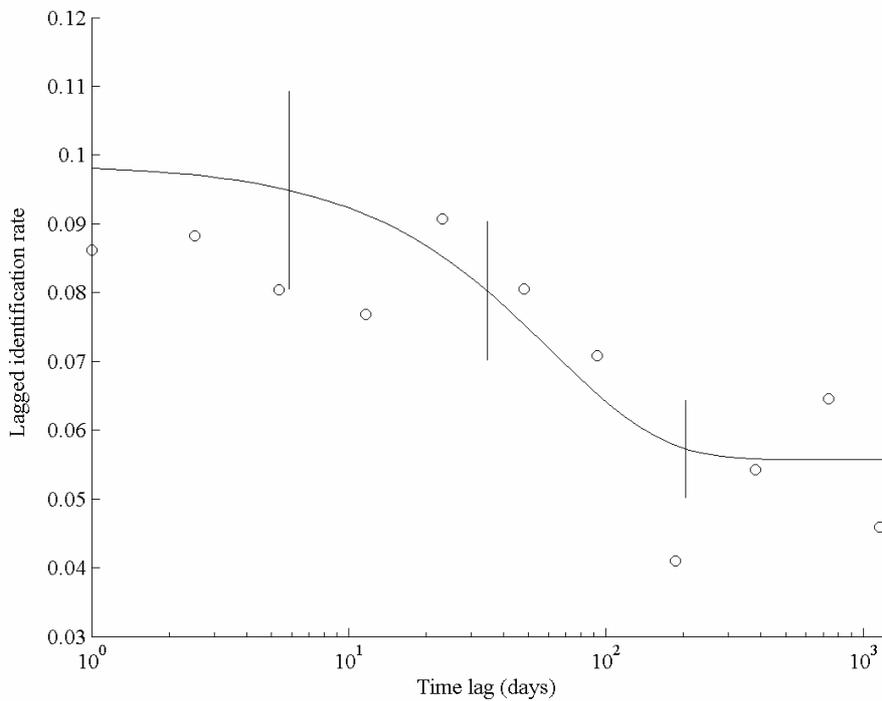


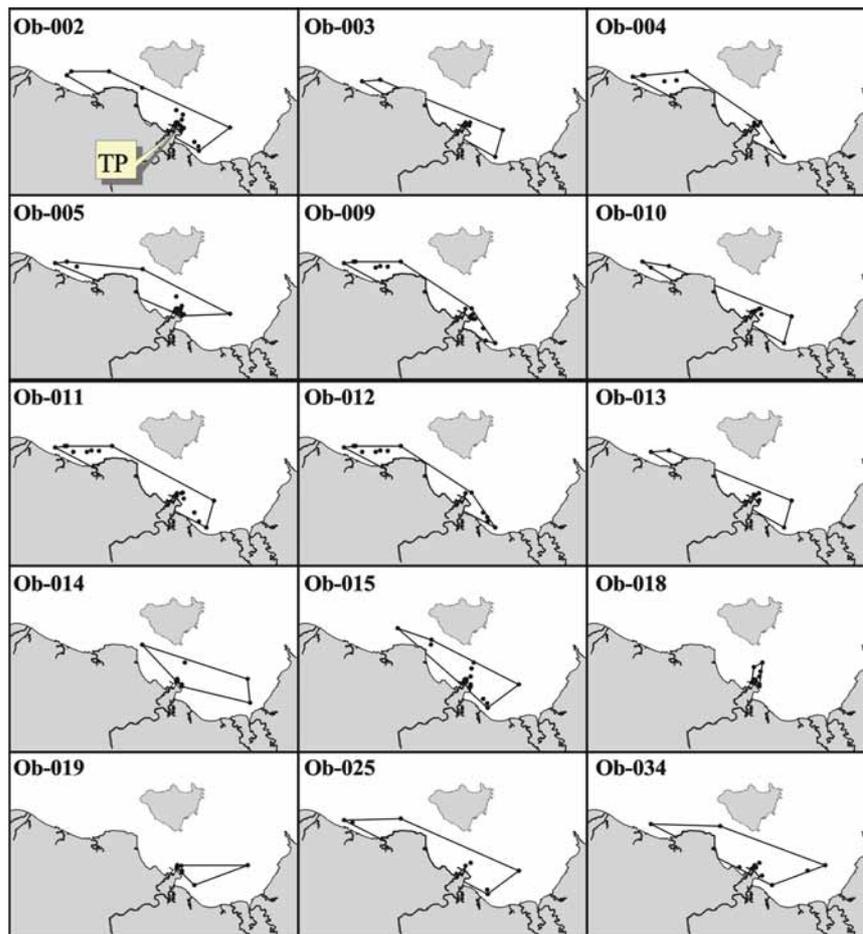
Figure 6.4 Lagged identification rates (○) for (a) adult Irrawaddy dolphins and (b) humpback dolphins in coastal waters of Cleveland Bay, together with the expected lagged identification rates and estimated standard errors (bars) from emigration and reimmigration models fitted to the data using maximum likelihood.

6.3.4 *Ranging patterns*

The MCP ranges of individuals of both species sighted on \geq eight occasions were similar in size and length (Fig. 6.5a, 6.5b, Table 6.2). The estimated range size of Irrawaddy dolphins varied from 4.7 km² to 108.3 km², with an overall mean of 69.1 \pm 7.43 km². Distances between the most extreme locations of each individual were between 4.5 km and 33.6 km long (27.4 \pm 2.18 km). The range of humpback dolphins was on average 74.8 \pm 13 km², ranging from 9.4 km² to 129.5 km². Range length varied from 15.4 km to 41.6 km, with an overall mean of 25.2 \pm 2.77 km. I found no interspecific differences in range size (Difference = -5.7 km², 95% CI = -32.7, 22.3, P = 0.678) and range length (Difference = 2.2 km, 95% CI = -6.3, 7.5, P = 0.553). Individual ranges of both species extended over similar areas, covering mainly the stretch of coastline southeast and northwest of Townsville's Port. The mean percent area overlap between individual ranges of both species was 45.8 \pm 1.71%, and none of the individual ranges showed spatial separation (range: 1.3%-85.4%). There was also considerable overlap among individual ranges at the intraspecific level (Mean \pm SE = Irrawaddy: 51.7 \pm 2.52%, humpback: 49.9 \pm 3.38 %).

The number of sightings needed to reach 90% of the estimated individual range was variable (Fig. 6.6a, 6.6b). Overall, the range size of most Irrawaddy and humpback dolphins continued to increase with number of sightings and more sightings are needed for range size to stabilize. Out of the 15 Irrawaddy dolphins, 11 reached 90% of their estimated range with 7 to 26 sightings (Fig. 6.6a). Five out of the nine humpback dolphins reached 90% of their estimated range with 6 to 25 sightings.

a) Irrawaddy dolphins



b) Humpback dolphins

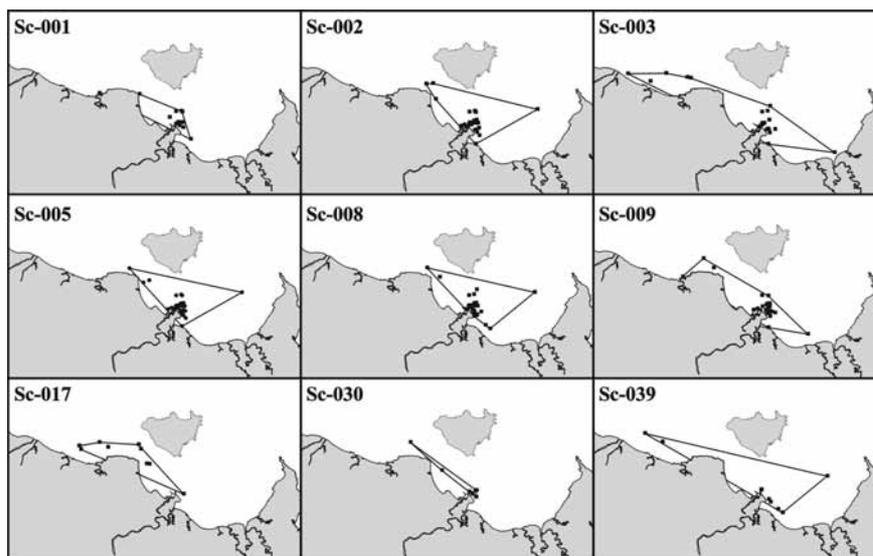


Figure 6.5 Minimum Convex Poygons (MCP) of individual Irrawaddy (a) and humpback (b) dolphins sighted on \geq eight occasions. Code in top left corner indicates the dolphin identification number. TP = Townsville's Port.

a) Irrawaddy dolphins

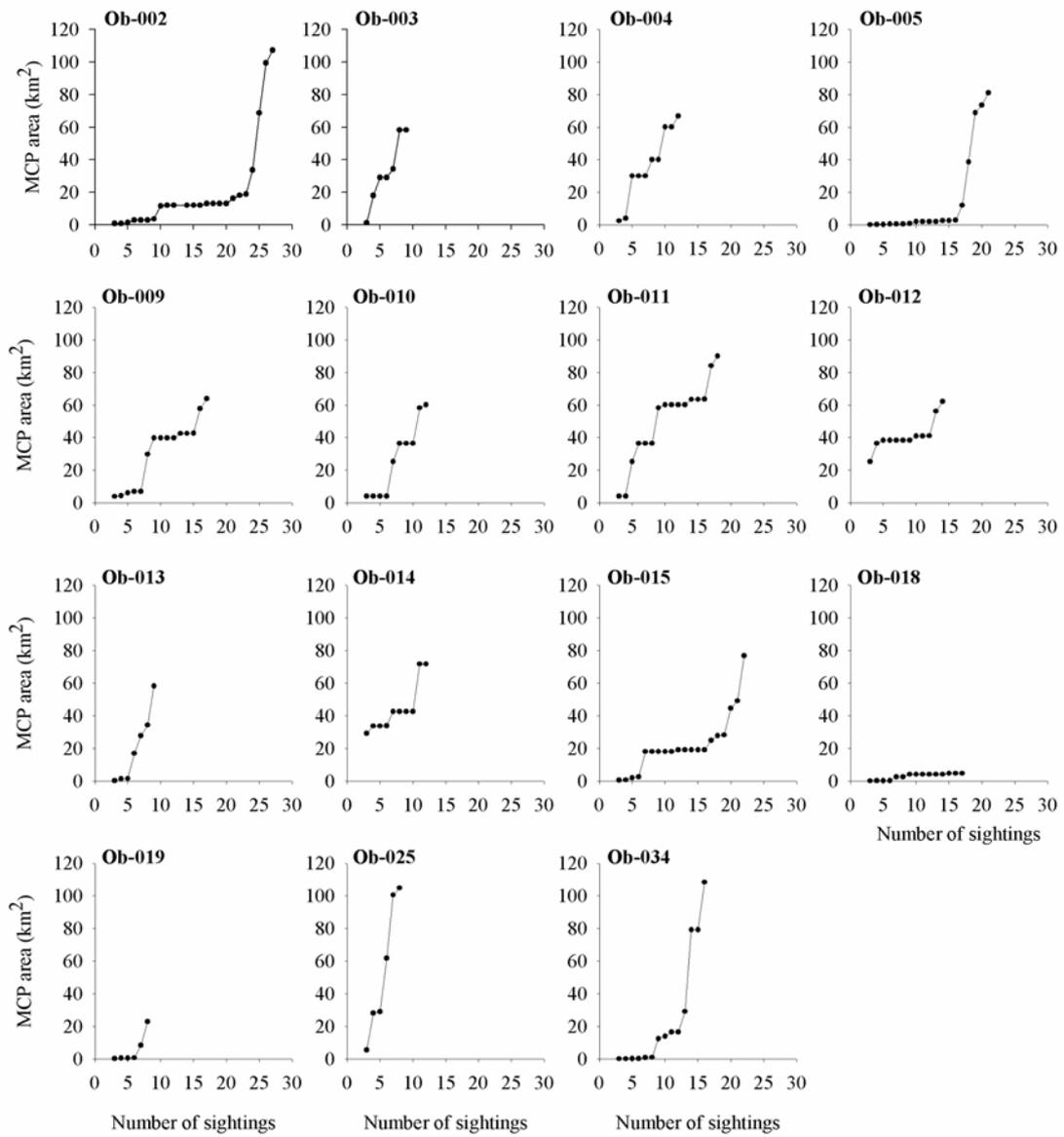


Figure 6.6 Area observation curves of Minimum Convex Polygons (MCP) with increasing numbers of sightings for individual Irrawaddy dolphins (a) and humpback (b) dolphins sighted on \geq eight occasions. Code in top left corner indicates the dolphin identification number. The * indicates that at least 90% of the estimated range size was reached for that individual.

b) Humpback dolphins

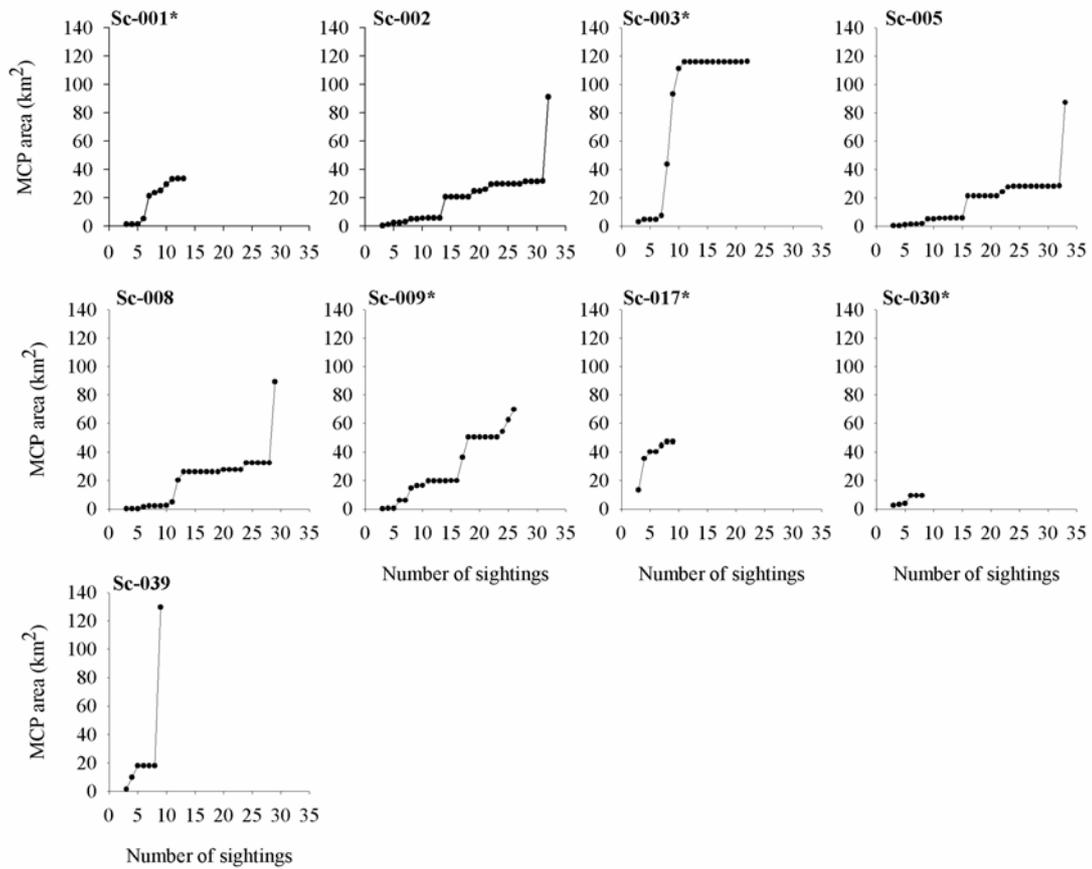


Figure 6.6 (continued). Area observation curves of Minimum Convex Polygons (MCP) with increasing numbers of sightings for individual Irrawaddy (a) and humpback (b) dolphins sighted on \geq eight occasions. Code in left corner indicates the dolphin identification number. The * indicates that at least 90% of the estimated range size was reached for that individual.

6.4 Discussion

6.4.1 *Site fidelity and residence times*

The low monthly sighting rates observed for both species suggest that the majority of animals do not reside in the study area permanently. However, yearly sighting rates (based on calendar years) suggest most animals come back from year to year to the study area. In fact, lagged identification rates and residence times estimated from emigration models suggested that most individuals of both species may spend a couple of days to a month or more inside the study area, with some animals residing permanently and/or others reimmigrating back into the study area at longer time lags. Although most humpback dolphins identified in this study were seen in more than one year (52%), the large proportion of animals seen only once (41%) indicates that there is a larger number of humpback dolphins that either die, or spend little time inside the study area in comparison to Irrawaddy dolphins. There is no evidence that such mortalities took place. Only eight humpback dolphins were found dead in the Townsville region between 1999 and 2001 (see Appendix 4, Haynes et al. 1999, Haynes and Limpus 2000, 2002, Limpus et al. 2003). Thus, it is likely that the large proportion of animals seen only once in the study area are occasional visitors and that the coastal waters of Cleveland Bay represent only a part of their home range.

The overall low standard distance deviations displayed by frequently sighted individuals of both species suggest that animals come back to particular areas within Cleveland Bay repeatedly. This localized pattern is indicative of preferential use of some areas in relation to others. These results correspond with the previous analysis in Chapter 5 on the space use patterns of Irrawaddy and humpback dolphins at the population level (i.e., schools of dolphins instead of individuals were used for analysis of space use) in Cleveland Bay, where it was shown that use of space by both species

was not random and animals tended to concentrate their activities in certain core areas.

Site fidelity is an attribute that appears to be common among some species of coastal delphinids (Santos et al. 2001, Bräger et al. 2002), however, our understanding of the factors that promote it is limited. Factors that may affect fidelity to a particular area include age (Newton 1993, Payne and Payne 1993, Kemp 2001), sex (Greenwood 1980, Johnson 1986), the spatial and temporal variability in the quality of a site (Switzer 1997a), previous reproductive and foraging successes (Switzer 1997b, a, Irons 1998), and avoidance of predators (Greenwood 1980, Schaefer et al. 2000). At this stage I cannot determine the relative importance of each of these factors in the apparent interannual fidelity displayed by adult Irrawaddy and humpback dolphins to Cleveland Bay. However, I discuss some hypotheses below.

For delphinids, patterns of space use have been regarded in part as responses to the risk of predation and prey availability (Heithaus and Dill 2002). As discussed in Chapters 4 and 5, Cleveland Bay support a highly diverse and abundant fish community including members of families (e.g., Leiognathidae, Haemullidae, Clupeidae, Engraulidae) (Robertson and Duke 1987, 1990) known to be prey of Irrawaddy or humpback dolphins (Heinsohn 1979, Barros et al. 2004). Additionally and as discussed in Chapter 4, adult tiger sharks *Galeocerdo cuvier*, a species that preys regularly on delphinids, occur in Cleveland Bay (Simpfendorfer 1992). In Cleveland Bay, individuals of both Irrawaddy and humpback dolphins showed scars resulting from interactions with sharks (personal observations) and dolphin remains have been identified among the stomach contents of tiger sharks caught in the study area (Simpfendorfer 1992). Because of these habitat attributes, I expect prey availability and predation to be important factors affecting site fidelity and residence

times of Irrawaddy and humpback dolphins in Cleveland Bay (see also discussions of Chapters 4 and 5).

Karczmarski (1999) hypothesized that the low levels of site fidelity displayed by humpback dolphins in Algoa Bay, South Africa, was a result of the low availability of prey resources, with animals forced to range over long distances in search of food. In contrast to Algoa Bay, Cleveland Bay is a large estuarine system receiving freshwater input from several rivers and creeks and fish are abundant (Robertson and Duke 1987, 1990). These differences in habitat characteristics may explain the higher interannual return rates of individuals of both species to Cleveland Bay, and the fit of emigration/reimmigration models to the data.

Alternatively, although predation risk might be potentially high in Cleveland Bay because of the presence of tiger sharks, animals might not be emigrating permanently from the study area because predation risk may be greater in unfamiliar habitats, or prey resources may be less abundant in other areas. I suggest that the site fidelity patterns and residence times of Irrawaddy and humpback dolphins inside and outside Cleveland Bay might reflect tradeoffs between the levels of predation risk and food availability within the study area and surrounding bays. The complexity of this pattern, implies that there must be mechanisms whereby animals acquire knowledge to adapt their behaviour to continuously changing conditions. Learning appears to be such a mechanism among mammals (Heyes and Galef 1996, Box and Gibson 1999).

In heterogenous environments, learning where and when to forage, and how to recognize and evade predators is likely to increase an individual's foraging success and survival (Gillingham and Bunnell 1989, Griffin and Evans 2003). Delphinids have several traits that favour social learning (i.e., transmission of information from conspecifics): 1) they live in spatially and temporally heterogeneous environments, 2)

have prolonged parental care, 3) have long lives, 4) form permanent and cohesive associations, 5) have advanced cognitive and communicative abilities (Connor et al. 1998, Whitehead 1998, Janik 2000). Irrawaddy and humpback dolphins may acquire a variety of behaviours and experiences during their first years of life that could influence their subsequent habitat choices. The foraging success of adult Irrawaddy and humpback dolphins may depend on them learning from their mothers and conspecifics about the abundance and predictability of resources in space and time. I suggest fidelity to the study area from year to year, and movements inside and outside of it by adult Irrawaddy and humpback dolphins may be a result of: 1) knowledge acquired from conspecifics, and 2) each individual's previous experiences about the spatial and temporal availability of prey resources and predators. In addition to foraging success, individuals experiencing high reproductive success at a particular site often have a higher probability of returning to the same area from year to year (Boulinier and Danchin 1997, Switzer 1997b). Socializing (i.e., socio-sexual behaviour) is among the predominant behaviours observed in Cleveland Bay together with foraging and travelling (see Chapter 4). Some animals might simply return to Cleveland Bay based on previous successful reproductive attempts or to have higher chances of finding a mate.

Most social polygynous mammals display male-biased dispersal from their natal range, whereas females show natal philopatry (Greenwood 1980). The high interannual sighting rate of most female Irrawaddy dolphins (six out of eight) and half of the female humpback dolphins (two out of four) identified in this study suggest female natal philopatry is likely in both of these species. Four male humpback dolphins were also among the animals with high interannual sighting rates indicating males of this species may also display fidelity to their natal site.

Long-term observations of coastal bottlenose dolphins in Shark Bay, Western Australia, and Sarasota, Florida indicated both males and females display natal philopatry (Connor et al. 2000b). In contrast, genetic studies on two populations of bottlenose dolphins (*Tursiops aduncus*) in southeastern Australia indicated females are philopatric whereas males tend to disperse from their natal site (Möller and Beheragaray 2004). Analysis of population structure, paternity and dispersal distances from genetic data will be fundamental in determining the level of natal philopatry displayed by Irrawaddy and humpback dolphins (as discussed in Chapter 10).

6.4.2 *Ranging patterns*

The sizes and lengths of the ranges that I estimated for Irrawaddy and humpback dolphins were within the range of those reported from photo-identification studies of other coastal delphinids. However, my study demonstrated that a large number of individual sightings (≥ 20) are needed in order to define the actual areas used by individual Irrawaddy and humpback dolphins in Cleveland Bay. The study of Hung and Jefferson (2004) on the ranging patterns of humpback dolphins in the Pearl River Estuary arrived at a similar conclusion.

Nevertheless, the available data provided an idea of the extent of individual movements and range overlap in the study area. It is apparent from sighting locations and MCP ranges that animals moved between the northwestern and south eastern section of Cleveland Bay. Sightings of both species in between these two areas were few, thus animals may have moved between these areas at times while we were not surveying (e.g., night hours) or passed through these areas relatively quickly. Individual ranges of both species were similar in size, length and location. These patterns of range overlap are indicative of similar space use patterns by both species and a lack of areas exclusive to one species (i.e., territories). This result supports the

findings in Chapter 5 on space use patterns and habitat preferences at the population level (i.e., schools of dolphins instead of individuals were used for analysis of space use,).

The substantial overlap between the ranges of individual Irrawaddy and humpback dolphins at the intraspecific level suggest that individuals that were frequently seen (i.e., animals identified on \geq eight occasions) in Cleveland Bay were often associated with each other. In contrast, individual humpback dolphins in the Pearl River estuary, though having overlapping ranges, rarely used similar areas. Hung and Jefferson (2004) suggested this was a result of the weak associations between individual animals. This geographical variation is possibly related to differences in the ecological constraints (e.g., prey availability, predation, dispersal costs) shaping ranging patterns and social structures across these two areas.

6.5 Chapter summary

- I used photo-identification data of Irrawaddy and Indo-Pacific humpback dolphins collected in Cleveland Bay between 1999-2002 to examine and compare their patterns of site fidelity, residence times, range size, and range overlap.
- Because dolphins spend most of their time underwater, estimating their site fidelity and ranging patterns in the wild is a difficult task. The analysis presented here was limited to a finite area, and was based on capture-recapture techniques (i.e., photo-identification) that do not provide continuous tracking of individuals in space and time. Additionally, strong association patterns between individuals in the analysis may limit our ability to extrapolate the patterns observed to the general population. Therefore, estimates of site

fidelity and ranging patterns presented here should be considered minimum estimates.

- Analysis of monthly and annual sighting rates indicated most animals were not permanent residents in the bay, but most used the area from year to year. The low standard distance deviations indicated that animals tended to come back to specific areas within the bay.
- Lagged identification rates suggested a model of emigration and reimmigration into the bay. Individuals of both species appeared to spend periods of days to a month or more inside the study area before leaving, and periods of over a month outside the study area before entering the bay again.
- Range sizes, length and location were similar between both species. From sighting locations and ranging patterns it is apparent that the movements of both species in the bay involved ranging southeast and northwest of Townsville's Port. The pattern of interspecific overlap in range patterns indicated lack of species-specific territories.
- The patterns of site fidelity and ranges in Cleveland Bay are likely a result of different ecological constraints imposed on both species. I suggest site fidelity patterns may reflect fluctuations in prey resource availability and levels of predation risk within Cleveland Bay. Because of their gregarious nature, strong association of mother calf-pairs, and ability to form long-term associations with other members, social learning may act as a mechanism by which animals gain knowledge about their heterogeneous environment and make decisions about their movement patterns.

Table 6.1 Survey effort in Cleveland Bay showing number of hours on the water searching for Irrawaddy and Indo-Pacific humpback dolphins between 1999 and 2002.

Year	Period covered	Searching effort (hrs)	
		Wet season (Jan-March)	Dry season (Apr-Nov)
1999	Jan-November	63.5	145.7
2000	Jan-November*	30.5	163.1
2001	Jan-October*	30.8	83.3
2002	May-October	NA	112.7
TOTAL		124.9	504.7

*Surveys during the month of February in both of these years were not possible due to bad weather conditions.

Table 6.2 Known range sizes and range lengths of Irrawaddy and Indo-Pacific humpback dolphins identified on \geq eight occasions or more in Cleveland Bay between 1999-2002. MCP = Minimum Convex Polygon.

Irrawaddy dolphins				
ID	Sex	Age	MCP range size (km ²)	Range length (km)*
Ob-002	F	Adult	107.2	31.7
Ob-003	?	Adult	58.2	28.5
Ob-004	?	Adult	66.8	31.9
Ob-005	F	Adult	81.1	33.6
Ob-009	?	Adult	63.9	31.9
Ob-010	?	Adult	60.0	30.3
Ob-011	?	Adult	90.0	31.9
Ob-012	?	Adult	62.2	31.9
Ob-013	?	Adult	58.2	28.5
Ob-014	?	Adult	71.8	22.7
Ob-015	F	Adult	76.9	24.9
Ob-018	F	Adult	4.7	4.5
Ob-019	?	Adult	22.8	12.3
Ob-025	?	Adult	104.8	33.6
Ob-034	F	Adult	108.3	32.8
Mean \pm SE			69.1 \pm 7.43	27.4 \pm 2.18
Indo-Pacific humpback dolphins				
ID	Sex	Age	MCP range size (km ²)	Range length (km)
Sc-001	?	Adult	33.7	20.6
Sc-002	M	Adult	91.1	21.1
Sc-003	M	Adult	116.3	41.6
Sc-005	M	Adult	87.2	22.0
Sc-008	F	Adult	89.2	21.1
Sc-009	M	Adult	69.6	26.6
Sc-017	F	Adult	47.1	22.4
Sc-030	?	Adult	9.4	15.4
Sc-039	?	Adult	129.5	35.8
Mean \pm SE			74.8 \pm 12.96	25.2 \pm 2.8

* Range length was calculated as the shortest distance between the two most extreme dolphin locations without crossing land.

Chapter 7

Social structure of Irrawaddy and Indo-Pacific humpback dolphins

In this chapter, I provide an assessment of the association patterns between identified individuals of Irrawaddy and Indo-Pacific humpback dolphins. I assess the temporal variation in their association patterns and apply mathematical models representing different social organizations to determine the type of association that best describes their social structure.

Chapter 7. Social structure of Irrawaddy and Indo-Pacific humpback dolphins

7.1 Introduction

Social structure is defined by the network of behavioural interactions between members of a society (Hinde 1976). In social mammals, differences in the spatial and temporal patterning of these interactions have given rise to a wide variety of social relationships between pairs of individuals (Wrangham and Rubenstein 1986, Connor et al. 1998). Understanding the patterns and characteristics of these relationships helps determine the social structure of an animal society. Differences and similarities in social systems across species are thought to be largely attributable to ecological pressures (e.g., predation, prey distribution), social factors (e.g., aggressive and mating behaviour), and phylogenetic history (Struhsaker 1969, Wrangham 1986). Thus, comparison of social structures within and among species can provide valuable insights into the adaptive nature and evolution of social systems.

Information on the social structure of cetacean species is usually obtained by quantifying the level of association among identifiable individuals occurring in close spatial proximity (e.g., schools, groups), and investigating how these associations change over time (Whitehead et al. 2000a). Among cetaceans, the plasticity of social organization in delphinids has attracted considerable interest, but detailed studies have been limited to a few species including killer whales, *Orcinus orca* (Baird and Whitehead 2000), long-finned pilot whales, *Globicephala melas* (Ottensmeyer and Whitehead 2003), Hector's dolphins, *Cephalorhynchus hectori* (Slooten et al. 1993, Bräger 1999), Atlantic spotted dolphins, *Stenella frontalis* (Herzing and Brunnick 1997), and bottlenose dolphins, *Tursiops sp.* (Wells 1991, Smolker et al. 1992, Bräger et al. 1994, Rossbach and Herzing 1999, Connor et al. 2000b, Quintana-Rizzo and

Wells 2001, Chilvers and Corkeron 2002, Owen et al. 2002, Lusseau et al. 2003).

These studies have shown social structures ranging from the stable matrilineal groupings of killer whales to the fluid fission-fusion grouping patterns of bottlenose dolphins.

Intraspecific and interpecific variations in this continuum of social structures appear to be dictated mainly by complex interactions between ecological and social factors. For example, the predominant fission-fusion society found in different populations of bottlenose dolphins appears to reflect an adaptation to a patchy and irregular distribution of prey resources, with animals spreading out to reduce intraspecific competition for food (Connor et al. 2000b). However, within these fission-fusion societies differences in the relationships formed between individuals are also influenced by their reproductive state, and mating strategy (Connor et al. 1992b, Connor et al. 1996, Connor et al. 2000a). For example, in Shark Bay Western Australia, males in pairs and trios form strong associations and cooperate to sequester and control the movement of individual females likely to be in estrus (Connor et al. 1992b)

Longitudinal studies of individual humpback dolphins have been conducted only in South Africa (Karczmarski 1999, Keith et al. 2002) and Hong Kong (Jefferson 2000). Analyses of association patterns from both of these regions agree that the social relationships between individual humpback dolphins appear to be very fluid, with only casual and short-lasting affiliations. Neither of these studies investigated how associations between pairs of individuals change over time. Studies of individual Irrawaddy dolphins are only recent (see Chapter 6, Parra and Corkeron 2001), and their social structure has not previously been reported .

In Chapters 4 and 6 I showed that Irrawaddy and humpback dolphins are present year round in Cleveland Bay, with some individuals showing strong inter-annual fidelity to this area. This situation provides an important opportunity for studying and comparing the social structure of two species of delphinids living under similar ecological conditions. Here, I investigate the social structure of Irrawaddy and Indo-Pacific humpback dolphins over four years (Objective 6 of this thesis, see Chapter 1) and relate differences in their social system to possible interspecific ecological, social and phylogenetic differences, recognizing that contemporary research suggest that Australia/Papua New Guinean populations of Irrawaddy and humpback dolphins are distinct from those elsewhere (Beasley et al. 2002a, Rosenbaum et al. 2003).

7.2 Methods

7.2.1 *Photo-identification surveys*

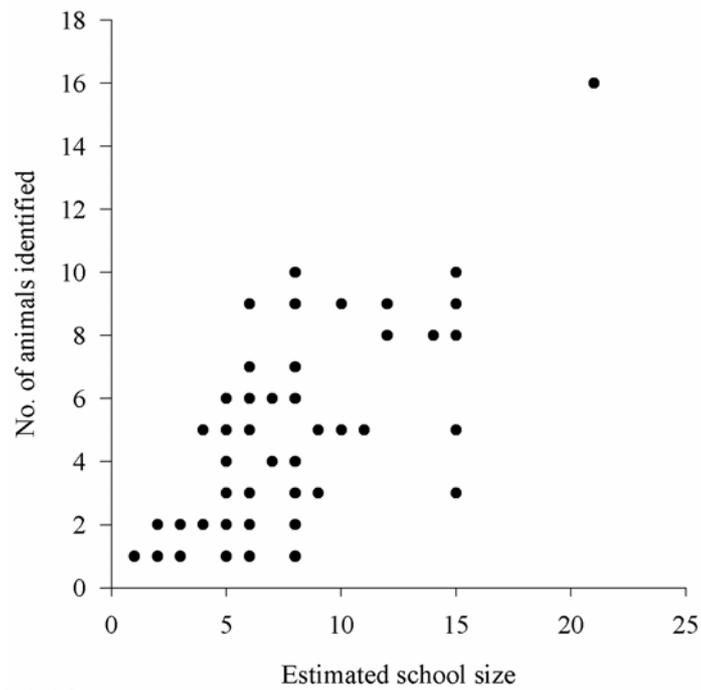
Boat survey procedures were described in Chapter 4 and photo-identification methodology in Chapter 6.

7.2.2 *Data analysis*

Association analyses were carried out in MATLAB 6.5 using SOCPROG 2.1, a series of MATLAB programs for analysing social structure (Whitehead 2004). For the analysis of association patterns, all dolphins identified within the same school during a single day (the sampling period) were considered associated. To ensure independent evidence of association, if an individual had been photographed and later resighted within the same day, the second school in which it was sighted was not included in the analysis. In many cases not all individuals in a school were photo-identified (Fig. 7.1), either because some individuals had not developed recognisable

marks, or because I failed to obtain excellent/good quality photographs. Therefore, there were occasions where associations between dyads were not detected, resulting in a downward bias in the association indices (Gowans et al. 2001, Chilvers and Corkeron 2002). To minimize this bias, only schools with 50% or more of the individuals identified were included in the analysis. Additionally, to provide a balance between the representativeness of the data (e.g., include the maximum number of individuals) and its reliability (e.g., include individuals with maximum sighting frequencies, Chilvers and Corkeron 2002)) association analyses were limited to individuals identified on four days or more.

a) Irrawaddy dolphins



b) Humpback dolphins

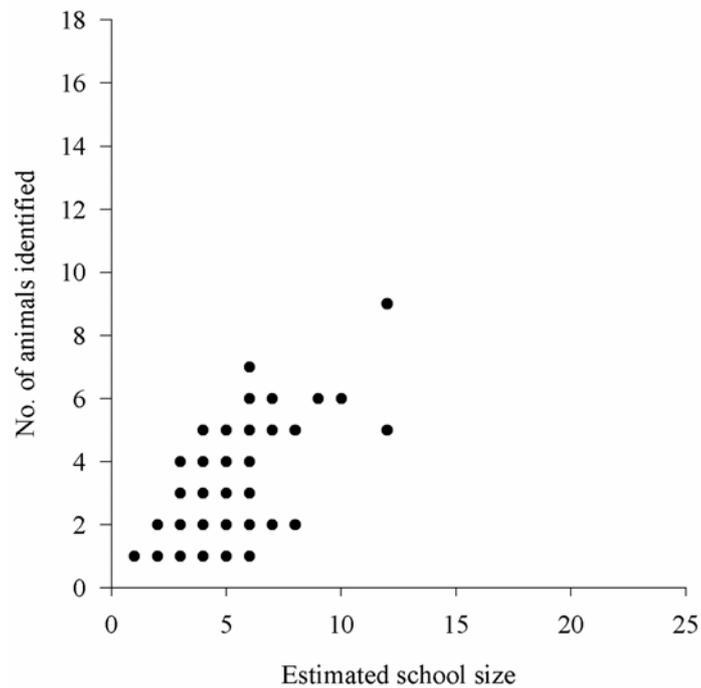


Figure 7.1 Relationship between the school size estimates of (a) Irrawaddy and (b) humpback dolphins and the number of animals photographically-identified within each school.

I used the Half-Weight Association Index (HWI) to estimate the strength of the relationship between dyads (Cairns and Schwager 1987):

$$HWI = \frac{x}{(x + \frac{1}{2}(Y_a + Y_b))}$$

where x is the number of sightings that included both dolphin A and B, Y_a is the number of sightings that included only individual A, and Y_b is the number of sightings that included only individual B. Values of the HWI range from 0 (individuals never sighted together) to 1 (individuals always sighted together). The HWI is the coefficient of association most commonly used in studies of dolphin social structure (Whitehead and Dufault 1999), and is considered to be appropriate when pairs of animals are more likely to be recorded when separate than when together, as is usually the case with cetaceans (Cairns and Schwager 1987, Smolker et al. 1992, Slooten et al. 1993). The resulting association matrices were displayed using dendrograms (with average-linkage cluster analyses) showing the degree of association between hierarchically-formed clusters.

To test if the association patterns of Irrawaddy and humpback dolphins provided evidence of preferred/avoidance associations, I used the test of random association developed by Bejder et al. (1998), and later modified by Whitehead (1999). In this test, random association matrices are produced in which the number of schools in which an animal was identified is kept constant within sampling intervals. With sufficiently short sampling intervals (e.g., days) this permutation method removes demographic effects (e.g., birth, death, migration) that could result in significant non-random associations due to non-social factors (Whitehead 1999). The test statistic was the standard deviation of the mean association indices. Simulations and field studies have shown that if some individuals have preferred companionships over several sampling periods, then the standard deviation of the observed association

indices is significantly higher ($P > 0.95$) than the random data (Gowans et al. 2001, Whitehead 2004). Association matrices were randomly permuted 20,000 times. Additional runs of the test showed P-values were stable after 20,000 randomizations.

Temporal variability in association patterns was investigated by estimating lagged association rates and comparing these to null association rates (Whitehead 1995). The lagged association rate is an estimate of the probability that if two animals are associating at some time, they will be associated various time lags later. The null association rate is the lagged association rate expected if individuals were associating at random. As not all individuals within the group were identified, lagged and null association rates were standardized by dividing the lagged association rate by the number of associates recorded on each occasion (Whitehead 1995). The temporal association patterns obtained for each species were then compared with mathematical models representing different social organizations proposed by Whitehead (1995). These models allow for different mechanisms of association to be evaluated by considering two classes of associates: 1) constant companions: permanent and stable associations over time until death or birth, and 2) casual acquaintances: associated individuals tend to disassociate over time. The model minimizing the adjusted Akaike Information Criterion for small-sample bias (AIC_c) was chosen as the best fit model (Burnham and Anderson 1998). The AIC_c acts as a measure of model fit and complexity, and the lower the AIC_c the better the model is supported by the data. Models differing by less than two units from the model with minimum AIC_c (ΔAIC_c) also provide good descriptions of the data (Burnham and Anderson 1998).

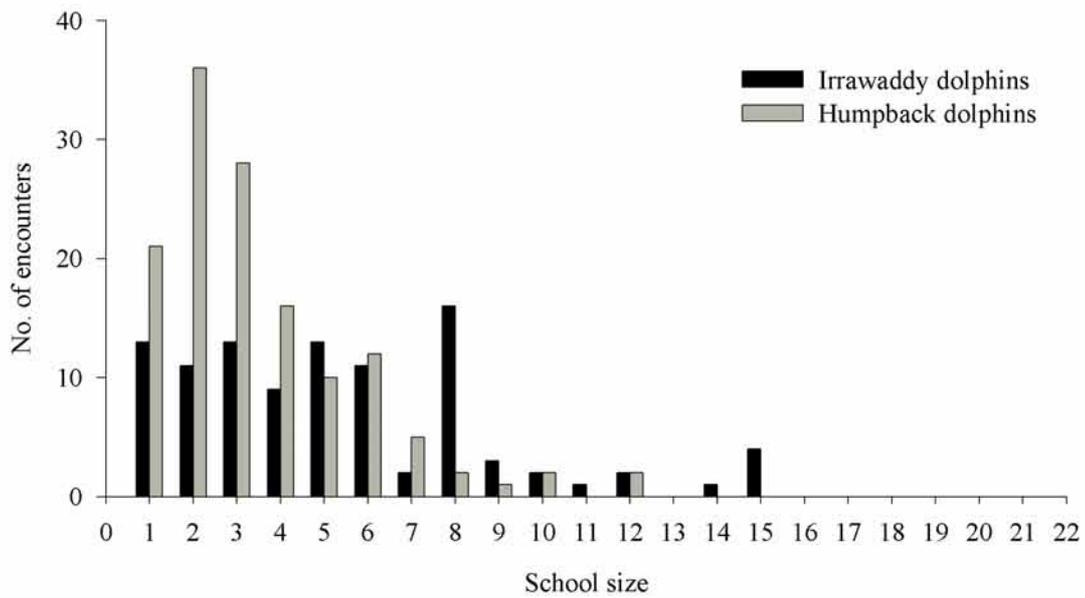
7.3 Results

7.3.1 *Schools sizes and association patterns*

As outlined in Chapter 4, I encountered 117 schools of Irrawaddy dolphins and 143 schools of humpback dolphins in Cleveland Bay Dugong Protected Area (hereafter Cleveland Bay) between 1999 and 2002. I also encountered 19 mixed-species schools that included individuals of both species at some point of the encounter (i.e., start, during, end). School size was estimated for 101 schools of Irrawaddy dolphins, 135 of humpback dolphins, and all mixed-species schools (Fig. 7.2). Average school size was 5.35 (SE = 0.35, median = 5, mode = 8) for Irrawaddy dolphins, and 3.5 (SE = 0.19, median = 3, mode = 2) for humpback dolphins. Mixed-species schools had an average of 6.2 (SE = 1.19, median = 5, mode = 2) Irrawaddy dolphins, and 3.8 (SE = 0.39, median = 5, mode = 2) humpback dolphins. As discussed in Chapter 4, Irrawaddy dolphins formed larger schools than humpback dolphins.

As discussed in Chapter 6, I photo-identified 63 Irrawaddy dolphins and 54 humpback dolphins in Cleveland Bay between 1999-2002. The truncation of the dataset to schools with 50% or more of individuals identified, and individuals sighted on four or more days, restricted the analyses of association patterns to 30 Irrawaddy dolphins and 14 humpback dolphins. All individuals in the analysis were adults, except for one Irrawaddy dolphin (OB-054) which was a juvenile. Sex was known for six Irrawaddy dolphins (all females) and eight humpback dolphins.

a) Single-species schools



b) Mixed-species schools

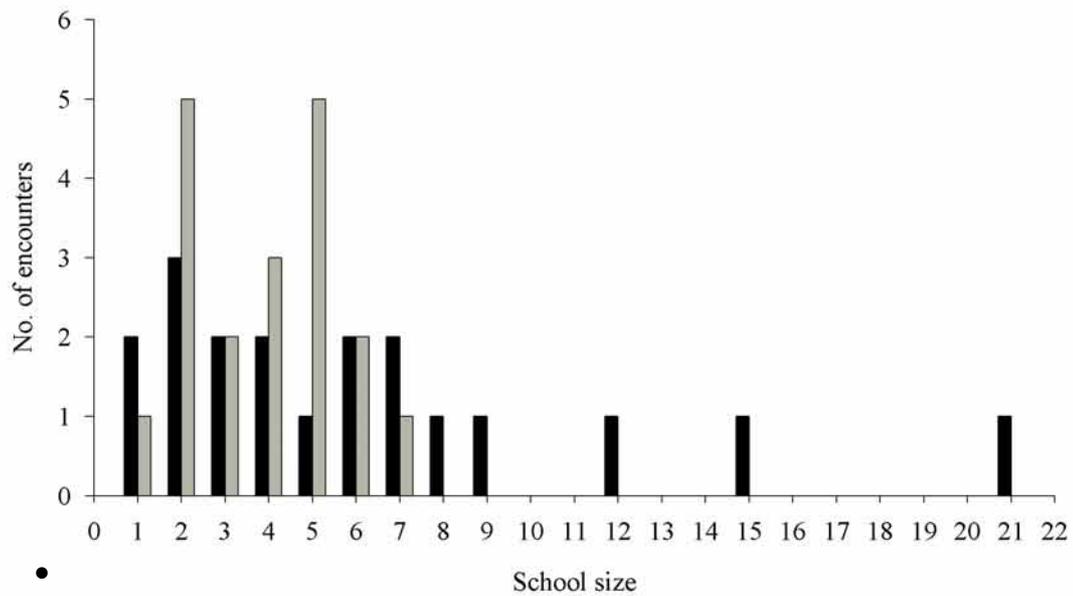


Figure 7.2 Estimated school sizes of Irrawaddy and humpback dolphins found in (a) schools involving only one single species and (b) schools involving at some point of the encounter (i.e., start, during, end) individuals of both species.

The standard deviation of the mean HWI of Irrawaddy and humpback dolphins was significantly higher than those from random data, indicating that individuals of both species showed preference in their associations over the four years of the study (Table 7.1, all tables have been placed at the end of this chapter to minimize interruption to the flow of the text, and printed on yellow colour paper for ease of location). The distribution of the maximum HWI observed for each individual shows that all Irrawaddy dolphins and humpback dolphins were more frequently seen with a particular companion that would be expected if all individuals associated at random (Fig. 7.3). Eighty percent of the Irrawaddy dolphins and 50% of humpback dolphins showed relatively strong associations at $HWI \geq 0.5$ (Fig 7.4).

The dendrograms from the average-linkage analysis showed similar patterns (Fig. 7.4). Overall, it appears that individual Irrawaddy dolphins form strong associations with more than one individual, while strong associations between humpback dolphins appear to be limited to pairs of animals. Individual Irrawaddy dolphins spent more time with another individual or with a group of individuals than would be expected by chance ($HWI > 0.15$, Table 7.1). Based on this, it appears from the dendrogram that individual Irrawaddy dolphins formed non- random associations with up to 11 individuals (Fig. 7.4). Relatively strong associations ($HWI \geq 0.5$) occurred between pairs and groups of five animals. Four of the six female Irrawaddy dolphins identified displayed strong associations with each other ($HWI \geq 0.5$).

In the case of humpback dolphins, groups of two to seven individuals formed associations more often than would be expected if all animals were associating at random ($HWI > 0.15$). Associations at $HWI \geq 0.5$ occurred only between pairs and trios of animals. SC-030 did not display a strong association with any other individual or group of individuals and associated at low levels with all individuals identified.

Three of the four male humpback dolphins identified were frequently seen with one another ($\text{HWI} \geq 0.5$).

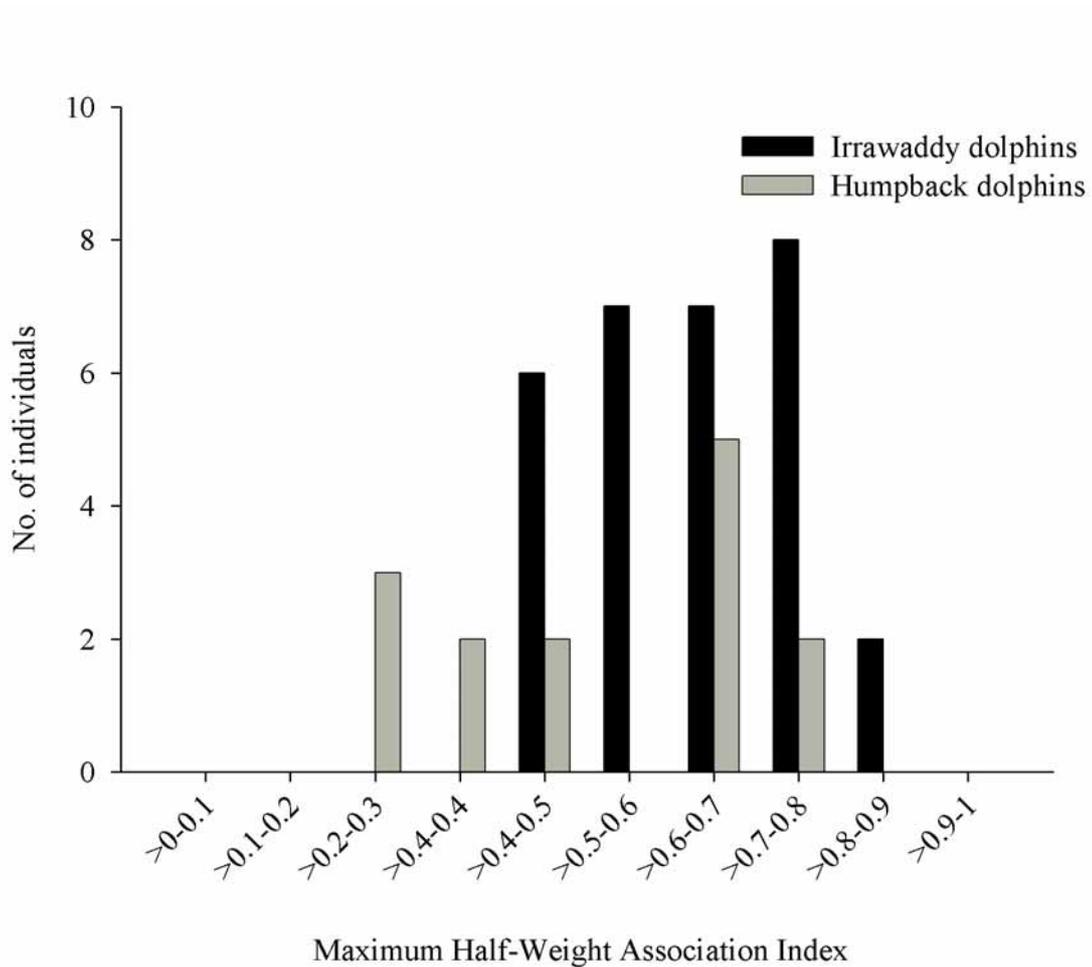
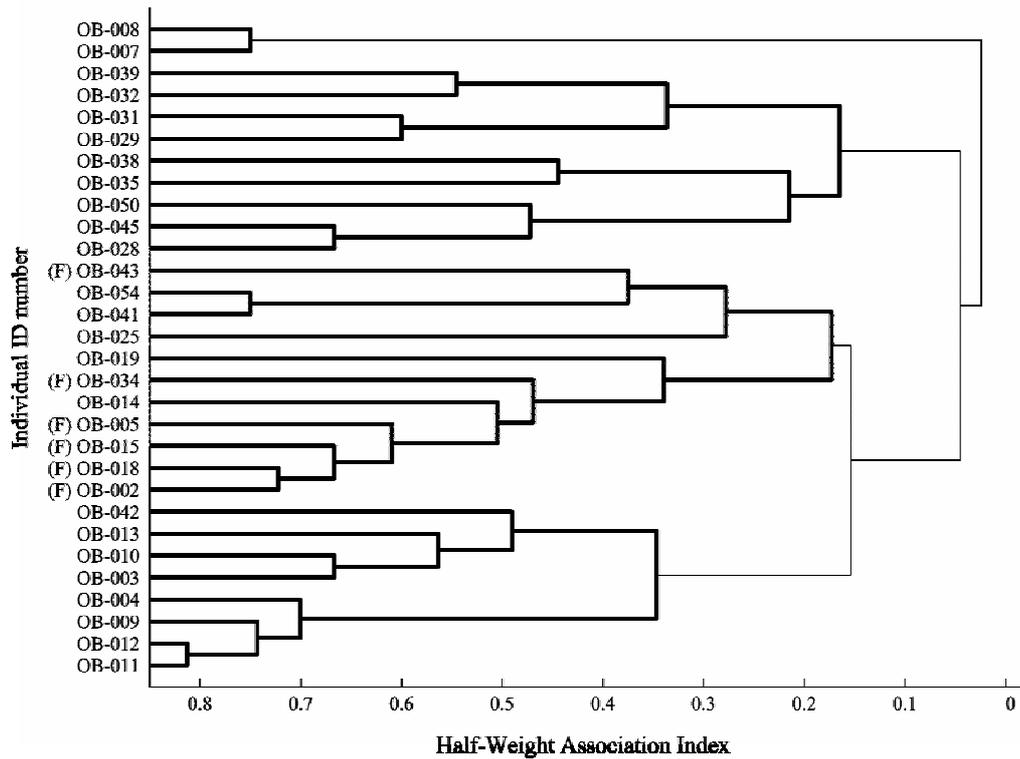


Figure 7.3 Distribution of maximum Half-Weight Association Indexes of Irrawaddy and humpback dolphins, using only individuals sighted \geq four days and in schools with \geq 50% of animals identified. The distribution suggest most animals formed strong associations with a particular companion

a) Irrawaddy dolphins



b) Humpback dolphins

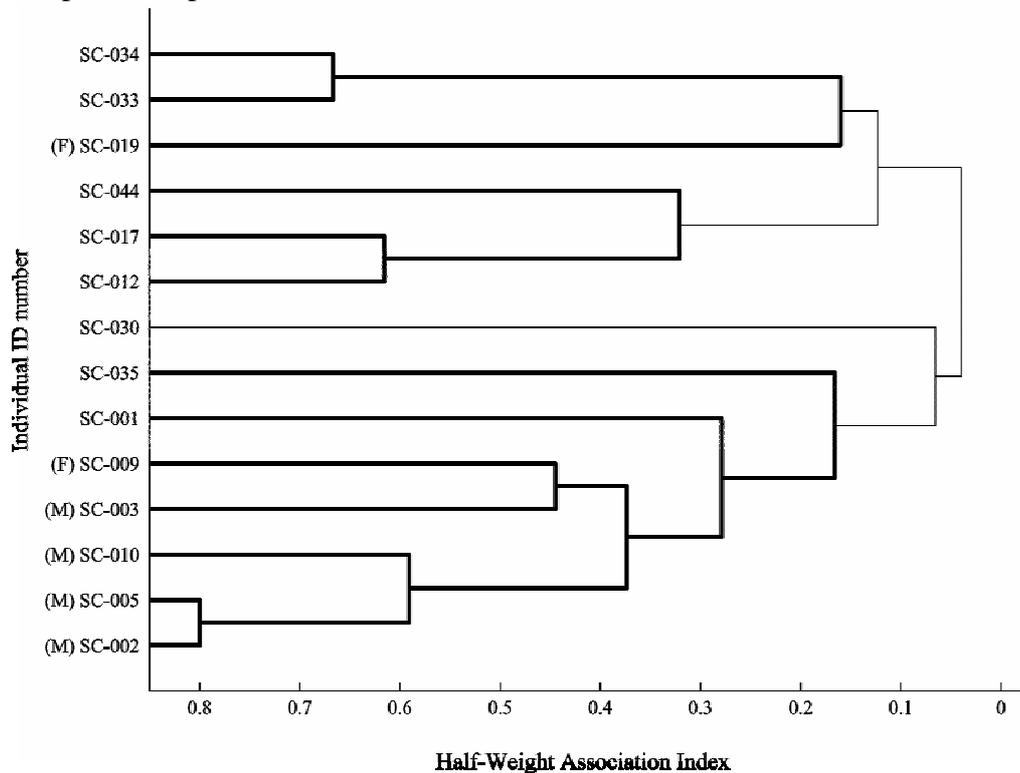


Figure 7.4 Average-linkage cluster analysis for associations between (a) Irrawaddy, and (b) humpback dolphins using only individuals sighted \geq four days and in schools with \geq 50% of animals identified. Associations higher than expected by chance are indicated in bold branches.

7.3.2 *Temporal patterns of association*

The standardized-lagged association rates of Irrawaddy and humpback dolphins were higher than the lagged association rate expected if individuals were associating at random (e.g., the null association rate) (Fig. 7.5). This result indicates that stable and long-term association patterns were present among individuals of both species.

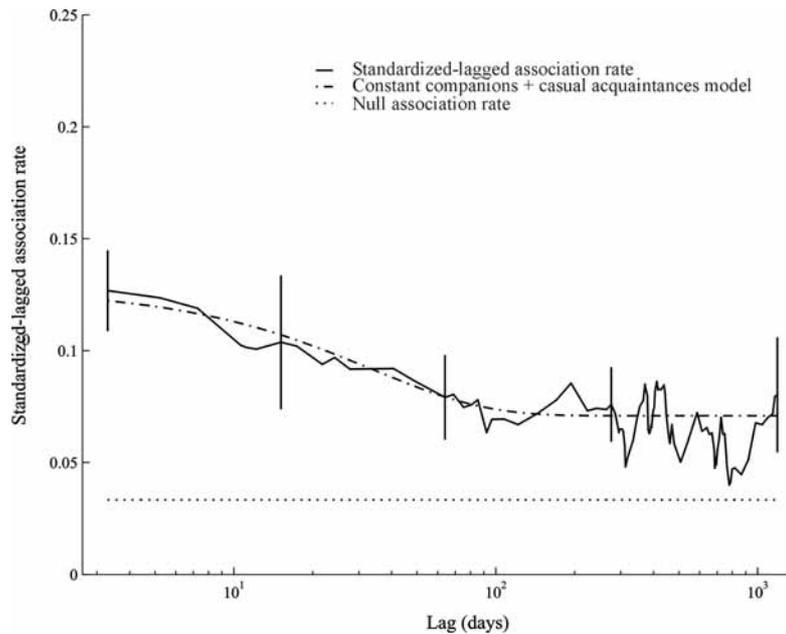
The relationship between lagged association rates and time lag for Irrawaddy dolphins showed that association rates were higher at short time lags (less than 10 days), decreased over periods of less than 100 days, and then stabilized above the null rate. The model that best described these temporal association patterns suggested that an individual Irrawaddy dolphin at any time had two types of associates: “constant companions” and “casual acquaintances” (Table 7.2, Fig. 7.5). The model curve stabilised at time lags of 101 days, indicating that some individual Irrawaddy dolphins had a mix of casual and constant companions for periods of up to three months, and a subset of constant companions that remained associated for periods of up to four years.

Given that there is little disassociation at short time lags (i.e. day), the mean number of associates an individual can have (casual + constant companions) can be estimated as the probability that an individual is still with its associates at time zero (probability = 1) divided by the standardized lagged association rate at that time (Whitehead 1995; Ottensmeyer and Whitehead, 2002). The value of the standard association rate at time zero was 0.128, thus, the mean number of associates an Irrawaddy dolphin had from one day to the other was approximately eight. The proportion of these associates that actually remain with a given individual as long-term constant companions can be estimated as the lagged association rate when the

model curve stabilizes, relative to the maximum rate predicted by the model (Whitehead 1995; Ottensmeyer and Whitehead, 2002). The model curve stabilized at a standardized lagged association rate of 0.057, 52% of the maximum (0.109). This indicates that the set of constant companions of a given Irrawaddy dolphin consisted of about four individuals.

The plot of standardized association rates for humpback dolphins suggests association rates were highest for time lags of less than 30 days, and then tended to decrease (Fig. 7.5). However, association rates did not drop below the null association rate and distinctive peaks at lags of 275 and 770 days suggesting long-lasting bonds among some individuals. For humpback dolphins, all models had similar AIC indicating that they fit the data equally well (Table 7.2). This uncertainty in model selection suggests a complex pattern of associations between individual humpback dolphins that may involve various associates with different levels of temporal stability.

a) Irrawaddy dolphins



b) Humpback dolphins

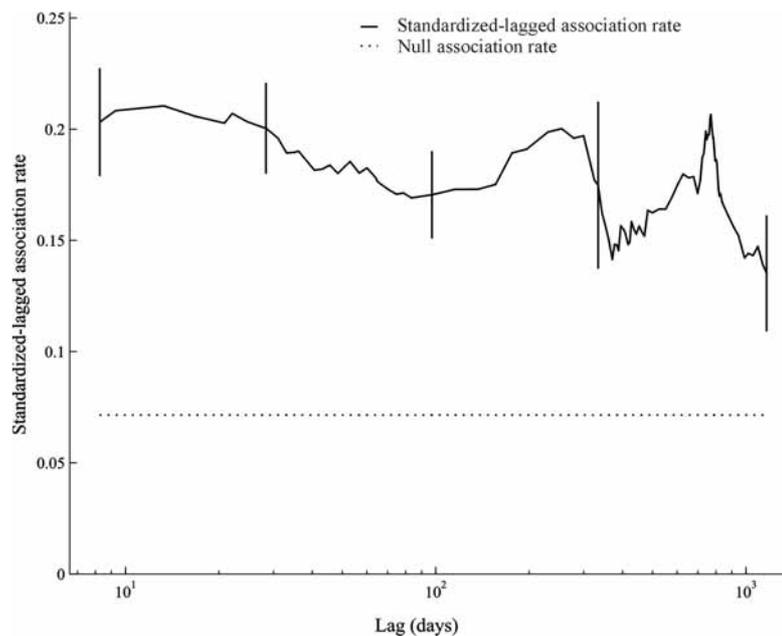


Figure 7.5 Standardized-lagged association rates for (a) Irrawaddy dolphins and (b) humpback dolphins, using only individuals sighted \geq four days and in schools with \geq 50% of animals identified. Standard error bars were estimated using jackknife procedures. The null association rate is the lagged association rate expected if individuals were associating at random. The model that best explained the observed temporal association rates of Irrawaddy dolphins (constant companions + casual acquaintances) is shown in a. All models in Table 7.2 fitted the temporal association rates of humpback dolphins. This result suggests a complex pattern of associations between individual humpback dolphins that may involve various associates with different levels of temporal stability.

7.4 Discussion

7.4.1 *Irrawaddy and humpback dolphins in Cleveland Bay*

The social structure of delphinids ranges from stable social groupings of permanent long-term affiliates to temporary aggregations of individuals with highly dynamic and fluid associations (i.e., fission-fusion society). Irrawaddy dolphins fit the former category, while humpback dolphins appear to be in-between these two extremes. Association patterns among individuals of each species indicated that individuals formed stronger associations with other members than would be expected if dolphins associated at random. However, while an individual Irrawaddy dolphin formed strong bonds with more than one individual, strong association among individuals humpback dolphins occurred mainly between pairs of animals. Additionally, associations of Irrawaddy dolphins were best described if constant companionship was considered an important mechanism of association, suggesting that long-lasting associations were a strong feature in this species. Long-lasting bonds in Irrawaddy dolphins formed among groups of five individuals, exactly the same size as the mean school size that I observed for Irrawaddy dolphins. Associations between individual humpback dolphins appear to be more dynamic involving different types of associates with variable temporal patterns. Nonetheless, temporal patterns of association indicated that long-term bonds between individual members do occur in these species.

The social structure of humpback dolphins has been described as highly fluid with individuals forming only casual and short-lasting affiliations typical of a fission-fusion society (Karczmarski 1999, Jefferson 2000, Keith et al. 2002). In Algoa Bay and Richards Bay, along the open coastline of South Africa, strong associations occurred only between pairs and occasionally trios. However, in Hong Kong there

was no evidence for strong bonds between pairs or among groups of individuals. My study showed that, although associations among all pairs of individuals appear to be casual, strong long-term bonds between pairs of animals were common.

7.4.2 *Factors influencing the structure of dolphin societies.*

Theories on the evolution of sociality in mammals emphasize the influence of ecological and social constraints in shaping social systems (Alexander 1974, Wrangham and Rubenstein 1986). Predation risk, distribution of food resources and mating relationships have been suggested as the principal factors driving grouping and association patterns in delphinids (Connor et al. 1998). However, it is also known that features of the social organization and behaviour of mammals may be constrained by their evolutionary history. For example, quantitative phylogenetic studies have shown that social systems in primates may be conserved among lineages even in the presence of considerable ecological variability (Di Fiore and Rendall 1994). What ecological, social or phylogenetic factors have been responsible for differences in the social system of Irrawaddy and humpback dolphins?

7.4.2.1 *Phylogeny*

A recent comparative study on groups sizes in the superfamily Delphinoidea (Delphinidae, Phocoenidae and Monodontidae) concluded that phylogeny plays an important role in the evolution of group size in Delphinoidea (Gygax 2002b). Closely related species are likely to share many aspects of their social and ecological adaptation as a result of their common evolutionary history. As discussed in Chapter 2, although not a definitive classification, the most recent systematic revision of the family Delphinidae places Irrawaddy dolphins in the subfamily Orcininae together with Killer whales, whereas humpback dolphins are grouped together with dolphins of

the genus *Stenella*, *Delphinus*, *Tursiops*, and *Lagenodelphis* in the subfamily Delphininae (LeDuc et al. 1999).

Interestingly, among delphinids the stable social organization described here for Irrawaddy dolphins is similar only to that of killer whales and long-finned pilot whales. . The social structure of the fish-eating *resident* (the name is not particularly descriptive of movement patterns) form of the killer whale is characterized by long-term associations between individuals with limited dispersal by both males and females from their natal range and maternal group (i.e., geographic and social philopatry Baird, 2000). Strong and long-term associations also exist between individual mammal-eating *transient* killer whales, even though dispersal of either sex from their maternal group can occur (Baird & Whitehead, 2000). Genetic and behavioural data suggest a similar social structure for long-finned pilot whales [subfamily Globicephalinae, \Amos, 1993 #5225; Ottensmeyer, 2003 #2885].

In contrast, some of the species closely related to humpback dolphins appear to live in fluid societies with fission and fusion of groups observed frequently (Norris et al. 1994, Connor et al. 2000b, Neumann 2001). In particular, the strong association patterns between pairs of humpback dolphins and the different levels of temporal stability in their association patterns, resemble the social structure seen in most coastal bottlenose dolphin communities (Connor et al. 2000b). Most populations of bottlenose dolphins (*Tursiops* spp.) live in fission-fusion societies, in which individuals associate in small schools that frequently change in composition. Nonetheless, within this fluid and dynamic social organization, strong long-term bonds between pairs of individuals exist (Connor et al. 2000b). This relationship of social structure and phylogeny indicates that some of the dissimilarities in the social structure of Irrawaddy and humpback dolphins can be attributed to their different evolutionary histories. As the

systematics of delphinids becomes clearer and more information is gathered on their social systems, comparative phylogenetic methods will help us elucidate their evolutionary similarity or dissimilarity.

7.4.2.2 *Social factors*

The effect of phylogenetic history on taxon traits does not mean that these traits are non-adaptive. Thus, ecological and social factors are also likely to play a role in shaping social systems. Kin-selection (whereby individuals are predicted to behave more altruistically and less competitively towards their relatives) is widely thought to play an important role in the evolution of strong and stable affiliations in group-living animals (Hamilton 1964, Emlen 1995). Strong affiliation among relatives is a salient aspect of various group-living mammal species. Examples include hyenas, *Crocuta crocuta* (Holekamp et al. 1997, Wahaj et al. 2004), some primates species (see Silk 2002 for examples), lions, *Panthera leo*, (Packer et al. 1991) and wild Asian, *Elephas maximus*, and African, *Loxodonta africana* elephants (Moss and Poole 1983, Fernando and Lande 2000). Nonetheless, kinship and sociality are not always related and stable groupings are also known to form among unrelated individuals, for example through by-product mutualism or reciprocal altruism, (Clutton-Brock 2002, Dugatkin 2002).

Given the lack of information on genetic relatedness among the individual Irrawaddy dolphins studied here, I could not determine if the strong and stable association patterns observed reflect a society structured by kin relationships or if groupings in this species follow a matrilineal organization such as that of killer whales and pilot whales. Similarly, it is not possible to assess if strong bonds between pairs of humpback dolphins are kin-based.

The pattern of male and female relationships and how these relationships are affected by ecological and social factors also influence the evolution of social structure (Wrangham 1986, Wrangham and Rubenstein 1986). There is no reliable method to determine the sex of Irrawaddy or humpback dolphins from surface observations, especially in their turbid habitats. From the few sexed animals, it appeared that female Irrawaddy dolphins formed strong associations with other females, and male humpback dolphins formed strong bonds with other males. The strong bond between female Irrawaddy dolphins may provide some form of communal care of calves resulting from kin selection or may be a form of reciprocal altruism between long-term associates. The strong bonds formed by the few male humpback dolphins identified may indicate cooperative alliances to herd females as those observed among bottlenose dolphins in Shark Bay (Connor et al. 1992b). Molecular studies determining the sex of individuals and assessing the degree of relatedness among school members should reveal if association patterns vary with sex and if kinship plays an important role in the formation of strong bonds in Irrawaddy and humpback dolphins (e.g., Möller and Beheregaray 2001, Krützen et al. 2003).

7.4.2.3 *Food availability and predation risk*

Although prey distribution and availability was not measured in Cleveland Bay, I suggest this is not likely to be a major factor shaping the social structure of Irrawaddy and humpback dolphins. This suggestion is based on a number of observations. First, both Irrawaddy and humpback dolphins appear to feed mainly on fish associated with estuarine areas, and at least at the prey family level there appears to be dietary overlap (see chapter 2). Second, in Cleveland Bay, space use patterns by both species overlap considerably, differences in their habitat preferences are not abrupt or substantial, and foraging takes place over similar areas. Based on this

information it would appear that both species share similar prey. If so there is no reason to expect that their grouping and association patterns are conditioned by food distribution and availability.

By associating with several individuals in a group or school, an individual may reduce its risk of predation through shared vigilance and detection, and reduction of chances of being attack and captured by predators (Pulliam 1973, Alexander 1974, Elgar 1989, Roberts 1996, Lingle 2001). As discussed in Chapters 4 and 5, large adult tiger sharks are found in Cleveland Bay and dolphin remains found in their in stomachs together with evidence from scarring on both species indicates predation does occur (Simpfendorfer 1992). Because of their overlapping distributions, levels of predation risk experienced by both species should be similar. However, there is the possibility that Irrawaddy dolphins experience higher rates of shark attacks due to their preference for shallower waters with seagrass meadows in comparison with humpback dolphins (see chapter 5). For example, in Shark Bay, bottlenose dolphins are found in larger group sizes in shallow water habitats with seagrass where tiger shark density is highest (Heithaus and Dill 2002). Predation risk is supposed to be higher in shallow habitats because of decreased echolocation efficiency by dolphins, due to biological noise being louder in these habitats and poor visual detection of tiger sharks over seagrass (Heithaus and Dill 2002). Investigation of the density and habitat use by sharks in Cleveland Bay will help determine the level of predation risk associated with different habitats and enhance our understanding of its influence on the social structure of Irrawaddy and humpback dolphins.

7.5 Chapter summary

- Comparison of social structures within and among species can provide valuable insights into the adaptive nature and evolution of social systems. In

this chapter, I use photo-identification data from Irrawaddy and Indo-Pacific humpback dolphins collected in Cleveland Bay between 1999-2002 to determine the structure and temporal patterns of association among individuals of each species.

- Analysis of association patterns indicated that individual Irrawaddy and humpback dolphins were more frequently seen with a particular companion than would be expected by chance. Cluster analysis showed that individual Irrawaddy dolphins may form strong associations with more than one individual. Strong associations between humpback dolphins appeared to be limited to pairs of animals.
- The relationship between lagged association rates and time lag for Irrawaddy dolphins suggested some individuals associated for short periods of time (days) but other remained affiliated for long-term periods (years). The model that best described this relationship suggested an individual Irrawaddy dolphin at any time had two types of associates: “constant companions” and “casual acquaintances”. The mean number of associates (constant companions + casual acquaintances) suggested by the model was approximately eight, of which four were constant companions.
- Short and long term associations also appear to be occurring among individual humpback dolphins. However, all the social models fit the data equally well suggesting a complex pattern of associations between individual humpback dolphins that may involve various associates with different levels of temporal stability.
- Differences in the social systems of both species could be explained by their different phylogenetic relationships among the Delphinidae. Within the family

Delphinidae, Irrawaddy dolphins seem to be most closely related to killer whales (i.e., both are placed in the subfamily Orcininae), the only other delphinid together with pilot whales (subfamily Globicephalinae) known to have a stable social structure composed of strong-long term associates. In contrast, humpback dolphins (subfamily Delphininae) are more related to bottlenose dolphins and other oceanic species characterized by fluid and dynamic social systems, where bonds among members vary in their temporal stability.

- The larger school size and number of associates of an Irrawaddy dolphin in comparison with a humpback dolphin may simply result from varying food distribution and availability among the home ranges of both species. However similar diet, space use patterns and habitat preferences indicate food distribution and availability should be similar for both species. Thus, the distribution and availability of food appears not to explain differences in social systems.
- Because of their preference for shallow waters with seagrass, the predation risk posed by tiger sharks present in Cleveland Bay may be higher for Irrawaddy dolphins than for humpback dolphins. Thus, strong bonds with more than one individual may serve as an antipredator strategy for Irrawaddy dolphins.
- The few sexed animals of both species provided limited insight into sex-specific bonds. In Irrawaddy dolphins, strong bonds among various females may provide a social function such as communal care of calves. Strong bonds between males in humpback dolphins may indicate cooperative alliances similar to those observed in bottlenose dolphins.

- Future studies involving genetic sampling of photo-identified individuals will be fundamental towards resolving the differences between the social structure of Irrawaddy and humpback dolphins.

Table 7.1 Mean and maximum half-weight association indices (HWI) of Irrawaddy and humpback dolphins. Observed and random mean HWI \pm SD and P-values are indicated for the random association test. The test statistic was the SD. P-values $>$ 0.95 indicate SD of observed data was significantly higher than that of random data.

Species	n	Mean HWI \pm SD		P	Maximum HWI \pm SD
		Observed	Random		
Irrawaddy dolphins	30	0.15 \pm 0.18	0.15 \pm 0.17	>0.999	0.63 \pm 0.11
Humpback dolphins	14	0.14 \pm 0.18	0.14 \pm 0.17	>0.999	0.52 \pm 0.20

Table 7.2 Mathematical models fitted to the standard lagged association rates ($g(d)$), describing the temporal association patterns of Irrawaddy and humpback dolphins as a function of time lag (td). Jackknife procedures were used to estimate standard errors of parameters. (Burnham and Anderson 1998). The model minimizing the adjusted Akaike Information Criterion for small-sample bias (AIC_c) was chosen as the best fit model for Irrawaddy dolphins (indicated in bold italics). There was not best model for humpback dolphins. The models are of the exponential form proposed by Whitehead (1995).

	Model	Model formula	No. of parameters	Estimates of parameters (\pm SE)	AIC_c	ΔAIC_c
Irrawaddy dolphins	Constant Companions	$g(td) = a1$	1	$a1 = 0.0776 (\pm 0.0130)$	19113	96
	Casual acquaintances	$g(td) = a2 * \exp(-a1 * td)$	2	$a1 = 0.0004 (\pm 0.0002)$ $a2 = 0.0908 (\pm 0.0166)$	19072	55
	<i>Casual acquaintances + Constant Companions</i>	<i>$g(td) = a2 + a3 * \exp(-a1 * td)$</i>	<i>3</i>	<i>$a1 = 0.0298 (\pm 0.0261)$</i> <i>$a2 = 0.0709 (\pm 0.0121)$</i> <i>$a3 = 0.0567 (\pm 0.0218)$</i>	<i>19017</i>	<i>0</i>
	Two levels of casual acquaintances	$g(td) = a3 * \exp(-a1 * td) + a4 * \exp(-a2 * td)$	4	$a1 = 0.0004 (\pm 8.8984)$ $a2 = 0.0004 (\pm 0.0005)$ $a3 = -0.7020 (\pm 6.4214)$ $a4 = 0.7927 (\pm 2.1545)$	19076	59
	Constant Companions	$g(td) = a1$	1	$a1 = 0.1870 (\pm 0.0147)$	11101	0
Humpback dolphins	Casual acquaintances	$g(td) = a2 * \exp(-a1 * td)$	2	$a1 = 0.0001 (\pm 0.0001)$ $a2 = 0.1931 (\pm 0.0188)$	11101	0
	Casual acquaintances + Constant Companions	$g(td) = a2 + a3 * \exp(-a1 * td)$	3	$a1 = 0.0380 (\pm 27.4130)$ $a2 = 0.1840 (\pm 1.6125)$ $a3 = 0.0280 (\pm 1319.2631)$	11102	1
	Two levels of casual acquaintances	$g(td) = a3 * \exp(-a1 * td) + a4 * \exp(-a2 * td)$	4	$a1 = 32.7703 (\pm 107.1323)$ $a2 = 0.0001 (\pm 0.0003)$ $a3 = 19.0394 (\pm 95.5775)$ $a4 = 0.1932 (\pm 0.5349)$	11105	4

Chapter 8

Abundance estimates of Irrawaddy and Indo-Pacific Humpback dolphins in Cleveland Bay, northeast Queensland, Australia

In this chapter, I use open mark-recapture population models to estimate the abundance of Irrawaddy and Indo-Pacific humpback dolphins in Cleveland Bay. I review and evaluate model assumptions. Finally, I discuss the implications of the abundance estimates obtained to the conservation of these two dolphin species.

Chapter 8. Abundance estimates of Irrawaddy and Indo-Pacific Humpback dolphins in Cleveland Bay, northeast Queensland, Australia

8.1 Introduction

Estimates of population size are an important aspect of the ecology of any species, and an integral part in the management of wildlife populations (Williams et al. 2002). For example, the estimation of sustainable removal levels of animal populations requires knowledge of abundance estimates and their variances (Wade 1998). Despite increasing concerns about the long-term survival of Irrawaddy dolphins, *Orcaella brevirostris*, and the Indo-Pacific humpback dolphins (hereafter humpback dolphins), *Sousa chinensis*, there are few estimates of their abundance even at local scales. Nonetheless, most of these estimates, particularly those of Irrawaddy dolphins, are worryingly small. Recent studies on freshwater populations of Irrawaddy dolphins throughout Southeast Asia revealed populations that number in the tens of animals, all facing potential extirpation in the near future (Beasley et al. 2002b, Krebs 2002, Smith et al. 2003). Long-term studies on humpback dolphins along the coast of South Africa and Hong Kong indicate that the populations are still viable (i.e., populations of hundreds to low thousands of animals), but emphasize they are under increasing threats from human activities adjacent to the coast (Jefferson 2000, Karczmarski 2000).

The conservation status of Irrawaddy dolphins and humpback dolphins in Australian waters is unknown (Corkeron et al. 1997, Parra et al. 2002, Parra et al. 2004). Most of the uncertainty about the status of these species is due to a lack of longitudinal studies on either species in Australian waters. This lack of knowledge has held back sound conservation and management efforts, and our ability to assess the

impact of human activities on local populations. Thus, population studies of Irrawaddy and humpback dolphins have been considered high priority under the Australian Cetacean Action Plan and the Great Barrier Reef Marine Park Whale and Dolphin Conservation Policy (Bannister et al. 1996, Great Barrier Reef Marine Park Authority 2000). In addition, the latest efforts to resolve the taxonomy of the members of the genera *Orcaella* and *Sousa* indicate that there is species/subspecies level separation between populations of these taxa in Australian/Papua New Guinea region and Asia (Beasley et al. 2002a, Rosenbaum et al. 2002), making the estimation of most basic population parameters (e.g., population size) particularly significant and urgent in Australian waters, as well as in Asia.

Obtaining accurate and precise estimates of the abundance of cetacean species is usually difficult, expensive, and time consuming (Gerrodette 1987, Taylor and Gerrodette 1993). Sampling and environmental variability affect our ability to estimate cetacean populations sizes and trends (Taylor and Gerrodette 1993, Forney 2000, Thompson et al. 2000). However, careful survey design and examination of the assumptions inherent in estimation methods results in relatively precise and unbiased estimates (Wilson et al. 1999, Read et al. 2003). Additionally, the use of power analysis can help address questions regarding the ability of monitoring programs to detect trends (Gerrodette 1987, Taylor and Gerrodette 1993).

Studies of naturally-marked individual and capture-recapture models have been used to estimate the population parameters of a wide number of taxa including several species of marine mammals (Hammond 1990, Hammond et al. 1990). Irrawaddy and humpback dolphins are reliably identified from marks and white pigmentation patterns on their dorsal fins (Corkeron 1990, Parra and Corkeron 2001). Here, I present the results of a four-year photo-identification and capture-recapture

study aimed at estimating the relative number of animals inhabiting the coastal waters of Cleveland Bay, northeast Queensland, Australia (Objective 7 of this thesis, see Chapter 1).

This study represents the first comprehensive assessment of the population size of Irrawaddy dolphins at a local level in Australian waters, and also provides the first point of comparison to previous estimates of humpback dolphin numbers in the region (Corkeron et al. 1997). Careful design of photo-identification surveys, analysis of photographs, model selection, and validation of capture-recapture assumptions provided precise estimates with minimal bias. Implications for the conservation and management of both species are discussed.

8.2 Methods

8.2.1 Data Collection

See chapter 4 for details of survey procedures, survey effort, and figure of study area; and chapter 6 for details of photo-identification methodology.

8.2.2 Data selection

As most fieldwork effort took place during the dry season (May-Nov), and most identified dolphins of both species (Irrawaddy: 98 %; Humpback: 94%) were captured during these months (Fig. 8.1), analysis of capture-recapture data were limited to animals captured within this season. Capture histories of each individual dolphin in the dry season were pooled by year (i.e., if an animal was photographed at least once during May-Nov it was considered captured for that year), resulting in four sampling occasions (1999, 2000, 2001, and 2002). Photographing Irrawaddy and humpback dolphins is time-consuming and weather dependent, thus this pooling was required in order to obtain adequate sample sizes.

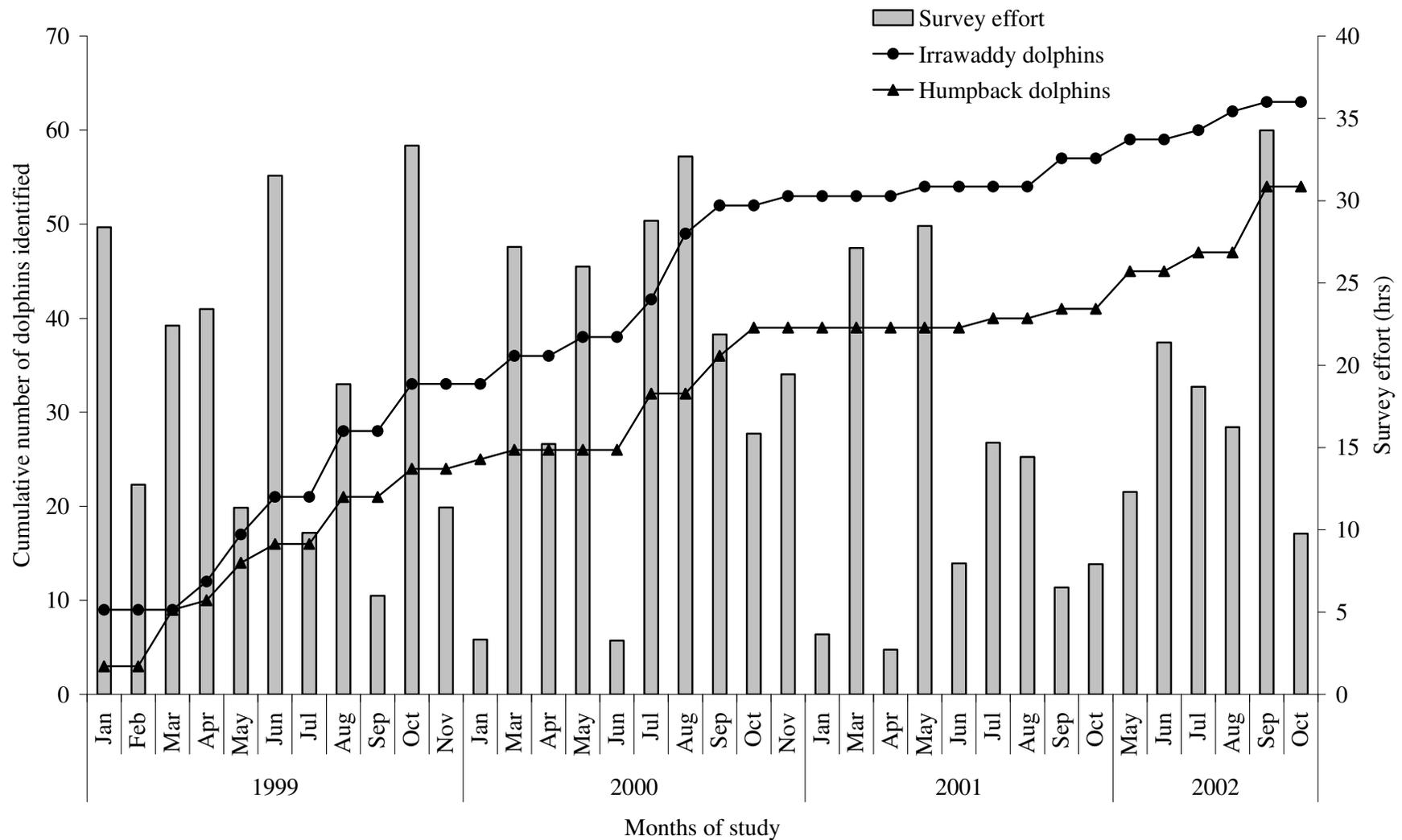


Figure 8.1 Discovery curves of the cumulative number of Irrawaddy and humpback dolphins identified between January 1999 and October 2002 in Cleveland Bay. The bars represent the number of survey hours spent in the field during each month of study.

8.2.3 *Estimating population size*

I defined the term “population” for both Irrawaddy and humpback dolphins as the number of individuals of each species frequenting the study area. Population sizes of Irrawaddy and humpback dolphins were estimated using Schwarz and Arnason’s parameterization of the Jolly-Seber open population model (Schwarz and Arnason 1996). This model provides abundance estimates while allowing entries (e.g., births, immigration) and losses (e.g., death, permanent emigration) in the population under study, and is suitable for long-term studies where the use of models assuming population closure is not reasonable. To model population size, I started with the most general Jolly-Seber model which allows for capture (p) and survival (Φ) probabilities to vary with time (t). Restrictions in the number of parameters estimated by the Jolly-Seber model can result in estimates with better precision (Pollock et al. 1990). Therefore, in addition to the general model, three conditional forms of the Jolly-Seber model were fitted to the data (Table 8.1, all tables have been placed at the end of this chapter to minimize interruption to the flow of the text, and printed on yellow colour paper for ease of location). The parameters of the Jolly-Seber models were estimated using maximum likelihood estimation using the computer program POPAN-5 (Schwarz and Arnason 1996, Arnason et al. 1998).

The appropriate model for inference among those fitted to the data was selected using the Akaike Information Criterion corrected for small sample sizes (AIC_c) (Burnham & Anderson, 1998). The AIC_c acts as a measure of model fit and complexity, and the lower the AIC_c the better the model is supported by the data. Models differing by less than two units from the model with minimum AIC_c (ΔAIC_c) also provide good descriptions of the data (Burnham & Anderson, 1998). In cases where more than one model provided a good description of the data, we followed the

principle of parsimony and selected the model with lower number of parameters as the most appropriate.

8.2.4 Total population size

Abundance estimates from Jolly-Seber models in this study pertain to the population of marked animals only. To include the unmarked portion of the population in our estimates the total population size of Irrawaddy and humpback dolphins in Cleveland Bay was derived as:

$$N_{total} = \frac{N}{\theta}$$

where N_{total} is the total population size, N is the estimate of marked animals from population models, and θ is the estimated proportion of animals that is identifiable (Williams et al. 1993, Wilson et al. 1999, Chilvers and Corkeron 2003). The proportion of identifiable individuals within the population (θ) for each year was estimated as the number of excellent and good quality photographs showing a recognisable individual from a random sample of 300 photographs from each species.

The variance of N_{total} was estimated as:

$$\text{Var}(N_{total}) = N_{total}^2 \left(\frac{\text{var } N}{N^2} + \frac{1 - \theta}{n\theta} \right)$$

where n is the total number of animals from which θ was estimated (Williams et al. 1993, Wilson et al. 1999, Chilvers and Corkeron 2003). Confidence intervals for total population size were calculated by assuming that the error distribution was the same as for the estimates from population models, with the lower and upper confidence limits equivalent to the number of standard errors away from the estimate.

8.2.5 *Validation of model assumptions*

The estimation of demographic parameters under Jolly-Seber capture-recapture models requires a number of assumptions about the nature of the population and the sampling of individuals. Violations of these assumptions can lead to bias in population estimates, making it important to assess and validate each assumption. Here, I used information on the biology of these two species and goodness-of-fit tests to evaluate potential violations of population analyses. The basic assumptions of the Jolly-Seber open model are:

1. *Mark recognition and mark loss*: marked animals are recognized with certainty if recaptured, and marks are not lost over the duration of the study. Failure to uphold these assumptions will result in upwardly biased estimates of population size (Pollock et al. 1990, Williams et al. 2002). To avoid any problems with mark recognition and mark loss, only good and excellent quality photographs were used to identify individuals. In addition, only individuals with long-lasting marks (e.g., notches on the dorsal fin; deep scars on back) were included in the analysis. Although marks may change with time, regular sampling over four years permitted me to monitor marked animals comprehensively and note changes or additions of new marks. Furthermore, additional marks (e.g., white pigmentation patterns, dorsal fin shape) often in association with notches and scars were also considered for individual identification. This practice helped me keep a record of an individual, even if the major feature of identification changed abruptly. In addition, to ensure consistency in the recognition of individuals and grading of photographs, only one experienced person was responsible for cataloguing

photographs over the entire duration of the study. Therefore, I consider the violation of these assumptions to be negligible.

2. *Homogeneous capture and survival probabilities*: every animal in the population has the same probability of capture in a given sampling period; and every marked animal has the same probability of survival between sampling periods. Heterogeneity in capture probabilities among individuals results in estimates of population size that are negatively biased (Pollock et al. 1990, Williams et al. 2002). There has been little work on the effect of heterogeneous survival probabilities on abundance estimates obtained from Jolly-Seber models (Williams et al. 2002). To test if these assumptions were met, I assessed the fit of the Jolly-Seber model to the data using the standard goodness-of-fit tests: Test 2 and Test 3 (see Burnham et al. 1987) implemented in the computer program U-Care (Choquet et al. 2002). These tests use a contingency table χ^2 analysis approach to test for specific patterns in capture-recapture data that might indicate violations of homogeneity in capture and survival probabilities. Test 2 deals with problems in capture heterogeneity, while Test 3 deals with heterogeneity in survival probabilities (Burnham et al. 1987). The pooled χ^2 statistics (Test 2 + Test 3) indicated that there was no evidence that the assumptions of homogeneous capture and survival probabilities were violated (Irrawaddy dolphins: $\chi^2 = 7.0$; $df = 4$; $P = 0.135$; humpback dolphins: $\chi^2 = 7.94$; $df = 4$; $P = 0.094$). Thus the Jolly-Seber model fitted the data.

It is important to note here that exact equality of capture probabilities and survival for all animals present in the study area at any sampling period is an assumption that is unlikely to be met in any sampling scheme of free ranging

animals (Pollock et al. 1990, Williams et al. 2002). Substantial negative bias in abundance estimates is expected if average capture probabilities are relatively low (e.g., $p < 0.5$) (Williams et al. 2002). In general, the average capture probabilities obtained in this study for both species were relatively high (> 0.5 , Table 8.1), thus I expect the effect of heterogeneity to be unimportant.

3. *No behavioural responses*: marked animals have the same probability of being recaptured as unmarked animals. If animals respond to capture in a way that increases (e.g., “trap-happy” behaviour) or decreases (“trap-shy” behaviour) their subsequent probability of capture estimates of population size will be biased. Trap-happy behaviour results in underestimation of population size, and trap-shy in overestimation (Pollock et al. 1990, Williams et al. 2002). Photo-identification uses existing marks to identify individuals and therefore animals are not subject to stress induced by capture, handling, or physical marking by the researcher. Boat approaches to take photographs were done at slow speed and parallel to the longitudinal axis of the school to minimize possible disturbance. As no physical interaction with the animal was needed for marking and the behavioural response to boats was minimized, the violation of this assumption was unlikely. Moreover, I carried out Pradel’s test for trap-dependence (Pradel 1993) using the program U-Care (Choquet et al. 2002). The test showed no indication of “trap-happy” or “trap-shy” behaviour by marked individuals (Irrawaddy dolphins: $Z = 0.0$; $df = 4$; $P = 1$; humpback dolphins: $Z = 0.67$; $df = 4$; $P = 0.497$).
4. *Permanent emigration*: all emigration from the sample area is permanent. Violations to this assumption are introduced when a significant portion of the

population is unavailable for capture during a given sampling occasion (i.e., temporary emigration) resulting in heterogeneity of capture probabilities (Kendall et al. 1997, Williams et al. 2002). Under random temporary emigration (i.e., every animal has the same probability of being a temporary emigrant) abundance estimates are unbiased (Kendall et al. 1997, Williams et al. 2002). In the situation where the probability of an animal emigrating depends on whether the animal was a temporary emigrant on the previous sampling period (i.e., Markovian emigration), the direction of the bias depends on the nature of the Markov process (Kendall et al. 1997, Williams et al. 2002). This assumption was unlikely to be violated. Though neither species resides permanently in the study area, both show high interannual site fidelity to the study area (see Chapter 6). As capture histories of each individual dolphin were pooled by year, most animals will have high probabilities of being captured during each year of sampling. In effect, estimates of the capture probabilities of both species were relatively high (Table 8.1); and there was no indication of heterogeneity in capture probabilities (see pooled χ^2 statistics of Test 2 + Test 3 above). These results indicated that most animals of both species were available during sampling.

5. *Instantaneous sampling*: sampling periods are instantaneous (i.e., population size does not change during sampling occasions). Violation of this assumption results in heterogeneity in survival probabilities, thus causing problems with estimation of abundance. The recommended design to minimize violation of this assumption is to select short sampling periods during which animals will experience negligible births, death, and migration. In general, delphinids are long-lived, and have low reproductive and high survival rates (Wells and Scott

1990, Woodley et al. 1997). The sampling occasions selected for analysis were relatively short in duration (6-7 months) in comparison to the dolphins' lifespan, thus we expect births and deaths to be insignificant during sampling periods. Capture probabilities of marked animals from Jolly-Seber models fitted to the data were relatively high for both species indicating migration during sampling periods was minimal (Table 8.1).

8.2.6 *Analysing the power to detect populations trends*

I used the method provided by Gerrodette (Gerrodette 1987) to investigate the ability of a series of population estimates to detect population trends:

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

where r is the annual rate of population change, n is the number of population estimates, CV is the coefficient of variation of the estimated total population size, $Z_{\alpha/2}$ is the one-tailed probability of making a Type I error (α) and Z_{β} is the probability of making a Type II error (β). The probability of Type I and II errors was set at 0.05 as this is the standard level of α and β used to claim a statistically significant effect, and high statistical power ($\text{Power} = 1 - \beta = 0.95$). I used the range of CV values obtained from the population estimates to investigate the time it will take to detect different rates of population change by conducting annual surveys.

8.3 Results

8.3.1 *Photo-identification and proportion of animals identifiable*

As discussed in Chapter 4, I spent a total of 630 hours in Cleveland Bay Dugong Protected Area (hereafter Cleveland Bay) searching for Irrawaddy and humpback dolphins between 1999-2002. During this period, 63 Irrawaddy dolphins and 54 humpback dolphins were identified (see Chapter 6). All identified animals

were adults, with the exception of one juvenile Irrawaddy dolphin. Overall, the cumulative number of identified individuals (i.e., rate of discovery) of both species did not decrease with time, suggesting populations were open for the duration of the study (Fig. 8.1). The initial increase in the discovery rate of new individuals of both species during 1999 (Fig. 8.1) is an attribute of the beginning of a study. However, the alternating increases and plateaus in the discovery curve later in the study suggest that there was a regular influx of new individuals to the study area throughout the study period. The rate of discovery of new individuals was not steep with an average of 1.7 ± 0.40 (mean \pm SE) Irrawaddy and 1.5 ± 0.35 humpback dolphins added to the catalogue per month. By the end of 2000, 84% of the identifiable Irrawaddy and 72% of humpback dolphins had been identified.

The analysis of random photographs of excellent and good quality for each year indicated that the proportions of Irrawaddy and humpback dolphins that could be reliably identified from the population were high (Table 8.1). The proportion of identifiable Irrawaddy and humpback dolphins varied from 0.63 to 0.78 and from 0.66 to 0.79, respectively depending on the year.

8.3.2 Population size of marked animals and model selection

Abundance estimates of marked animals (N) from the four Jolly-Seber models fitted to the data are presented in Table 8.1. Note that because of the specific structure of each model, some parameters are not identifiable and thus N cannot be estimated for all years (Schwarz & Arnason, 1996). In the full time-dependent Jolly-Seber model (ϕ_t, p_t), N could only be estimated for the second and third years (i.e., 2000, 2001). For the other three models, estimates of N are available for all periods except 1999. For each year where a comparison is available, abundance estimates of marked animals for both species did not vary greatly between models.

Based on the AIC_c values the model that best fitted the data for Irrawaddy and humpback dolphins was the model in which capture probabilities vary with time and survival probabilities were constant (φ_{\bullet}, p_t , Table 8.1). The full time dependent model (φ_t, p_t) and the constant model ($\varphi_{\bullet}, p_{\bullet}$) also provided good fit to the data (i.e. ΔAIC_c scores within 2 units of best model) of both species, with similar estimates of N to the best model (Table 8.1)

Following the principle of parsimony, I selected as best model for both species the constant capture-constant survival model ($\varphi_{\bullet}, p_{\bullet}$) as it has a lower number of parameters than all other models. Estimates of N from the constant capture-constant survival model varied from 42 to 53 marked Irrawaddy dolphins and from 27 to 41 marked humpback dolphins.

8.3.3 Total Population size

Taking into account the proportion of identifiable individuals for each year and the selected model for each species the total number of Irrawaddy dolphins using the study area was estimated as 76 ± 6.0 (mean \pm SE; CV = 0.08; 95% CI = 65-88) in 2000; 64 ± 7.4 (mean \pm SE; CV = 0.11; 95% CI = 51-80) in 2001; and 67 ± 9.4 (mean \pm SE; CV = 0.14 95% CI = 51-88) in 2002 (Table 8.1). Estimates of total population size for humpback dolphins were 52 ± 7.1 (mean \pm SE; CV = 0.14; 95% CI = 40-68) in 2000; 34 ± 6.3 (mean \pm SE; CV = 0.19; 95% CI = 24-49) in 2001; and 54 ± 9.6 (mean \pm SE; CV = 0.18; 95% CI = 38-77) in 2002 (Table 8.1).

8.3.4 Power to detect population trends

With the different levels of precision obtained in the abundance estimates, it is clear that the time required to detect a population trend in either species by carrying annual surveys will decrease with increasing rates of population change (Fig. 8.2,

Table 8.2). With the highest level of precision obtained for the abundance estimates of Irrawaddy dolphins (CV = 0.08), I estimated that it will take eight years to detect a population change of 5% p.a., but two years to detect a 20% p.a. change. The total percentage change in the population of either species that will have occurred by the time a 5% or 20% p.a. increase or decrease is detected is high (Table 8.2). By the time a trend is detected in the populations of either species, numbers would have increased or decreased substantially. For example, a population of 76 Irrawaddy dolphins (CV = 0.08) decreasing at 5% per year, would consist of only 55 individuals by the time such trend was detected. If the rate of decline was 20% per year, only 49 individuals would remain by the time the trend was detected.

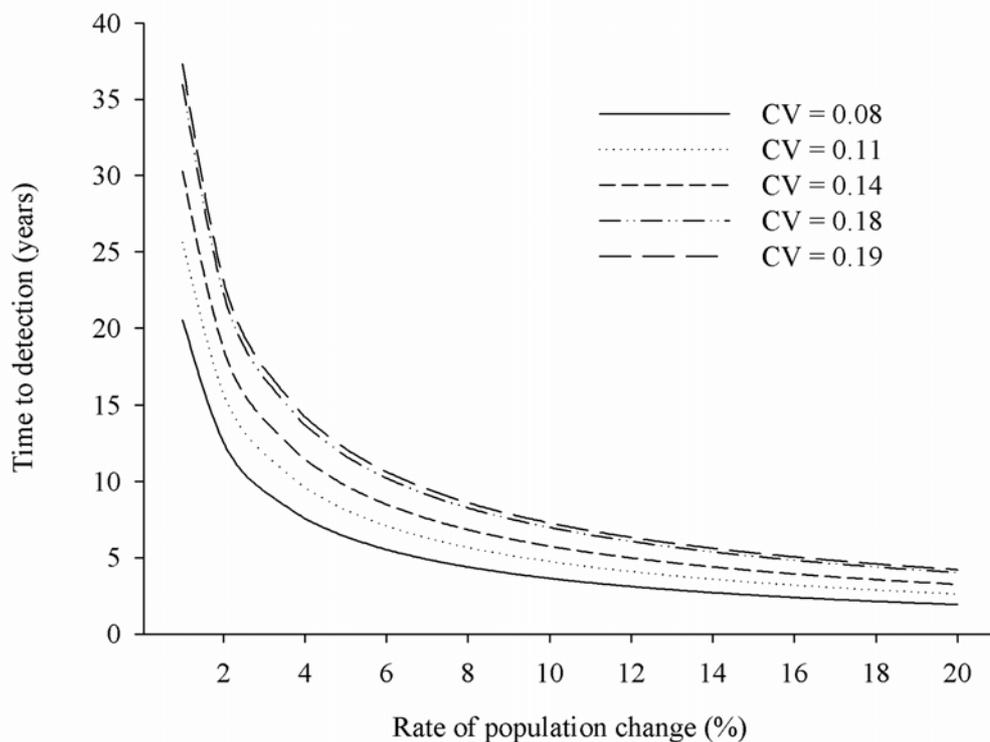


Figure 8.2 Relationships between different rates of population change, time until trend detection, and coefficient of variation (CV) for annual population estimates. The CVs used to present data variability are the values obtained for population estimates of Irrawaddy and humpback dolphins. The probability of type I (α) and Type II (β) errors was set at 0.05.

8.3.5 Discussion

The size of an animal population is a major determinant of its persistence in time. Small populations are more prone to extinction than large stable populations because of loss of genetic variability and environmental and demographic stochasticity (Caughley and Gunn 1996). Although there has been controversy over how large populations need to be to ensure persistence, recent studies across many vertebrate taxa indicate that the minimum size required for a population to be viable (i.e., the smallest size a population can have to have a 99% probability of persistence for 40 generations) in the long-term is thousands to tens of thousands of individuals (Reed et al. 2003).

The results of this study indicate that a very small number of Irrawaddy and humpback dolphins inhabit the coastal waters of Cleveland Bay. By detailed examination of the assumptions involved in mark recapture analyses with open population models, I was able to derive what I consider to be relatively unbiased and precise abundance estimates for both species. I estimated that less than a hundred individuals of each species used the study area between 1999 and 2002. Although these estimates pertain only to the number of animals of both species using the study area, such low numbers pose serious concerns about the long-term survival of both species in this local region. For example, population viability analysis of well known coastal dolphin species (i.e., bottlenose dolphin, *Tursiops truncatus*, and Hector's dolphin, *Cephalorhynchus hectori*) indicated that populations of less than a hundred animals face very high extinction probabilities (Thompson et al. 2000, Burkhart and Slooten 2003). Future studies on population structure and dispersal patterns of Irrawaddy and humpback dolphins will be fundamental to determine extinction risks and appropriate management strategies in this region (see Chapter 10).

With no previous estimates of population size, it is impossible to assess if populations of both species in this region have been stable, increasing or decreasing over the years. Irrespective of the historical abundance of Irrawaddy and humpback dolphins in the study area, there is evidence that local populations of both species have been subject to anthropogenic mortality in the past. Between 1967 and 1992 at least 544 cetaceans were caught in shark nets set for bather protection along the Queensland coast (Paterson, 1990, Anon. 1992). Though the species composition for most dolphin catches in shark nets is unknown, there is an indication that Irrawaddy and humpback were among the species most frequently caught in the Townsville region. For example, of 24 dolphins caught in shark nets between 1968 and 1976 in the study area, 15 were Irrawaddy dolphins (63%) and 6 (25%) were humpback dolphins (Heinsohn 1979). Despite the lack of information on past bycatch of dolphins in commercial gillnets in this region, I regard some mortality in commercial gillnets as inevitable because: 1) they are mainly set in waters close to the coast, and 2) there is evidence from elsewhere that both species are vulnerable to gillnetting practices (Amir et al. 2002, Smith et al. 2003). Thus, it is very likely that anthropogenic activities such as shark nets and gillnetting have contributed to the current low numbers.

The data collected in this study do not provide an insight into the current trends of local populations of Irrawaddy and humpback dolphins. It is also clear from the analysis of statistical power of mark-recapture methods that increases or declines in abundance will be extremely difficult to detect within the space of a few years, unless changes in population size are very high (> 20% p.a.) or survey intensity is increased. At such high levels of annual change, local populations of Irrawaddy and

humpback dolphins could have decreased to very low levels by the time trend is detected.

In addition, the estimation of trends becomes more complex if we take into account the apparent open nature of both populations. The alternating increases in the number of individuals identified through the study period indicate that the populations of Irrawaddy and humpback dolphins in the study area are potentially open to immigration. My previous studies on site fidelity patterns of identified individuals suggest that there is substantial movement of animals out of the study area, but that a great proportion tend to return into the study area following a model of emigration + reimmigration (see Chapter 7). It is therefore important, that future survey coverage include areas to the north and south of the study area, to assess population structure and how movement of individuals between these areas might affect abundance estimates at a local level.

As discussed in Chapter 6, although most humpback dolphins identified in this study were seen in more than one year (52%), there is a large proportion of animals that were only seen once (41%). This result suggests that a large number of humpback dolphins only visited Cleveland Bay occasionally, and as a result my estimates of population size may be underestimates. In the case of Irrawaddy dolphins, only a small proportion of the animals identified were seen once (12%) only, while 63% were seen in more than one calendar year (see Chapter 6), thus estimates for Irrawaddy dolphins should reflect local population sizes.

The low population numbers of Irrawaddy and humpback dolphins and our inability to detect trends reinforce the assertions of other marine mammal studies that scientific proof of decline or increase should not be a necessary criterion for enacting conservation measures of these species (Taylor and Gerrodette 1993, Wilson et al.

1999, Thompson et al. 2000). Against this background, the first priority of managers should be to reduce and control all direct threats to local populations while minimising the impacts of management decisions on different stakeholder groups.

The current level of protection offered to Irrawaddy and humpback dolphins in Cleveland Bay is good. Because of its status as a Dugong Protected Area Type A since 1997, gillnetting is currently banned in the study area. In addition, shark nets to protect bathers were replaced with baited drumlines in 1992 and the number of dolphins killed at a regional level has declined (Gribble et al. 1998). Despite this high level of protection in relation to entanglement in mesh nets, the effectiveness of the current protection provided to local dolphins will depend strongly on the maintenance of high quality habitat within and outside the study area. For example, adjacent areas to Cleveland Bay offer different levels of protection regarding mesh netting practices. Bowling Green Bay to the south is a Dugong Protected Area Type B, where mesh netting activities are allowed to continue, but with rigorous safeguards and restrictions. In Halifax Bay, North of Cleveland Bay, there are no regulations regarding mesh netting practices *per se*. The number of fishers licensed to operate gillnets throughout the Great Barrier Reef Marine Park has been reduced by > 50% since 1997 (Darren Cameron, Great Barrier Reef Marine Park Authority, personal communication 2004). Nonetheless, entanglement threats pose some risk to the maintenance of local populations.

The open nature and low abundance estimates of both populations suggest that in order to maintain viable population sizes of Irrawaddy and humpback dolphins conservation approaches will need to consider the establishment of large protected areas or a network of small protected areas connected by corridors. The basis for such protected areas and networks already exists within the Great Barrier Reef Marine Park

along the east coast of Queensland. As discussed in Chapter 2, the Great Barrier Reef Marine Park is located off a coast with relatively low human population density and is one of the best protected marine ecosystems in the world. First, 33% of the Great Barrier Reef Marine Park was zoned as 'no-take' from mid 2004 (<http://www.reefed.edu.au/rap/>). Second, the new Great Barrier Reef Coast Marine Park established in November 2004, extends the Great Barrier Reef Marine Park zoning from low water to high water or to the seaward edge of mangrove forests. However, as discussed in Chapter 10, the suitability of these protected areas for the conservation of coastal dolphins is not understood because of the lack of information about the distribution and abundance of Irrawaddy and humpback throughout most of the Queensland coast.

Although it is difficult to be certain about the status of Irrawaddy and humpback dolphins in Queensland waters, local populations of both of these species appear to be small and are unlikely to be in the order of several tens of thousands at the state level. This conclusion is substantiated by: 1) the low numbers of Irrawaddy and humpback dolphins sighted during aerial surveys covering most of the east Queensland Coast between 1987 and 1995 (i.e.; 29 sightings of Irrawaddy dolphins and 54 sightings of humpback dolphins (Corkeron et al. 1997, Parra et al. 2002); 2) the low number of sightings during boat-based line transect surveys in selected areas of northeast Queensland (22 sightings of Irrawaddy dolphins and 14 sightings of humpback dolphins, see Chapter 3); 3) the small population estimates of humpback dolphins in Moreton Bay, an area approximately four times the size of my study area, (i.e., 119 individuals for the period of August 1985-February 1987, and 163 individuals for May 1984-February 1986, Corkeron et al. 1997).

Given their apparent small populations and likely status as species endemic to Australian/Papua New Guinean waters, precautionary conservation measures are essential to ensure the long-term survival of Irrawaddy and humpback dolphins in Australian waters. Although the preservation of suitable habitat is necessary, the recovery and persistence of small populations cannot occur without an understanding of the demography and population genetics of Irrawaddy and humpback dolphins. As discussed in Chapter 10, future research in these areas will provide important insights for their management at local and regional levels.

8.4 Chapter summary

- Estimates of population size are an important aspect of the ecology of any species, and an integral part in the management of wildlife populations. The lack of estimates of population size for Irrawaddy and humpback dolphins along the east coast of Queensland is a major impediment to the successful conservation of viable populations of Irrawaddy and humpback dolphins in this region.
- In this chapter, I used photo-identification data collected between 1999-2002 and open mark-recapture models to provide abundance estimates of Irrawaddy and humpback dolphins inhabiting the coastal waters of Cleveland Bay, northeast Queensland. I also used power analysis methods to assess the ability of annual surveys to detect different rates of population change.
- Detailed examination of the assumptions involved in open mark-recapture population models suggest that the abundance estimates presented here for both species were relatively unbiased and precise. I estimated that less than a hundred individuals of each species used the study area between 1999 and 2002 (Table 8.1).

- With no previous estimates of population size, it is impossible to assess if populations of both species in this region are stable, increasing or decreasing. However, it is certain that both species have been subject to anthropogenic mortality in the past due to entanglement in shark nets set for bather protection, and in gillnets.
- The power analysis indicated that even with relatively unbiased and precise abundance estimates ($CV = 0.08$) population trends will be extremely difficult to detect within the space of a few years unless changes in population size are very high ($> 20\%$ p.a.).
- Because of their small population sizes, Irrawaddy and humpback dolphins are particularly vulnerable to local extinction. Detection of population trends should not be a necessary criterion for enacting conservation measures of both species.
- The prospects for the conservation of both species along the east coast of Queensland are good. However, the suitability of these protected areas for the conservation of coastal dolphins is not understood because of the lack of information about their distribution and abundance at a regional level.
- Given their apparent small populations and their likely status as species/subspecies endemic to Australian/Papua New Guinean waters, precautionary conservation measures are essential to ensure the long-term survival of Irrawaddy and humpback dolphins in Australian waters.

Table 8.1 (opposite page) Abundance estimates of (a) Irrawaddy and (b) humpback dolphins in Cleveland Bay between January 1999-October 2002. Model notation follows Lebreton et al. 1992: φ = survival probability; p = capture probability; t = time dependent effect; and \bullet = constant effect. Other notations: n = number of animals captured; p = capture probability; N = estimate of number of marked animals; SE = standard error; CV = coefficient of variation; CI = confidence interval; Proportion ID = proportion of identifiable animals; N_{total} = estimate of total population size after correcting for proportion of identifiable individuals; np = number of estimable parameters in model; ΔAIC_c = difference between AIC_c and minimum AIC_c obtained; and na = not available. The model that best fitted the data of both species according to the Akaike Information Criterion corrected for small sample sizes (AIC_c) was model (φ_{\bullet}, p_t) . Models (φ_b, p_t) and $(\varphi_{\bullet}, p_{\bullet})$ also provided good fit to the data (i.e. ΔAIC_c scores within 2 units of best model) of both species. Following the parsimony principle model $(\varphi_{\bullet}, p_{\bullet})$ was selected as the most appropriate because has less number of parameter.

a)

Irrawaddy dolphins																	
Jolly-Seber models	Year	n	p	Marked animals					Proportion ID	Total population				np	Model selection		
				SE	N	SE	CV	95% CI		Ntotal	SE	CV	95% CI		AIC	AICc	ΔAIC_c
(φ_b, p_t)	1999	32	na	na	na	na	na	na	0.78	na	na	na	na	8	171.1	171.8	1.9
	2000	43	0.9	0.07	48	4.5	0.09	40-58	0.70	69	7.0	0.10	57-84				
	2001	28	0.6	0.10	45	6.1	0.14	35-59	0.67	68	9.5	0.14	51-89				
	2002	32	na	na	na	na	na	na	0.63	na	na	na	na				
(φ_b, p_{\bullet})	1999	32			na	na	na	na	0.78	na	na	na	na	7	173.6	174.3	4.4
	2000	43	0.7	0.06	54	4.5	0.08	46-64	0.70	78	7.1	0.09	65-93				
	2001	28			42	5.0	0.12	33-53	0.67	62	7.8	0.13	49-80				
	2002	32			43	6.5	0.15	32-58	0.63	69	10.9	0.16	51-94				
(φ_{\bullet}, p_t)	1999	32	na	na	na	na	na	na	0.78	na	na	na	na	7	169.2	169.9	0.0
	2000	43	0.9	0.07	49	4.3	0.09	41-58	0.70	70	6.7	0.10	58-84				
	2001	28	0.6	0.09	44	5.4	0.12	35-56	0.67	66	8.5	0.13	52-85				
	2002	32	0.8	0.13	43	7.2	0.17	31-59	0.63	68	11.9	0.17	48-95				
$(\varphi_{\bullet}, p_{\bullet})$	1999	32			na	na	na	na	0.78	na	na	na	na	5	170.1	170.8	0.9
	2000	43	0.7	0.06	53	3.6	0.07	46-60	0.70	76	6.0	0.08	65-88				
	2001	28			43	4.6	0.11	35-53	0.67	64	7.4	0.11	51-80				
	2002	32			42	5.6	0.13	32-54	0.63	67	9.4	0.14	51-88				

Table 8.1 Continued

b)

Humpback dolphins																
Jolly Seber	Year	n	p	Marked animals					Proportion ID	Total population				Model selection		
				SE	N	SE	CV	95% CI		Ntotal	SE	CV	95% CI	np	AICc	ΔAIC_c
(φ_b, p_t)	1999	20	na	na	na	na	na	na	0.77	na	na	na	na	8	155.9	1.8
	2000	25	0.8	0.13	32	5.9	0.18	23-46	0.66	49	9.1	0.19	34-70			
	2001	13	0.5	0.13	26	6.1	0.23	17-41	0.79	34	7.8	0.23	21-53			
	2002	30	na	na	na	na	na	na	0.77	na	na	na	na			
(φ_b, p_{\bullet})	1999	20			na	na	na	na	0.77	na	na	na	na	7	156.8	2.6
	2000	25	0.7	0.08	35	5.3	0.15	26-47	0.66	53	8.4	0.16	39-72			
	2001	13			24	4.9	0.20	16-35	0.79	30	6.2	0.21	20-45			
	2002	30			45	6.5	0.14	34-60	0.77	59	8.7	0.15	44-78			
(φ_{\bullet}, p_t)	1999	20	0.7	0.10	na	na	na	na	0.77	na	na	na	na	7	154.1	0.0
	2000	25	0.7	0.10	34	4.1	0.12	27-43	0.66	51	6.6	0.13	40-66			
	2001	13	0.5	0.13	25	5.2	0.21	17-38	0.79	32	6.7	0.21	21-48			
	2002	30	0.8	0.23	35	9.3	0.27	21-59	0.77	46	12.2	0.27	27-77			
$(\varphi_{\bullet}, p_{\bullet})$	1999	20			na	na	na	na	0.77	na	na	na	na	5	155.1	1.0
	2000	25	0.7	0.09	34	4.5	0.13	27-44	0.66	52	7.1	0.14	40-68			
	2001	13			27	4.9	0.18	19-38	0.79	34	6.3	0.19	24-49			
	2002	30			42	7.3	0.18	30-59	0.77	54	9.6	0.18	38-77			

Table 8.2 Effect of different annual rates of population change on the number of years required to detect population trends of Irrawaddy and humpback dolphins with yearly survey intervals ($t=1$). Data variability is specified at $CV = 0.08$ for Irrawaddy dolphins and 0.14 for humpback dolphins. These CVs correspond to the highest level of precision obtained for the abundance estimates of Irrawaddy and humpback dolphins (see Table 8.1). The probability of Type I (α) and II (β) errors was set at the 0.05 level.

	CV	Rate of change (r)	Number of surveys required (n)	Number of years to detection (t(n-1))	Total % change at detection for decreasing population $(1-r)^{t(n-1)}-1$	Total % change at trend detection for increasing population $(1+r)^{t(n-1)}-1$
Irrawaddy	0.08	0.05	7	6	-0.28	0.36
		0.1	5	4	-0.32	0.41
		0.15	4	3	-0.34	0.43
		0.2	3	2	-0.35	0.42
Humpback	0.14	0.05	11	10	-0.39	0.60
		0.1	7	6	-0.45	0.73
		0.15	5	4	-0.49	0.78
		0.2	4	3	-0.52	0.81

Chapter 9

Behavioural interactions between Irrawaddy and Indo-Pacific humpback dolphins

In this chapter, I provide the first description and quantitative assessment of behavioural interactions between free ranging Irrawaddy and Indo-Pacific humpback dolphins. I suggest possible explanations for these interactions and their potential implications for the structure and functioning of coexisting communities of Irrawaddy and Indo-Pacific humpback dolphins.

Chapter 9. Behavioural interactions between Irrawaddy and Indo-Pacific humpback dolphins

9.1 Introduction

The study of behavioural interactions between coexisting species can provide information on ecological interactions (e.g., competition, predation) that play an important role in the dynamics, structure and conservation of animal communities (Martin and Martin 2001b, a, Soule et al. 2003). Systematic observations of behavioural interactions provide the initial step in determining their possible functions (Abrams 2001). Interspecific interactions among cetaceans are common and complex. However, studies of sympatric communities of cetaceans and the type of interactions that take place between them are scarce.

Among cetaceans, delphinids are the most diverse and widespread group with several species coexisting in space and time and potentially interacting. Sympatric delphinids have been reported to travel, play, forage, mate, care (e.g., alloparental care) and display aggressive behaviour during interspecific interactions (Corkeron 1990, Herzing and Johnson 1997, Frantzis and Herzing 2002, Herzing et al. 2003, Pitman et al. 2003, Psarakos et al. 2003). Interactions are not only limited to other dolphins but might also include other cetacean species (see examples in: Jefferson et al. 1991, Shelden et al. 1995, Palacios and Mate 1996, Ross and Wilson 1996, Weller et al. 1996, Baird 1998, Baraff and Asmutis-Silvia 1998, Pitman et al. 2001, Shelden et al. 2003).

Irrawaddy, *Orcaella brevirostris*, and Indo-Pacific humpback dolphins (hereafter humpback dolphins), *Sousa chinensis*, occur in sympatry over a significant part of their geographical range (Stacey and Arnold 1999, Jefferson and Karczmarski 2001). Despite great overlap in their distribution no observations of interactions in the

wild have been reported. However, when Irrawaddy and humpback dolphins have been held together in captivity, humpback dolphins chased and harassed Irrawaddy dolphins confining them to a small portion of the pool (Stacey and Leatherwood 1997). Kamminga et al. (1983) suggested that specialized dolphins forced Irrawaddy dolphins inshore, but a justification for this statement was not given.

In Australia, Irrawaddy and humpback dolphins occur in sympatry throughout most of the coastline of Queensland, Northern Territory and Western Australia (Parra et al. 2002, Parra et al. 2004). Recent studies on the ecology of both species in northeast Queensland indicate considerable overlap in their space use patterns (see Chapters 5, and 6), thus the potential for interspecific interactions is high. In this study I describe the behavioural interactions observed between Irrawaddy and humpback dolphins between January 1999 and October 2002 in Cleveland Bay Dugong Protected Area (hereafter Cleveland Bay), northeast Queensland, Australia (Fig. 9.1), with the aim of addressing the following question: “How do these coexisting delphinids behave towards each other? (Objective 8 of this thesis, see Chapter 1) These observations are important for understanding the potential ecological interactions that occur within sympatric communities of Irrawaddy and humpback dolphins.

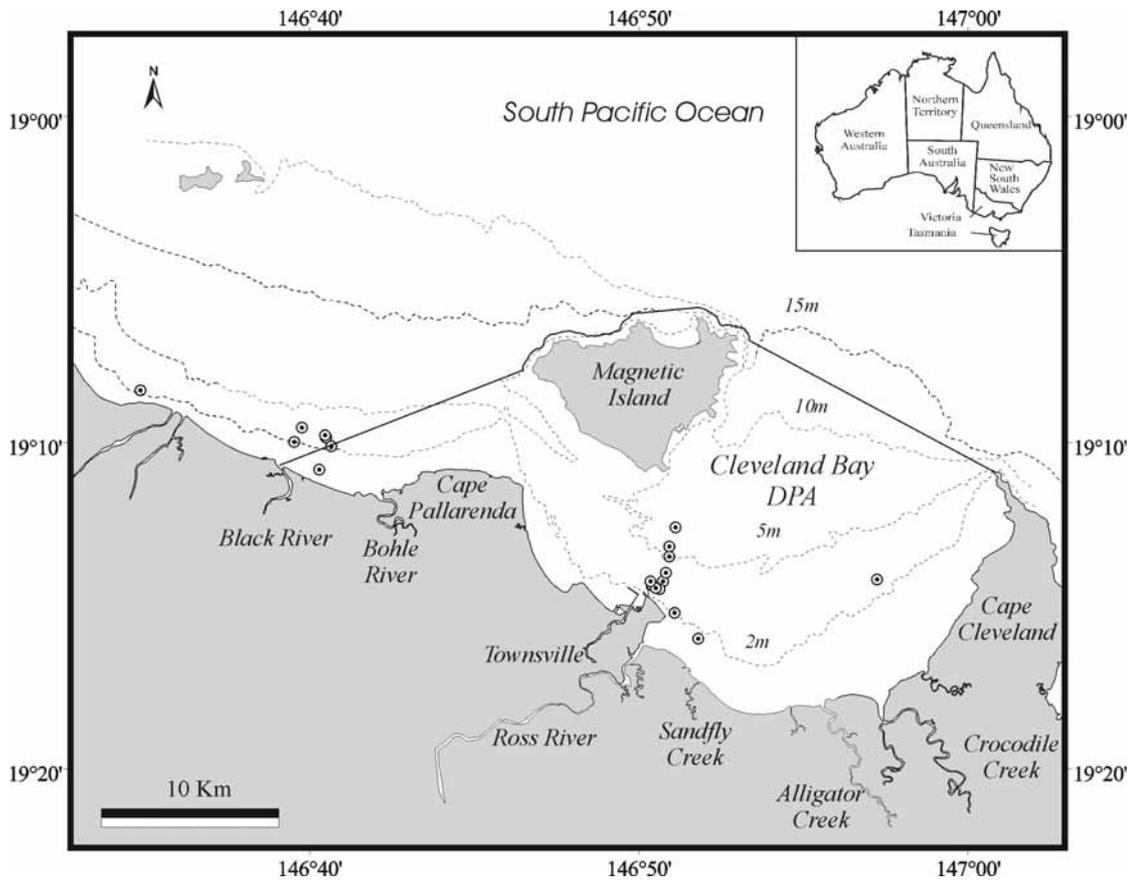


Figure 9.1 The study area with locations of the interspecific interactions observed between Irrawaddy and humpback dolphins (⊙) during 1999-2002. Solid line (—) indicates limits of the Dugong Protected Area (DPA).

9.2 Methods

9.2.1 Data Collection

See Chapter 4 for details of survey procedures and survey effort. See Chapter 6 for details of photo-identification methodology.

9.2.2 Interspecific interactions

I defined an interspecific interaction to occur when: at least one Irrawaddy dolphin was sighted $\leq 100\text{m}$ of at least one humpback dolphin for some or all the duration of an encounter. Once an interaction started, I scanned the schools of each species and recorded school size, age composition of the school, and behaviour every

5 minutes. Interactions were classified as follows based on: 1) different behavioural criteria and 2) whether or not activity between interacting individuals persisted for more than 50% of the duration of the encounter:

- Affiliative: animals less than a body length apart, travelling together in synchronous and directional movement, minimum physical contact
- Aggressive-sexual: rapid and persistent chase of one or more animals by another(s), usually accompanied by sudden and forceful contact using the rostrum, head or side of body, and often resulting in one animal being lifted partially out of the water. Included in this category were events of sexual interaction where such behaviour preceded potential copulation attempts by one of the species. Potential copulation attempts were inferred from the direct observation of animals swimming belly to belly. I defined copulations as 'potential' as the sex of the individuals involved could not usually be confirmed.
- Avoidance: abrupt and immediate departure by one species to distances > 100m usually followed by disappearance of one of the interacting dolphin schools in response to the action of the other.
- Forage: Individuals moving in various directions without an obvious pattern. Dolphins dive frequently and steeply downwards (often preceded by fluke up or peduncle arches), with extended submersion times. Rapid accelerations and erratic movement at the surface, indicative of animals chasing fish. Animals seen directly pursuing a fish (e.g., fish jumping at surface) or with fish in mouth, birds circling the school and seen catching fish at the water surface close to where dolphins surfaced.

The identity of the dolphins involved in each interaction was obtained from photo-identification catalogues developed during this study (see Chapter 6). The gender of some identified animals was inferred from social interactions (see Chapter 4).

I used two sample randomization tests (Manly 1997) to test for interspecific differences in school size and age composition of schools of Irrawaddy and humpback dolphins when they were first sighted interacting (i.e., member(s) of each species within 100 meters). Randomization procedures were repeated a large number of times (i.e., 5000) and the significance of the test evaluated by recording the number of times the differences obtained from randomization was greater than the observed value (Manly 1997). All tests were two-tailed and evaluated at $\alpha = 0.05$. To avoid an uncontrolled inflation of overall Type-I error rates in the multiple pairwise comparisons, the False Discovery Rate (FDR) correction procedure for multiple testing was used to adjust *P*-values (Benjamini and Hochberg 1995). Confidence intervals around the effect sizes (i.e., differences between means were obtained by non-parametric bootstrapping using the bias corrected and accelerated method (BCa) (Efron and Tibshirani 1993).

9.3 Results

9.3.1 School size and age composition

Between 1999 and 2002, a total of 19 interactions between Irrawaddy and humpback dolphins were recorded in Cleveland Bay and adjacent waters (Fig. 9.1). Interactions were seen every year of the study and during both the wet (December-March) and the dry season (April-Nov) (Fig. 9.2). Most interspecific interactions took place around the Townville Port and Black River mouth areas in shallow waters (mean \pm SE = 5.2 \pm 0.35 m), close to the coast (mean \pm SE = 1.6 \pm 0.28 km) and river

mouths (mean \pm SE = 2.7 ± 0.32 km) (Fig. 9.1). Out of the 19 occasions individuals of both species were seen interacting, eight were interactions already underway (i.e., both species were already in close spatial cohesion when I first saw them), while on 12 occasions humpback dolphins were the ones initiating the interaction (i.e., humpback dolphins approached school of Irrawaddy dolphins). The time I was able to observe interactions ranged from less than 5 minutes to 3 hours and 50 minutes.

The number of individuals observed at the time I first sighted an interaction varied from one to 21 Irrawaddy dolphins (mean \pm SE = 6.2 ± 1.19) and one to seven humpback dolphins (mean \pm SE = 3.8 ± 0.39). Overall, the number of Irrawaddy dolphins at the start of the interaction was higher than the number of humpback dolphins (Table 9.1). Interacting schools were mainly composed of adults, with Irrawaddy dolphin schools showing higher numbers of adults and calves than humpback dolphins (Table 9.1). These differences in school size and age composition refer to the animals observed in each school when an individual or individuals of both species were first seen within 100m of each other, however, interactions involving physical contact did not always involve all members in this close spatial cohesion (see below).

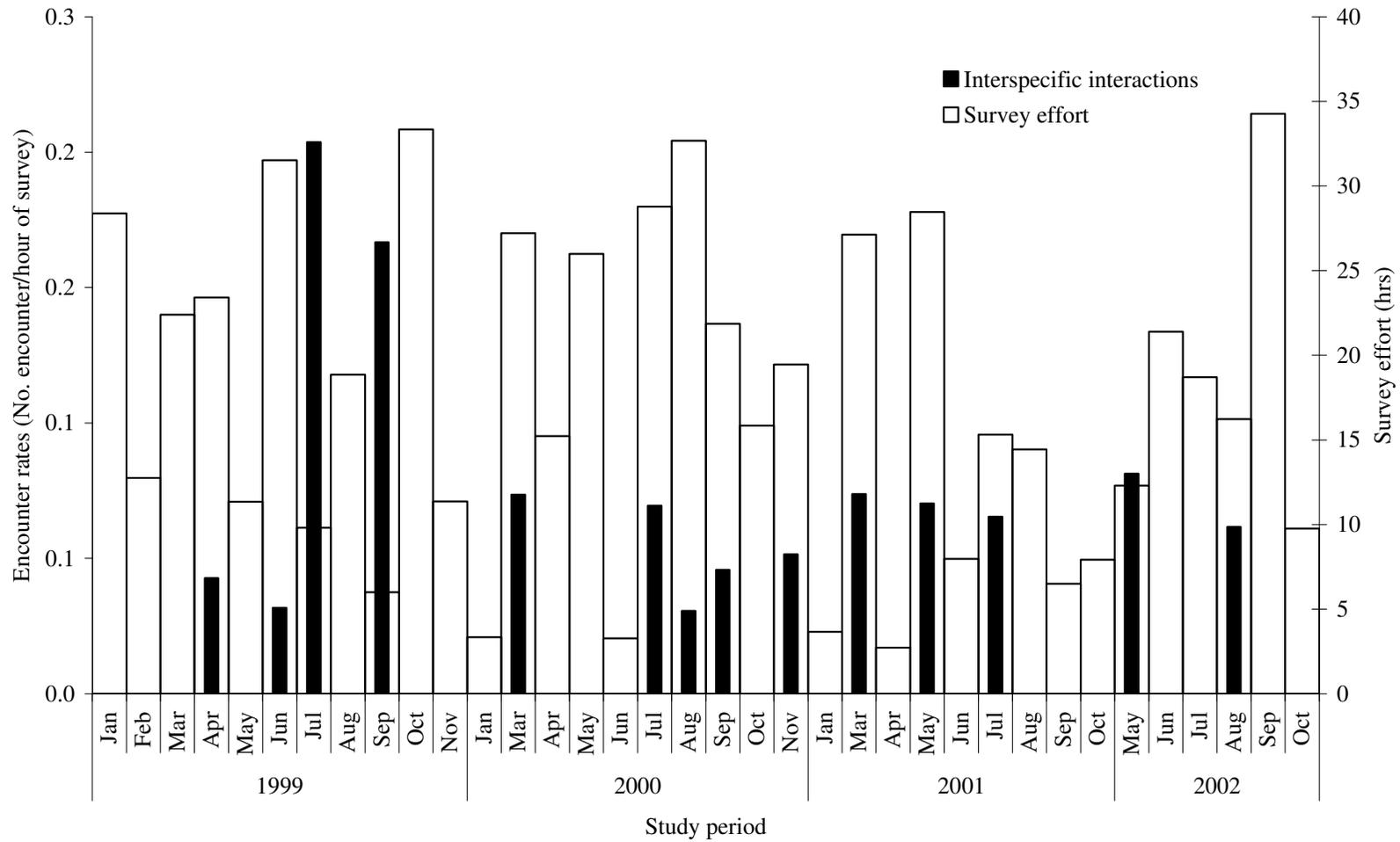


Figure 9.2 Encounter rates (No. encounters/hours of survey effort) of interactions between Irrawaddy and humpback dolphins in Cleveland Bay between 1999-2002.

9.3.2 Type of interspecific interactions

Interspecific interactions were mainly of an aggressive-sexual nature (53%), followed by affiliative (21%) activities (Fig. 9.3). Not all members first seen in close spatial cohesion participated in activities characterizing aggressive and affiliative interactions. During 73% of the aggressive-sexual interactions observed, the number of Irrawaddy dolphins involved was two (Fig. 9.4), and these were typically an adult and a calf (Fig. 9.5). The number of humpback dolphins participating in aggressive-sexual interactions varied from two to five (Fig. 9.4), and these were mainly adult animals (Fig. 9.5). In seven of the aggressive-sexual encounters, I was able to confirm from photo-identification data and behavioural observations that the adult Irrawaddy dolphins involved were females. In these same seven aggressive-sexual interactions, all the humpback dolphins involved except two (i.e., unknown sex) were males.

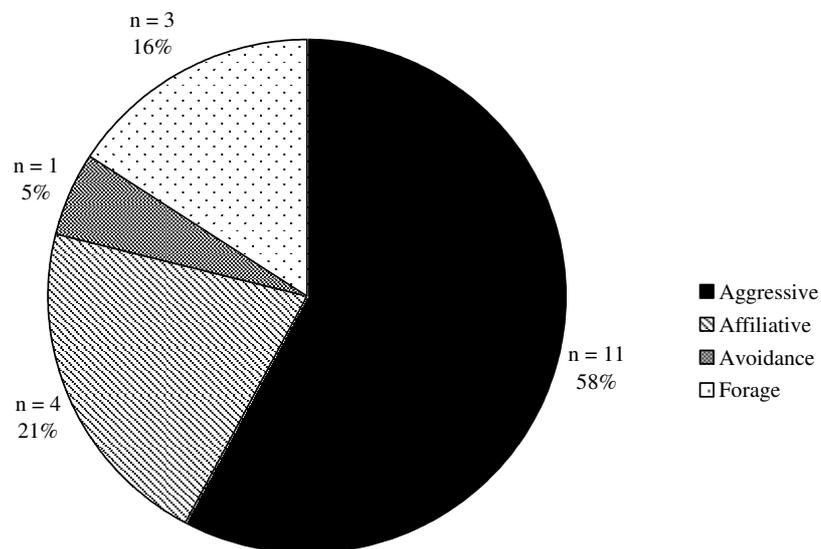


Figure 9.3 Relative frequency (%) of interactions observed between Irrawaddy and humpback dolphins

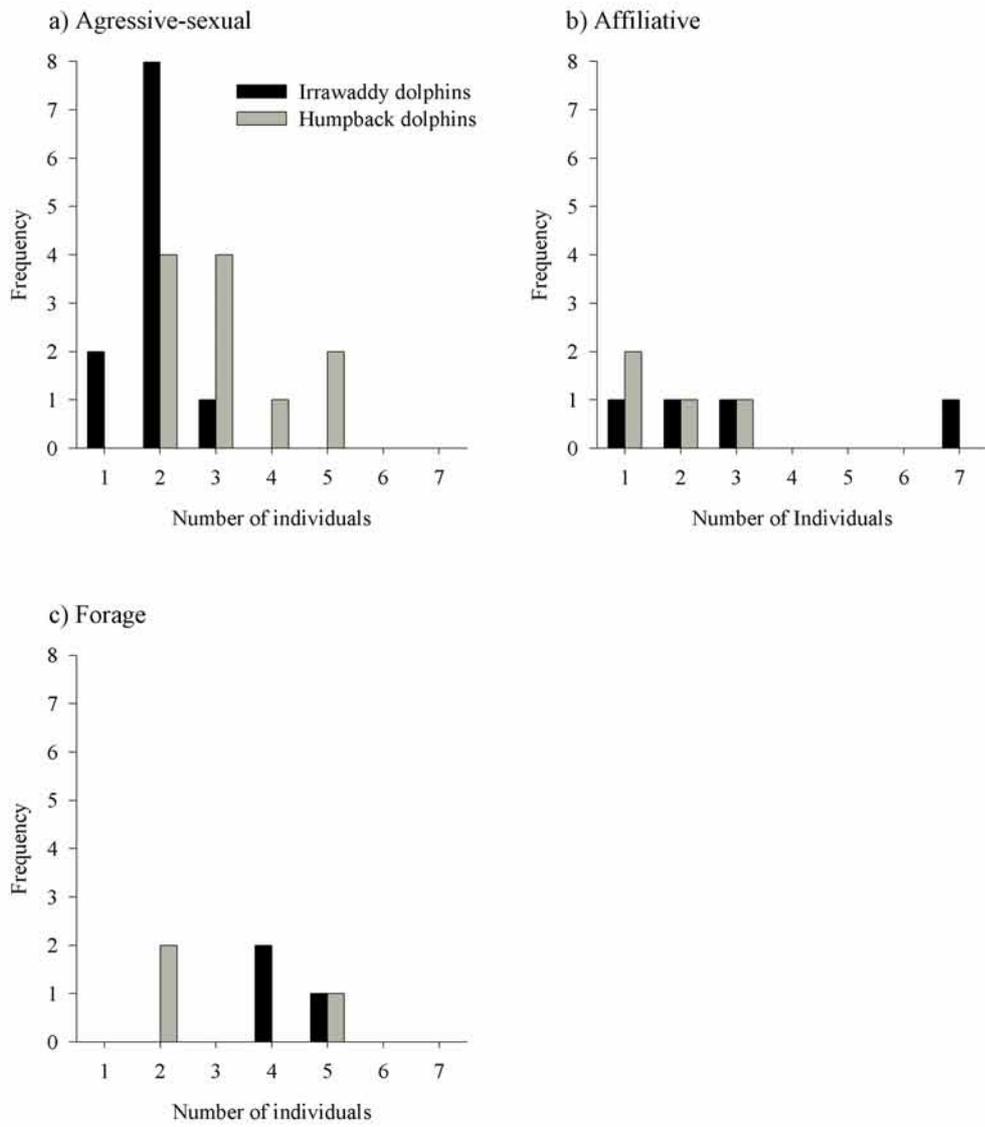
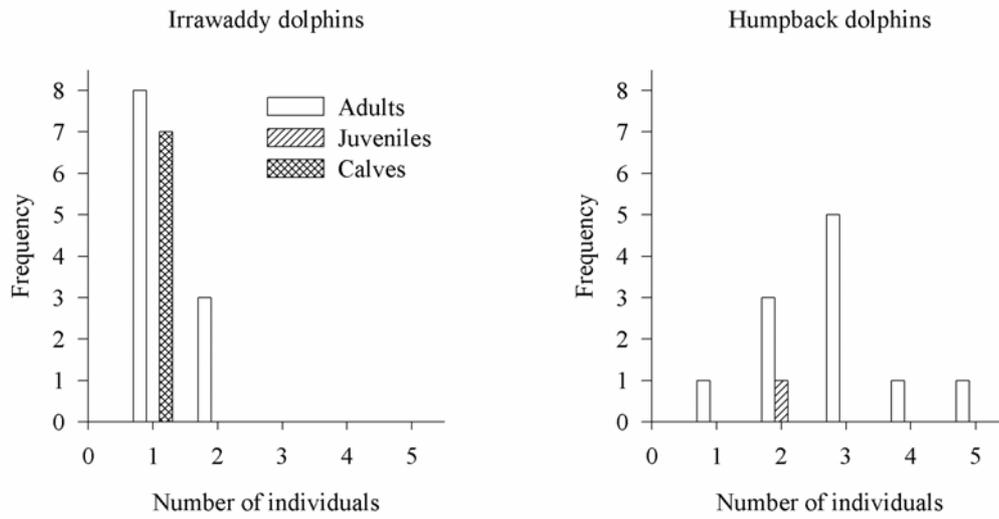
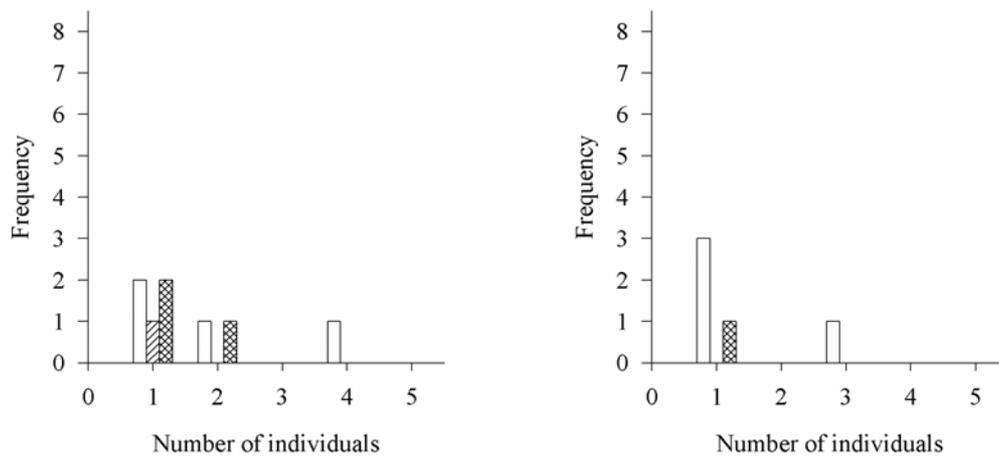


Figure 9.4 Frequency distribution of the number of Irrawaddy and humpback dolphins seen during a) aggressive-sexual, b) affiliative and c) foraging interactions.

a) Aggressive-sexual



b) Affiliative



c) Forage

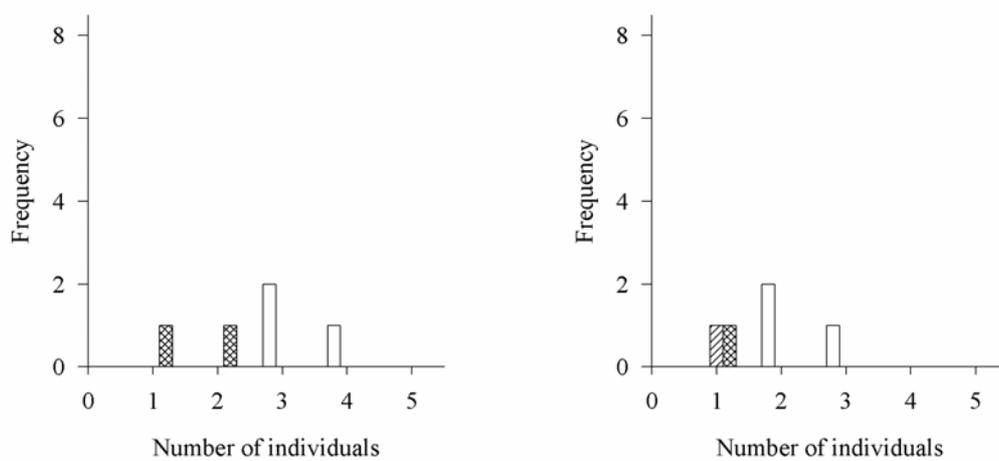


Figure 9.5 Frequency distribution of the number of adults, juveniles and calves of Irrawaddy and humpback dolphins seen during a) aggressive-sexual, b) affiliative, and c) foraging interactions.

During all the aggressive-sexual interactions observed, humpback dolphins were the ones initiating, chasing, and seeking physical contact with Irrawaddy dolphins, while the latter tried to swim away or resist the interaction using the rostrum, head or side of body against humpback dolphins. Irrawaddy dolphins were never observed to help conspecifics involved in aggressive/sexual interactions.

Affiliative interactions involved one to seven Irrawaddy dolphins and one to three humpback dolphins (Fig. 9.4). Irrawaddy dolphins engaging in affiliative interactions were mainly adults with calves, while humpback dolphins were mostly adults (Fig. 9.5). I could determine the sex of only some of the animals involved in affiliative interactions on only two occasions: 1) two male humpback dolphins and one female Irrawaddy dolphin and its calf, and 2) one female Irrawaddy dolphins and its calf, and one female humpback dolphins and its calf.

Foraging interactions consisted of four to five Irrawaddy dolphins and two to five humpback dolphins (Fig. 9.4), including mainly adults of both species (Fig. 9.5). The only avoidance interaction observed involved an adult and a juvenile humpback dolphin approaching three adult Irrawaddy dolphins, with the latter swimming in opposite direction as humpback dolphins got closer than 100m and disappearing.

9.3.3 *Description of interspecific interactions*

In the next section, I provide general descriptions from field-notes and video footage of particular encounters that characterize the most common type of interactions I observed between Irrawaddy and humpback dolphins in the study area.

9.3.3.1 *Aggressive-sexual*

On 23rd of July 2001, five adult humpback dolphins and two Irrawaddy dolphins (adult and calf) were observed interacting between 8:45 AM and 12:35 PM.

From previous encounters and constant association with a calf, the adult Irrawaddy dolphin was known to be a female. Throughout the encounter, four out of the five humpback dolphins, three known to be males, and both of the Irrawaddy dolphins were seen in close physical contact, swimming together in a tight formation with Irrawaddy dolphins in the middle and humpback dolphins flanking them side by side (Fig. 9.6a). Animals showed no consistent direction of movement, and none of the individuals made dives longer than 2 minutes. During the encounter, all four humpback dolphins charged the Irrawaddy dolphin calf several times, lifting it in part out of the water and pushing it away from the adult female (Fig 9.6b). Fresh tooth scars were seen on the right side of the calf behind its head as a result of this interaction. The female Irrawaddy dolphin was seen repeatedly pushing the calf out of the way of humpback dolphins and in head collisions with the latter during these intense physical interactions. These physical contact bouts lasted less than a minute and were often followed by Irrawaddy dolphins swimming away from humpback dolphins and changing direction of movement with humpback dolphins chasing and flanking both Irrawaddy dolphins as they try to swim away. After approximately 40 minutes into the interaction, all four humpback dolphins were seen various times submerging and positioning themselves upside down belly to belly with the female Irrawaddy dolphin swimming slowly at the surface (Fig. 9.6c). Animals continued this type of behaviour with bouts of intensive physical interaction followed by slow travel in tight formation with the humpback dolphins swimming belly to belly for the rest of the encounter. Animals were lost at 12:35 PM due to bad weather.

a)



b)



c)



Figure 9.6 Photographs of aggressive-sexual interaction observed on 23rd of May 2001: a) Adult and calf Irrawaddy dolphin swimming in a tight formation with adult humpback dolphins b) Irrawaddy dolphin calf lifted partly out of the water by one of the humpback dolphins, while another humpback dolphin circles it; c) adult and calf Irrawaddy dolphin at surface with a humpback dolphin swimming underwater belly to belly with adult Irrawaddy dolphin.

9.3.3.2 *Affiliative*

On 23rd of August 2002, between 9:43 AM and 10:03 AM, a school of nine Irrawaddy dolphins composed of seven adults and two calves were seen in close spatial cohesion with an adult humpback dolphin and calf. Both species were swimming in the same direction keeping an approximate distance of 50-100 meters. About two minutes into the encounter, the two humpback dolphins (female and calf) approached an Irrawaddy dolphin adult female and calf and swam synchronously side by side (within a body length apart) in a constant direction with no physical contact and staying mainly at the surface. The rest of the Irrawaddy dolphins kept swimming in the same direction but further apart from the latter four animals. From previous photo-identification and their constant association with calves, I knew both adults involved were females. Soon after 10:03 AM the humpback dolphins were lost while the Irrawaddy dolphins kept travelling in the same direction.

9.4 Discussion

Behavioural interactions between wild Irrawaddy and Indo-Pacific humpback dolphins had never been observed prior to this study. My observations indicate that in Cleveland Bay, where both species coexist, interactions occur on a regular basis. While some encounters appear to be neutral, with Irrawaddy and humpback dolphins foraging or travelling together, most observations involved interspecific aggression and sexual interactions.

Previous observations of captive animals suggested that humpback dolphins are dominant and behave aggressively towards Irrawaddy dolphins (Stacey and Leatherwood 1997). The asymmetric and frequent aggressive/sexual interactions observed in this study correspond with this pattern. During these interactions humpback dolphins behaved aggressively towards Irrawaddy dolphins, while

Irrawaddy dolphins appeared submissive, making every effort to escape from humpback dolphins.

Aggressive/sexual behaviour has been observed on numerous occasions among dolphin species; however the reasons behind these interactions remain unclear. In the Bahamas, encounters between Atlantic spotted dolphins (*Stenella frontalis*) and bottlenose dolphins (*Tursiops truncatus*) are characterized mainly by affiliative and aggressive/sexual interactions (Herzing and Johnson 1997, Herzing et al. 2003). Aggressive/sexual interactions between these species generally involve aggressive displays followed by interspecific copulations between adult and juvenile males of both species (Herzing and Johnson 1997, Herzing et al. 2003). Similar interactions have been observed between adult male spotted dolphins (*Stenella attenuata*) and spinner dolphins (*Stenella longirostris*) of unknown sex off Oahu, Hawaii (Psarakos et al. 2003). Herzing (1997) suggested that participation in these interactions may serve as a mechanism by which males of both species build strong bonds resulting in interspecies coalitions. These interspecies coalitions appear to play an important role in agonistic aid among both species during other interspecific encounters. During the four years of study in Cleveland Bay, no interspecific aid was observed during agonistic interactions. In addition, the sex of animals involved in aggressive sexual interactions also differed from those observed in the Bahamas. Thus, it seems interactions between Irrawaddy humpback dolphins may serve other functions.

On the occasions where sex of animals was known, aggressive/sexual interactions between Irrawaddy and humpback dolphins in Cleveland Bay were directional from adult male humpback dolphins towards female Irrawaddy dolphins accompanied by their calves. During these interactions the aggressive displays observed from humpbacks toward the Irrawaddy dolphins calves resemble the

interactions observed between bottlenose dolphins (*T. truncatus*) and harbour porpoises (*Phocoena phocoena*) in the Moray Firth, Scotland (Ross and Wilson 1996). These violent events appear to serve a skill-developing function where bottlenose dolphins learn and practice skills involved in infanticidal attacks of conspecifics (Patterson et al. 1998). Although the killing of immature humpback dolphins by conspecifics has not been observed, socializing interactions between male humpback dolphins and females with calves involve similar aggressive displays towards calves followed by sexual interactions with the females (personal observations).

Intraspecific infanticide inflicted by males or females occurs in a wide variety of mammals and is considered an adaptive behavioural strategy to enhance the reproductive success of the perpetrator (Agrell et al. 1998, Ebensperger 1998). Infanticide inflicted by males is thought to increase access to breeding females. For example, in a pride of African lions (*Panthera leo*) that has been overtaken by a new band of males, females whose cubs have been killed become sexually receptive sooner than if their cubs had survived and tended to mate with most of the new males (Packer and Pusey 1983a, b). Studies on mating strategies of bottlenose dolphins indicate that females become attractive to males within one to two weeks of losing their calves (Connor et al. 1996). Thus aggressive/sexual interactions between Irrawaddy and humpback dolphins may serve a physical training or skill development function that would have beneficial effects for male humpback dolphins during interactions with female conspecifics. Since there is no evidence for infanticide in humpback dolphins, testing these hypotheses will depend on further collection of behavioural data including age and sex of animals involved in such interactions within and among species.

Alternatively, aggressive/sexual interactions may form a mechanistic basis for some competitive interactions and patterns of resource partitioning between these two species of coastal dolphins. Interspecific aggression can mediate patterns of space use among coexisting species and is expected when closely related species occur in sympatry (Robinson and Terborgh 1995, Garcia and Arroyo 2002). In species with great spatial overlap interspecific aggression may confer the dominant species priority of access to highest quality resources (Robinson and Terborgh 1995, Martin and Martin 2001a), restrict species with lower competitive ability to “competition refuges” (Durant 1998) , or result in the gradual displacement or exclusion of the weaker competitor (i.e., interference competition) (Tannerfeldt et al. 2002).

Irrawaddy and humpback dolphins are present year round in Cleveland Bay and their spatial distribution and ranges overlap considerably (see Chapter 5). Most of the interactions observed occurred in areas known to be used heavily by both species for foraging activities (i.e., Townsville Port and Black River mouth; see Chapter 5). Thus, it is clear that both species have a high chance of encountering each other in Cleveland Bay and interactions may reflect competition for space or food. Despite similarities in their occurrence and space use patterns, there are slight differences in their habitat preferences. As discussed in Chapter 5, Irrawaddy dolphins prefer shallower waters with seagrass meadows, and waters closer to river mouths than humpback dolphins. These differences in habitat selection may partly be a result of the aggressive/sexual encounters between both species. It is possible then that Irrawaddy dolphins use shallower water areas close to river mouths as “competition refuges” (Durant 1998) to avoid encounters with dominant humpback dolphins. This would support the statement by Kamminga (Kamminga et al. 1983) that Irrawaddy dolphins are forced into inshore waters by more specialized dolphins. In this context,

the key to the coexistence of both of these species might rely on the spatial heterogeneity of the coastal ecosystem. If habitat selection is the result of aggressive interactions with humpback dolphins, Irrawaddy dolphins in allopatric situations should expand their preferences to include deeper habitats in coastal waters. Studies of habitat use in allopatric populations of both species are needed to test this hypothesis.

Evidence of interspecific mating has been recorded among captive (Sylvestre and Tasaka 1985, Zornetzer and Duffield 2003) and wild odontocetes (Reyes 1996, Baird et al. 1998, Yazdi 2002, Willis et al. 2004). Interspecific mating can arise as a result of ecological or behavioural factors leading to a decrease in conspecific mates (Dowling and Secor 1997, Wirtz 1999). For example, it has been suggested that the natural hybridization between harbour porpoises and Dall's porpoises in Haro Strait is a result of the apparent decline in local harbour porpoise numbers (Willis et al. 2004). In Cleveland Bay, abundance estimates of both species for 2000, 2001, and 2002 indicate that Irrawaddy dolphins are slightly more abundant than humpback dolphins (see Chapter 8). It is possible that the aggressive/sexual interactions observed here reflect an indiscriminate pursuit of female Irrawaddy dolphins by male humpback dolphins, merely because of their lower encounter rate with conspecific mates.

Studies on interference interactions among terrestrial mammalian carnivores and birds have demonstrated that these interactions can have important effects on individual fitness, and population demography (Linnell and Strand 2000, Martin and Martin 2001b). We do not yet know enough about Irrawaddy and humpback dolphins to provide a full list of hypotheses explaining possible adaptive or non-adaptive reasons behind the interactions observed and if they are actually having an effect of the fitness of individuals involved or demography of populations. Additionally, the

variation in the type of interactions recorded adds to the complexity of the possible ecological and demographic processes that might be involved. However, this study adds to the growing evidence that interspecific interactions among sympatric delphinids are common and complex and thus may play an important role in the structure and functioning of coexisting communities. The challenge for future research will be to go beyond recording these interactions, and to determine whether they actually reflect specific ecological interactions (e.g., interspecific competition) and the context of their consequences to individuals and populations.

9.5 Chapter summary

- Interspecific interactions among cetaceans are common and complex. However, studies of sympatric communities of cetaceans and the type of interactions that take place between them are limited.
- In this chapter, I describe the behavioural interactions observed between Irrawaddy and humpback dolphins between January 1999 and October 2002 in Cleveland Bay, northeast Queensland, Australia.
- Interspecific interactions were observed across the four years of study and were mainly of aggressive-sexual nature (53%), followed by affiliative (21%) activities, foraging (16%), and avoidance (5%) (Fig. 9.3).
- During all the aggressive/sexual interactions humpback dolphins were the dominant species in initiating chasing, and seeking physical contact with Irrawaddy dolphins, while the latter tried to swim away or showed resistance to the interaction by using its rostrum, head or side of body against the perpetrator(s). The individuals involved in aggressive/sexual interactions appear to be mainly adult-male humpback dolphins and adult-female Irrawaddy dolphins with calves.

- The predominant aggressive/sexual interactions observed may reflect : 1) a physical training or skill development function that would have beneficial effects for future interactions between male humpback dolphins and their female conspecifics; 2) a mechanistic basis for some competitive interactions and patterns of resource partitioning between these two coastal dolphins; and 3) a relative scarcity of female humpback dolphins.
- Although the motives behind these interactions are not yet clear, this study adds to the growing evidence that interspecific interactions among sympatric delphinids are common and complex and thus may play an important role in the structure and functioning of coexisting communities.

Table 9.1 Differences in size and age composition of schools of Irrawaddy and humpback dolphins when they were first sighted interacting (i.e., member(s) of each species within 100 meters). Significant P-values are indicated in bold italics.

School Size	Irrawaddy	Humpback	Difference	95% CI of difference	<i>P</i>
Mean	6.2	3.8	2.4	0.42-5.07	0.062
SE	1.19	0.39			
Median	5	4			
Mode	2	5			
Range	1-21	1-7			
School composition					
Adults					
Mean	4.7	3.0	1.7	0.21-3.74	0.083
SE	0.90	0.29			
Median	4	3			
Mode	1	3			
Range	1-16	1-5			
Juveniles					
Mean	0.2	0.5	-0.3	-0.63-0.00	0.376
SE	0.16	0.16			
Median	0.0	0.0			
Mode	0.0	0.0			
Range	0-3	0-2			
Calves					
Mean	1.2	0.4	0.8	0.16-1.63	0.033
SE	0.3	0.1			
Median	1.0	0			
Mode	0.0	0			
Range	0-5	0-2			

Chapter 10

General discussion and synthesis

In this chapter, I provide a summary of the major results of this study and discuss these results in relation to their contribution to the conservation and management of Irrawaddy and Indo-Pacific humpback dolphins. I discuss how my results have contributed towards the understanding of Irrawaddy and Indo-Pacific humpback dolphins' coexistence, and outline and prioritize future research directions for the management of Irrawaddy and Indo-Pacific humpback dolphins.

Chapter 10. General discussion and synthesis

10.1 Introduction

As explained in Chapter 1, some species of coastal dolphins are among the most threatened cetaceans (Thompson et al. 2000, DeMaster et al. 2001). Despite these concerns, our lack of knowledge about their biology and behavioural ecology has limited our ability to effectively conserve and manage most wild populations. Irrawaddy and Indo-Pacific humpback dolphins (hereafter referred to as humpback dolphins) are two of the least known and most threatened dolphin species inhabiting coastal waters of the Indian and west Pacific Ocean region. Prior to this study very little was known about these two species in Australian waters and there was an urgent need for ecological studies (Chapter 2, Parra et al. 2002, Parra et al. 2004). This study has greatly improved our knowledge of the behavioural ecology of Irrawaddy and humpback dolphins and should serve as a basis for their conservation and management in Australian waters.

My thesis has also contributed towards an understanding of the mechanisms underlying the coexistence of sympatric coastal dolphin communities. Many species of coastal and oceanic dolphins live in sympatry; however ecological studies have mainly focused on single species. As a result, little is known about how coexisting delphinids partition resources or of the underlying mechanisms explaining this process. The loss of upper predators can have profound effects on the structure and functioning of marine (Estes et al. 1998, Jackson et al. 2001) and terrestrial ecosystems (Estes 1996, Linnell and Strand 2000). Thus understanding the patterns and processes of coexistence among predators is fundamental to the effective conservation of biodiversity.

My contribution to the knowledge of these two species is summarized and synthesised below. First, I summarize the major results obtained under each of the objectives specified in the introduction of this thesis. Second, I discuss the implications of my results for the conservation and management of Irrawaddy and humpback dolphins. Third, I explain how my results contribute towards our understanding of their coexistence. Finally, I outline directions for future research that should: 1) improve our knowledge of the behavioural ecology of both species, 2) enhance our ability to assess the impact of human activities on local populations, and 3) elucidate some of the underlying ecological processes structuring dolphin communities.

10.2 Major results of this study

10.2.1 Objective 1. Review the current state of knowledge of Irrawaddy and humpback dolphins in Australian waters (Chapter 2)

I reviewed the distribution, population status, and conservation threats of Irrawaddy and humpback dolphins in Australian waters. Data from stranding databases, museums, and unpublished sightings by wildlife agencies and aerial surveys showed that Irrawaddy and humpback dolphins are widely distributed along coastal waters of Queensland, Northern Territory and Western Australia. Irrawaddy dolphins were recorded from approximately the Brisbane River (27° 32'S, 152° 49'E) on the east coast of Queensland to Broome (17° 57'S, 122° 14'E) on the west coast. Humpback dolphins occurred from approximately the Queensland - New South Wales border (31° 27'S, 152° 55'E) to Ningaloo Reef (22° 17'S, 113° 48'E) in Western Australia.

Both species are commonly observed close to the coast in sheltered, shallow estuarine waters. Because of their coastal distribution, the major threats to Irrawaddy

and humpback dolphins in Australian waters are: 1) entanglement in gillnets set in shallow waters for fishing purposes; 2) entanglement in shark nets set for bather protection; 3) habitat degradation and loss due to coastal zone development, pollution, boat traffic, and overfishing of prey resources; and 4) ineffective management measures to alleviate 1-3.

The status of populations of Irrawaddy and humpback dolphins in Australian waters is unknown because of the poor to non-existent information on their distribution, abundance, and levels of anthropogenic mortality. However, the information available from the few studies throughout their geographical range indicates that both species occur in discrete, geographically localized populations and are susceptible to anthropogenic threats. My review concluded that information on the behavioural ecology of both of these species in Australian waters is urgently needed in order to improve conservation and management efforts.

10.2.2 Objective 2. Investigate the spatial distribution patterns of Irrawaddy and humpback dolphins in northeast Queensland (Chapter 3)

Data on the spatial distribution of Irrawaddy and humpback dolphins were obtained in October-November 2001, during vessel-based line transect surveys in the Far Northern Section and Central Section of the Great Barrier Reef Marine Park, northeast Queensland. I used Geographic Information Systems (GIS), randomization tests and a suite of spatial analysis techniques to examine the relationships between the spatial distribution of Irrawaddy and humpback dolphins, and three simple, readily quantified, environmental variables: distance to land, distance to river mouths, and water depth.

At both study sites, Irrawaddy and humpback dolphins were sighted mostly in waters less than 15 m deep that were within 10 km of the coast and within 20 km from

the nearest river mouth. Randomization tests indicated that the distribution of Irrawaddy and humpback dolphins in both study areas was strongly influenced by proximity to the coast. Proximity to river mouths and water depth also appeared to influence the spatial distribution of both species, with Irrawaddy dolphins occurring closer to river mouths and in shallower water than humpback dolphins. However, this pattern was not consistent across study areas. Results from Mantel tests suggested that all environmental data had a patterning effect on the spatial distribution of both species in the Far Northern Section study area, while in the Central Section distance to land and distance to rivers emerged as the most important variables affecting their spatial distribution.

The resultant information identified relationships between the dolphins and environmental features that can be used to develop spatially-explicit conservation and management strategies. The conservation utility of this approach was illustrated by comparing the distribution patterns observed for both dolphin species and the current zoning of the Great Barrier Reef Marine Park for the areas surveyed. I showed that, despite the huge area closed to extractive industries throughout the Great Barrier Reef Marine Park (33% of 344,400 km²) under the current zoning, Irrawaddy and humpback dolphin populations in the study areas surveyed are still under threat from netting activities, as much of the coastal waters where the animals occurred are not protected.

10.2.3 Objective 3. Investigate the occurrence patterns and school dynamics of Irrawaddy and humpback dolphins in Cleveland Bay (Chapter 4)

I conducted boat-based surveys between 1999-2002 in Cleveland Bay, northeast Queensland, to assess the patterns of occurrence, school size, and school age

composition of Irrawaddy and humpback dolphins. Both species were present year-round in Cleveland Bay and their occurrence did not vary with year or season.

Irrawaddy and humpback dolphins used the study area mainly for foraging and travelling activities. These findings emphasize the importance of Cleveland Bay as a feeding area for local populations of Irrawaddy and humpback dolphins.

I found that overall, schools of Irrawaddy dolphins were larger in size than those of humpback dolphins, and were composed of a larger number of adults and calves. The mean size of the schools of Irrawaddy dolphins did not change with behavioural activity, whereas the school size of humpback dolphins varied significantly with behaviour. Schools of humpback dolphins engaged in socializing activities had considerably more members than schools that were foraging, foraging behind trawlers, or travelling. Additionally, schools foraging behind trawlers were larger than schools foraging independently of trawlers, or travelling. Interspecific differences in school size and age composition may be a result of their different evolutionary history, habitat preferences and/or social structure.

10.2.4 Objective 4. Determine the space use patterns and habitat preferences of Irrawaddy and humpback dolphins in Cleveland Bay (Chapter 5).

Little is known about the spatial dynamics and habitat preferences of many species of coastal dolphins. I used the data collected during boat-based surveys in Cleveland Bay in combination with a Geographic Information System, kernel range estimators and distance based approaches to investigate the space use patterns, spatial overlap, and habitat preferences of Irrawaddy and humpback dolphins. The results indicated that dolphins of both species made preferential use of certain areas within

the study area. Core areas (50% kernel range) were located close to river mouths and the Port of Townsville.

The predominant behavioural activities of both species within and outside their core areas were foraging and travelling. The behaviour of Irrawaddy dolphins did not show any variation according to time and location (i.e., inside or outside core area). In contrast, humpback dolphins foraged mainly inside the core area in the early morning hours (i.e., 06:00-08:00), while later in the morning (i.e., 08:00-10:00) foraging activities shifted to locations outside the core area. Foraging behind trawlers, an activity recorded only for humpback dolphins, occurred mainly inside their core area around the Port of Townsville.

The representative ranges (95% kernel range) of Irrawaddy and humpback dolphins overlapped considerably, with shared areas used heavily and similarly by both species. Despite the high spatial overlap and concordance in space use patterns of both species, there were significant differences in their habitat preferences. Within their representative range, Irrawaddy dolphins preferred shallow (0-2 m) waters with seagrass meadows, and occurred closer to river mouths than humpback dolphins. Humpback dolphins showed preference for deeper water (2-5 m), followed by shallow water with no seagrass and dredge channels. These differences in habitat preferences appear to be one of the principal factors promoting the coexistence of Irrawaddy and humpback dolphins.

10.2.5 Objective 5. Assess the site fidelity and ranging patterns of Irrawaddy and humpback dolphins in Cleveland Bay (Chapter 6).

During boat-based surveys in Cleveland Bay, I used photo-identification techniques to identify individual dolphins (63 Irrawaddy dolphins and 54 humpback dolphins) from marks on their dorsal fins. I used these data to assess their site fidelity

and ranging patterns. Photo-identification does not allow continuous tracking of individual animals, thus the sighting rates, standard distance deviations, residence times, and range sizes and length presented here for both species are minimum estimates.

Analysis of monthly and annual sighting rates and standard distance deviations indicated that most animals were not permanent residents in the study area, but most use it from year to year, coming back to specific locations. Sighting patterns of identified individuals followed a model of emigration and reimmigration. Individuals of both species appeared to spend periods of days to a month or more inside the study area before leaving, and periods of over a month outside the study area before re-entering.

The ranging patterns of both species, as indicated by minimum convex polygons (MCP), were similar in size, length and location. Area observation curves of MCP ranges indicated a larger number of sightings are needed to estimate the actual range size of both species. However, it is clear from their MCP ranges that individuals of both species commonly used and moved between regions southeast and northwest of the Port of Townsville. The high degree of interspecific overlap in ranging patterns indicated a lack of species-specific territories. I suggest site fidelity and ranging patterns within the study area reflect fluctuations in prey resource availability and levels of predation risk within Cleveland Bay.

10.2.6 Objective 6. Investigate the social structure of Irrawaddy and humpback dolphins (Chapter 7)

The standard deviation of the observed association indices among individuals of both species were significantly higher than those expected under a random scenario indicating that individuals of both species showed preference in their associations.

Dendrograms of association matrices revealed that individual Irrawaddy dolphins formed strong associations with more than one individual, while strong associations between humpback dolphins appeared to be limited to pairs of animals. Association patterns among the few animals of known gender suggest that female Irrawaddy dolphins formed strong associations with other females, and male humpback dolphins formed strong bonds with other males.

Analysis of the temporal variability of associations between pairs of individuals showed that the social structure of Irrawaddy dolphins is based on long-lasting associations. An individual Irrawaddy dolphin was estimated to have five constant companions at any time. Associations between individual humpback dolphins appeared to be more fluid and dynamic involving different types of associates with variable temporal patterns. Nonetheless, long-term bonds between individual members did occur among humpback dolphins.

The social structure of these two sympatric coastal delphinids is consistent with their postulated phylogenetic relationships within the family Delphinidae. The stable social organization of Irrawaddy dolphins is similar to that of the killer whale, to which they appear to be closely related. Similarly, humpback dolphins are closely related to several delphinids with fluid social structures.

Interspecific differences in the social structure of Irrawaddy and humpback dolphins are also likely to reflect social and ecological constraints. Future studies involving assessment of predation risk, food availability, and genetic sampling of photo-identified individuals will be fundamental towards resolving the relative importance that ecological and social factors might play in the social structure of both of these species.

10.2.7 Objective 7. Estimate the population size of Irrawaddy and humpback dolphins inhabiting Cleveland Bay (Chapter 8)

Based on the open population model that best fitted the data, I estimated that less than a hundred individuals of each dolphin species used Cleveland Bay between 1999 and 2002. A power analysis indicated that increases or declines in abundance would be extremely difficult to detect within the space of a few years unless annual declines in population size are worryingly high (> 20% p.a.) or survey intensity is increased. The low population numbers and our inability to detect trends reliably indicate that conservation actions towards Irrawaddy and humpback dolphins should not rely on field data indicating population change. Given their apparent small populations and likely status as species endemic to Australian/Papua New Guinean waters, conservation measures to ensure the long-term survival of Irrawaddy and humpback dolphins in Australian waters are needed urgently.

10.2.8 Objective 8. Describe behavioural interspecific interactions that may occur between Irrawaddy and humpback dolphins (Chapter 9)

I observed a total of 19 interactions between Irrawaddy and humpback dolphins in Cleveland Bay. These interspecific interactions were mainly of aggressive-sexual nature (53%), followed by affiliative activities (21%), foraging (16%), and avoidance (5%). During aggressive-sexual interactions, humpback dolphins were dominant in initiating chasing, and seeking physical contact with Irrawaddy dolphins, while the latter tried to swim away or showed resistance to interaction by using their rostrum, head or side of body against perpetrator(s). Individuals engaging in aggressive-sexual interactions appeared to be mainly adult-male humpback dolphins and adult-female Irrawaddy dolphins with calves.

The predominant aggressive/sexual interactions I observed may reflect: 1) a physical training or skill development function that has beneficial effects for male humpback dolphin interactions with female conspecifics; 2) a mechanistic basis for some competitive interactions and patterns of resource partitioning; and 3) scarcity of humpback dolphins female conspecifics. This study adds to the growing evidence that interspecific interactions among sympatric delphinids are common and complex and thus may play an important role in the structure and functioning of coexisting communities.

10.3 Implications for the conservation of Irrawaddy and humpback dolphins

One of the major aims of this study was to provide information necessary to improve our ability to conserve and manage Australian populations of Irrawaddy and humpback dolphins. Recent morphological and molecular studies suggest that Australian/Papua New Guinea populations of Irrawaddy and humpback dolphins may represent different species/subspecies from populations elsewhere (Beasley et al. 2002a, Rosenbaum et al. 2003). Consequently, Irrawaddy and humpback dolphins have extremely high biodiversity value, as they are likely to be the only endemic species/subspecies of dolphins found in Australian/Papua New Guinean waters. This taxonomic change will necessitate reconsideration of their status by the IUCN and under Australian Commonwealth and State laws. In this context, the results from this study are of particular importance as they have provided information on the dolphins' distribution, abundance, habitat preferences, and movement patterns that has the potential to improve our ability to conserve and manage local populations of Irrawaddy and humpback dolphins. Based on my results, I discuss below some of the issues and challenges inherent in the development of future conservation and

management strategies, and the implications of these results for the conservation of Irrawaddy and humpback dolphins.

10.3.1 Conservation of coastal-estuarine ecosystems and the need for behavioural ecology studies

It is clear from this study and others elsewhere (Stacey and Arnold 1999, Jefferson and Karczmarski 2001) that coastal and estuarine waters are important habitats for Irrawaddy and humpback dolphins. Furthermore, populations of both species in these coastal estuarine habitats appear to be relatively small (see Chapter 8). Small populations are more prone to extinction than large populations because of loss of genetic variability and environmental and demographic stochasticity (Caughley and Gunn 1996). Consequently, the loss of even a small number of individuals can have serious detrimental effects in such populations. Thus, it is apparent that the maintenance of high quality habitats along the coastal zone (i.e., habitats with high densities of dolphins, and where survival and reproduction rates are high) will play a key role in the conservation and long-term survival of Irrawaddy and humpback dolphins. The identification of high quality habitats for Irrawaddy and humpback dolphins will be dependant on studies of their behaviour and ecology at local and regional levels. Maintenance of habitat quality will depend on the reduction of direct (e.g., gillnetting) and indirect (e.g., pollution) anthropogenic threats to populations within these areas.

10.3.1.1 Conservation prospects for Irrawaddy and humpback dolphins along the Queensland Coast

The potential for the conservation and management of Irrawaddy and humpback dolphin populations along the Queensland coast is relatively good. The

Great Barrier Reef Marine Park (GBRMP) along the east coast of Queensland covers approximately 42% (4,312 km) of Queensland's total coastline (10,343 km)

(Fig.10.1).

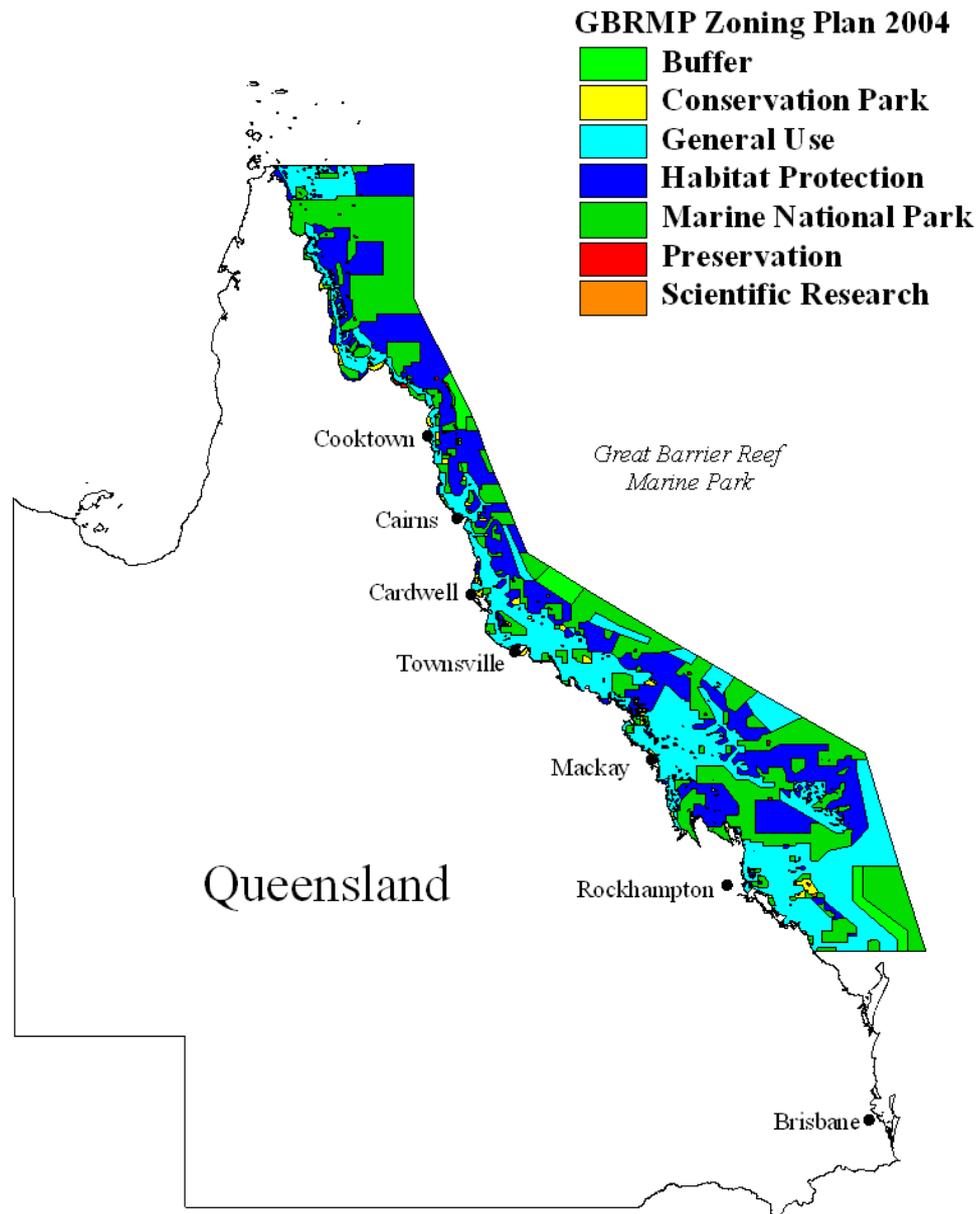


Figure 10.1 Map of the Great Barrier Reef Marine Park (GBRMP, 344,400 km²) zoning plan as of July 2004.

The current zoning of the GBRMP offers different levels of protection for marine species ranging from areas designated as “General Use” where most anthropogenic activities are allowed except for oil drilling and mining to “Preservation Zones” where most anthropogenic activities are banned (Fig. 10.1). In addition to these areas there are: 1) the Great Barrier Reef Coast Marine Park (GBRCMP) which extends the Great Barrier Reef Marine Park zoning from low water to high water or to the seaward edge of the mangrove forests; 2) Dugong Protected Areas (DPA) where netting activities are restricted (DPA Type A, activities prohibited: offshore set, foreshore set and drift nets. River set nets allowed, with modification (prohibited in Hinchinbrook and Shoalwater Bay). or less heavily restricted (DPA Type B), and 3) Areas A, B And C within the Special Management Area of Princess Charlotte Bay (PCB) which offer different restrictions to netting activities. Because of their coastal distribution and habitat preferences (see Chapters 3 and 5), the protection afforded to coastal waters within 10 km of the shore is relevant to Irrawaddy and humpback dolphins.

To estimate the level of protection offered to areas that are potentially suitable habitat for Irrawaddy and humpback dolphins (i.e., coastal waters within 10 km of the shore), I used a digital map prepared by my colleague Alana Grech that provides spatial data on different activities throughout the GBRMP. As discussed in Chapter 2, I considered boating activities, catchment run-off, netting, and trawling activities as potentially threatening to Irrawaddy and humpback dolphins and their habitats. I also assumed each activity carries the same threat pressure to the dolphins.

Information on the number of registered recreational boats in the GBR was obtained from Queensland Transport. This information was divided into regions and interpolated out from the coast to a distance of 15 km (Sutton, pers comm.).

According to the number of boats per region I defined four categories of risk: 1) low risk (between 1-300 boats), 2) medium risk (300-1000 boats), 3) medium-high risk (1000-3000 boats) and 4) high risk (>3000 boats). The risk assessment for catchment run-off followed the format given by the Water Quality and Action Plan, Nov 2001 (Great Barrier Reef Marine Park Authority 2001): 1) low risk, 2) medium risk, 3) medium-high risk, and 4) high risk. Risk rankings for each catchment were based on: 1) the relative increase of sediment export from 1850 to the present, and 2) increases in agricultural activity in land adjacent to catchments (Great Barrier Reef Marine Park Authority 2001). Catchment risk was interpolated out from the coast to the edge of the GBRMP. According to management regimes in each zone within the GBRMP, netting pressure was divided into five categories: (1) netting prohibited or highly restricted (Preservation, Marine National Park, Conservation Park, Buffer, Scientific Research (GBRMP), Scientific Research, Marine National Park B, Buffer, Preservation (GBRCMP)), (2) level 1 restrictions (DPA A and PCB Area A), (3) level 2 restrictions (PCB Area B), (4) level 3 restrictions (DPA B and PCB Area C) and (5) limited restrictions to netting (General Use, Habitat Protection (GBRMP), General Use A, General Use B, Marine National Park A, Estuarine Conservation, Conservation Park, Habitat Protection (GBRCMP)).

I considered areas of high level of protection those where: 1) boating activity was of low risk; 2) catchments had a low risk of discharging poor quality water 3) netting was not permitted or strongly restricted (up and including level 2 restrictions); and 4) trawling was prohibited. Given these restrictions, I estimated that approximately 14% (3,604 km²) of the potential habitat for Irrawaddy and humpback dolphins (25,605 km²) within the GBRMP is highly protected (Fig. 10.2). All of these

highly protected areas are located in very remote sites, north of the urban coast of Queensland.

This information indicates that a moderate proportion of the potential habitat of Irrawaddy and humpback dolphins is well protected within the GBRMP. However, the actual level of protection offered by these areas to populations of both species is unknown. The reason for this uncertainty is that we lack comprehensive data on the occurrence, distribution, abundance, and habitat use of Irrawaddy and humpback dolphins for almost all areas along the Queensland coast. The same situation extends to the whole range of both species in Australian waters. This result emphasizes the need for studies on the distribution and relative abundance of these two species, as these will provide some of the information that is necessary for their conservation and management. We need to establish where along the northern tropical waters of Australia these two species occur in high densities (i.e., hotspots) and provide high levels of protection to these areas and surrounding waters. These studies will be particularly important near urban areas where anthropogenic impacts are likely to be high, and where populations are already under increasing threats.

Public education and community involvement are a key component in any type of conservation program. Increasing public awareness about the biology, importance and conservation issues and threats faced by Irrawaddy and humpback dolphins will play a key role in their conservation, particularly in areas where hotspots are close to urban areas (e.g., Cleveland Bay, Hinchinbrook Island).

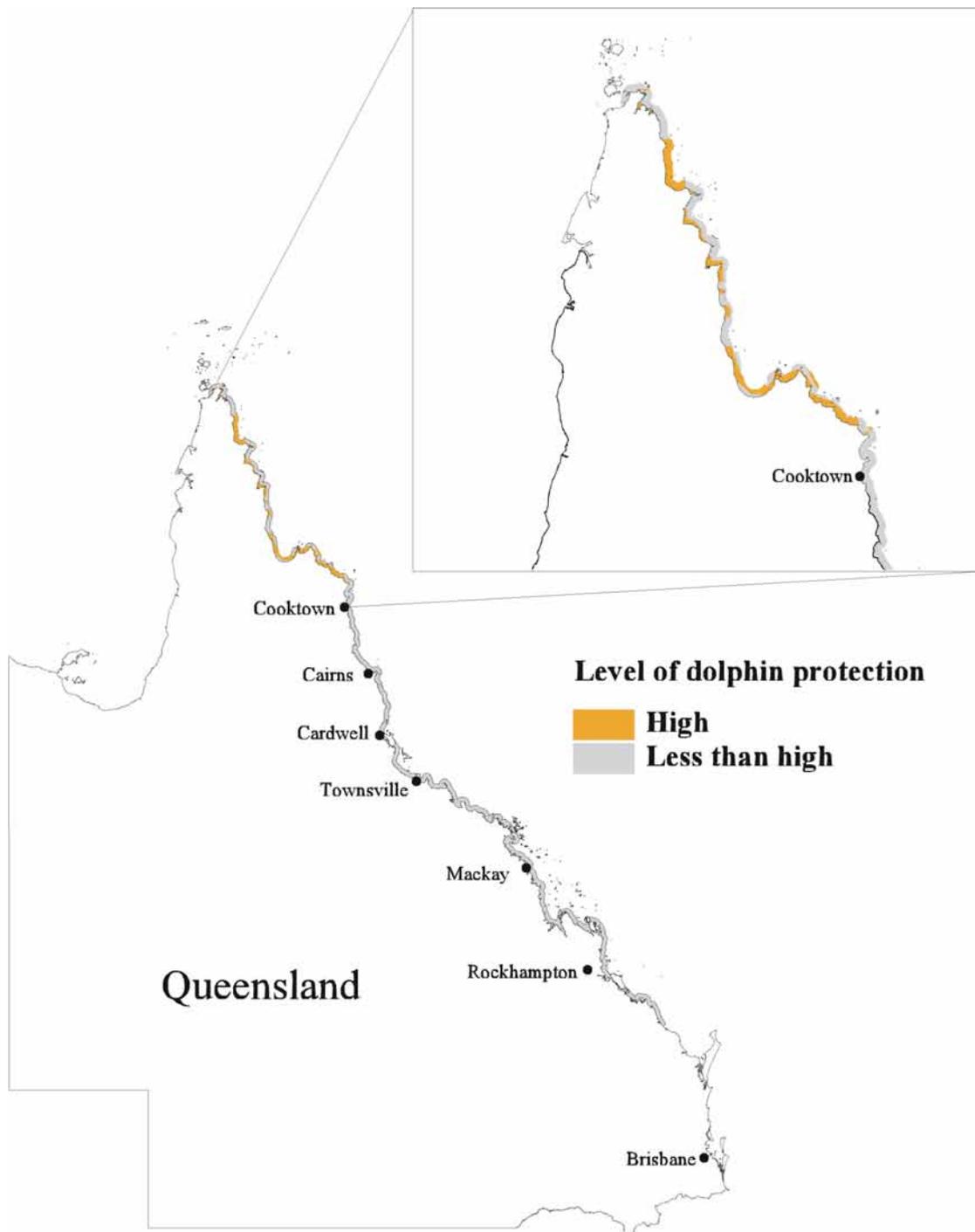


Figure 10.2 Level of protection offered to areas of potential habitat of Irrawaddy and humpback dolphins within the Great Barrier Reef Marine Park. Areas of potential habitat were defined as coastal waters within 10 km from the nearest coastline. I considered areas of high level of protection those where: 1) boating activity was of low risk; 2) catchments had a low risk of discharging poor quality water 3) netting was not permitted or strongly restricted (up and including level 2 restrictions); and 4) trawling was prohibited.

10.3.2 Problems faced by Irrawaddy and humpback dolphins along the urban coast of Queensland

Australia is sparsely populated in comparison with more highly populated countries in the Indo-Pacific region. However, increasing development and preference of human settlements for coastal locations, especially in the east, southeast and southwest has become an important issue affecting the sustainability of many of Australia's marine and coastal resources (Zann 1995). Queensland is the fastest growing state in Australia with an annual growth rate of 2.3% and a population of 3.84 million (Queensland Government 2004). The highest levels of population growth are along the urban coast between Cooktown and Brisbane (Fig 10.2) and locations adjacent to these areas (Queensland Government 2004). This concentration and rapid population growth along the east coast of Queensland has put increased pressure on coastal ecosystems (Queensland Environmental Protection Agency 1999)

Several coastal areas along the east coast of Queensland represent potentially important habitats for Irrawaddy and humpback dolphins. Many of these areas are located along the urban coast of Queensland and it is in these areas that reduction of threats will be essential for the conservation of local populations. In this study, I have identified several aspects of the behavioural ecology of Australian Irrawaddy and humpback dolphins that make them particularly vulnerable to human activities. Although they are based primarily on results from Cleveland Bay, near the city of Townsville, they should serve as a basis for conservation and management of Irrawaddy and humpback dolphins in other areas along the Queensland coast pending further studies.

10.3.2.1 Site fidelity and habitat degradation and loss

Species with high levels of site fidelity are vulnerable to population declines as a result of habitat degradation and loss, particularly when those species occupy relatively restricted habitats (Warkentin and Hernandez 1996). Irrawaddy and humpback dolphins in Cleveland Bay showed high levels of site fidelity with most animals returning to the coastal waters of Cleveland Bay from year to year (Chapter 6). Such site fidelity potentially conveys several ecological benefits including reduction in the costs and risks involved in relocating to new sites, and familiarity with resources and predators (Greenwood 1980).

The various habitats within the home range of Irrawaddy and humpback dolphins are unlikely to be of the same quality. Consequently, degradation and loss of coastal habitats can lead to an increase in distance among habitable patches and/or reduction in number of remnant habitats (i.e., habitat fragmentation, Andren 1994). The modification of coastal habitats may cause shifts in prey and predator distribution and abundance, resulting in species regularly using the area not finding suitable habitats and having lower survival probability. For example, a large scale loss of seagrass habitat in Hervey Bay, immediately south of the Great Barrier Reef Marine Park, following a cyclone and two floods resulted in unprecedented deaths and decline of local dugongs (Preen and Marsh 1995). Identification and conservation of coastal habitats along the east coast of Queensland that are regularly used by Irrawaddy and humpback dolphins should be a priority. In the case of Cleveland Bay, it is clear that this area represents an important habitat for both species and efforts to maintain or improve current levels of protection inside and in adjacent areas will play a key role in the persistence of local populations in this area.

10.3.2.2 *High vessel traffic*

In Cleveland Bay, areas highly used by Irrawaddy and humpback dolphins (i.e., the Port of Townsville, river mouths) overlap with areas of high vessel traffic. High vessel traffic in shallow coastal areas can cause serious injuries and mortalities to coastal dolphins (Wells and Scott 1997), reduce their access to particular areas within their home range (Allen and Read 2000), affect their acoustic communication (Van Parijs and Corkeron 2001), and alter their behaviour (Lusseau 2003, Constantine et al. 2004). All of these effects can be potentially detrimental to the small populations of Irrawaddy and humpback dolphins inhabiting Cleveland Bay.

Although the high use of these areas by Irrawaddy and humpback dolphins could be interpreted as evidence that both species have become habituated to vessel traffic in the area, behavioural studies assessing their behavioural response to vessels are needed. The acoustic communication and group cohesion of humpback dolphins is affected by boat traffic and noise (Van Parijs and Corkeron 2001). Post mortem investigation on stranded humpback dolphins in Hong Kong suggests that some deaths may have been caused by boat strikes (Parsons & Jefferson, 2000). Voluntary transit lanes and speed limits set in other areas along the Queensland coast for protection of dugongs have low levels of compliance (Groom 2003). Thus enforced vessel lanes and/or speed restrictions to protect Irrawaddy and humpback dolphins from vessel strike or disturbance should be considered as a precautionary measure in areas of high vessel traffic.

10.3.2.3 *Pathogen pollution*

Recent studies have shown that pathogen pollution may have considerable negative effects on populations of coastal marine mammals (Kreuder et al. 2003). The carcasses of three humpback dolphins recovered in the Townsville region between

2000 and 2001 were infected with *Toxoplasmosis gondii* (Bowater et al. 2003), a terrestrial parasite that can be fatal or have deleterious effects to the health of marine mammals (e.g., infection with *T. gondii* is one of the leading causes of mortality of southern sea otters along the California coast, Kreuder et al. 2003). Given the small number of Irrawaddy and humpback dolphins in Cleveland Bay, the incidence of this pathogen is of serious concern. The introduction of this parasite to the coastal ecosystem appears to be linked to runoff of contaminated water with cat faeces or litter carrying oocyst of *T. gondii* (Miller et al. 2002). Thus controls on the disposal of cat faeces, and improvements of the treatment of stormwater and sewage discharges will be fundamental as a precautionary measure. Monitoring of the incidence of this pathogen in stranded animals and studies on its potential sources are also needed to determine areas of high risks associated with *T. gondii* infection.

10.3.2.4 Gillnets

Entanglements in gillnets and shark nets set for bather protection have long been recognized as a major threat for Irrawaddy and humpback dolphins (Cockcroft 1990, Paterson 1990, Hale 1997). Gillnetting throughout Cleveland Bay is prohibited due to its status as a Dugong Protected Area type A; however the coastal waters of Cleveland Bay DPA do not include the full home range of Irrawaddy and humpback dolphins using this area. Part of the representative ranges I estimated for both species and part of one of the core areas identified for Irrawaddy dolphins lie just outside the northern limit of Cleveland Bay DPA (Chapter 5). In addition, sighting patterns of identified individuals indicate animals spent considerable amounts of time outside this study area (Chapter 6).

The areas adjacent to Cleveland Bay DPA offer different levels of protection from entanglement in gillnets. Bowling Green Bay to the south, is a Dugong Protected

Area Type B, where gillnetting activities are allowed with safeguards and restrictions. However, Halifax Bay to the north, is a “General Use” zone and there are no area-specific regulations regarding netting practices. Thus, entanglement in gillnets still poses a risk to the maintenance of local populations when individuals are outside the study area, a potentially serious threat to populations occurring in low numbers.

10.4 Habitat selection as a principal mechanism explaining the coexistence between sympatric Irrawaddy and humpback dolphins:

Understanding the mechanisms underlying the coexistence of species remains one of the major unresolved issues in community ecology (Tokeshi 1999). As explained in Chapter 1, no comprehensive studies have been carried out on the behavioural ecology of coexisting delphinids, and therefore little is known of the ecological processes (e.g., resource partitioning) shaping their coexistence. Thus, one of the aims of this study was to identify ecological and behavioural factors that may mediate the coexistence of sympatric communities of Irrawaddy and humpback dolphins.

Differential use of space, difference in activity patterns, and temporal segregation in space use have been proposed as strategies adopted by sympatric mammal species to promote coexistence (Johnson and Franklin 1994, Palomares et al. 1996, Fedriani et al. 1999, Johnson et al. 2000, Neale and Sacks 2001). Irrawaddy and humpback dolphins in Cleveland Bay showed: 1) high degree of spatial overlap, 2) concordance in space use patterns; and 3) similarity in their behavioural activities according to space (Chapter 5). Thus segregation into exclusive ranges in space and difference in behaviour patterns do not seem to be important factors promoting the coexistence of Irrawaddy and humpback dolphins. A difference in the behavioural activities of both species that might, in part, promote the sharing of space while

alleviating interspecific interactions was that of foraging behind trawlers. I did not see Irrawaddy dolphins engaging in this behaviour, whereas humpback dolphins frequently foraged behind trawlers, especially within the core areas common to both species around the Port of Townsville.

Temporal separation in space use might contribute to space sharing between these two species. I did not address this question in this study, as simultaneous tracking of schools of both species was not feasible. Nonetheless, both species co-occur year round in the study area with no seasonal interspecific differences, both displayed similar behavioural patterns with time of day throughout their ranges (see Chapter 4), and interspecific encounters were observed across the four years of study (see Chapter 9). Thus although detailed studies on temporal interactions between Irrawaddy and humpback dolphins are needed, in Cleveland Bay both species appeared to use similar areas, at similar times, for similar purposes.

Difference in habitat selection is considered one of the principal mechanisms promoting coexistence (Rosenzweig 1981, Morris 2003). If species select different habitats within a common shared space they should have no difficulties coexisting. As discussed in Chapter 5, despite considerable overlap and concordance in their space use patterns, Irrawaddy and humpback dolphins exhibited differences in their habitat preferences. While Irrawaddy dolphins preferred shallow (0-2 m) waters with seagrass meadows, and occurred closer to river mouths, humpback dolphins showed preference for slightly deeper water (2-5 m), followed by shallow water with no seagrass and dredge channels. Thus the considerable interspecific overlap in space appears to be promoted by the mosaic of habitats found within the coastal waters of Cleveland Bay. In conclusion, I suggest that interspecific differences in habitat selection play a key role in the coexistence of sympatric communities of Irrawaddy and humpback

dolphins. This study supports the increasing acknowledgement that the key to coexistence relies on spatial heterogeneity (Chesson 1985, Chesson 2000).

10.4.1 What underlies the interspecific differences in habitat selection between Irrawaddy and humpback dolphins?

Habitat selection in delphinids has been directly related to the distribution of their prey and predators (Heithaus and Dill 2002), and to physiographic and hydrographic features that may affect indirectly prey availability or reflect prey specializations by individual species (Gowans and Whitehead 1995, Davis et al. 1998, Smith and Whitehead 1999, Baumgartner et al. 2001, Benson et al. 2002, Davis et al. 2002, Jaquet and Gendron 2002). Considering that Irrawaddy and humpback dolphins use the coastal waters of Cleveland Bay for foraging, differences in their habitat preferences may be related to differences in their diet.

Quantitative studies on the diet of Irrawaddy and humpback dolphins are scarce, especially for marine Irrawaddy dolphins (Chapter 2). Based on the available data, both species appear to be opportunistic-generalist feeders, eating a wide variety of coastal, estuarine and reef-associated fishes both on the bottom and within the water column. There appears to be some dietary overlap with both species feeding on prey belonging to the same family and even genus (Chapter 2, Appendices 3 and 4). However, there also appears to be some dietary differences. All stomach contents of Irrawaddy dolphins from Cleveland Bay contained cephalopods, whereas humpback dolphins contained only fish and crustaceans (Heinsohn 1979). Stomach contents from humpback dolphins in Hong Kong contained a very small proportion of cephalopods. As mentioned in Chapter 5, several species of cephalopods are abundant in shallow water (≤ 1 m deep) close to the coast, and along breakwaters of Cleveland Bay (Jackson 1991). Therefore, if Irrawaddy dolphins feed disproportionately on

cephalopods in comparisons to fish, this could explain their preferences for shallower waters. This difference in feeding habits could also reflect differences in their facial morphology (see discussion in Chapter 5)

I suggest diet partitioning is likely, but that it does not fully explain the differences in habitat selection between Irrawaddy and humpback dolphins. First, similar fish families and genera are present in the stomach contents of both species indicating prey overlap. Second, both species use similar areas for foraging, and foraging schools of both species have been recorded within 100 m of each other in Cleveland Bay. Thus, it is likely that other constraints may be responsible for their differences in habitat selection.

My observations on the interspecific interactions of both species showed that encounters between Irrawaddy and humpback dolphins are common and predominantly of an aggressive/sexual nature (Chapter 9). During these encounters humpback dolphins were dominant. The nature of these interactions (e.g., competition, skill development, scarcity of conspecifics) is not yet fully understood. Nonetheless, regardless of their function, the high levels of aggressive interactions among sympatric species are likely to lead to habitat segregation. For example, interspecific aggression among sympatric birds plays a key role in determining habitat selection and priority of access to productive habitats (Robinson and Terborgh 1995, Martin and Martin 2001a). Among terrestrial mammals there are also several examples where interspecific aggression (including in some cases interspecific killing) has led to habitat displacement by dominant species (e.g., Johnson and Franklin 1994, Durant 1998, Linnell and Strand 2000, Loveridge and MacDonald 2002, Tannerfeldt et al. 2002).

Different factors (e.g., competition, predation, environmental conditions) with variable strengths and magnitudes may act simultaneously in the process of habitat selection (Rosenzweig 1981, 1991). I suggest that habitat partitioning between sympatric Irrawaddy and humpback dolphins is partly mediated by the aggressive exclusion of Irrawaddy dolphins by humpback dolphins (see Chapter 9). As a result, shallow waters, close to river mouths and seagrass meadows may act as refuges for Irrawaddy dolphins, places where encounters with dominant and aggressive humpback dolphins will be less likely. This interference interaction and subsequent habitat displacement is difficult to prove without experimental manipulation, however studies of habitat use in allopatric populations of both species may help us test this hypothesis. If habitat selection is the result of aggressive interactions with humpback dolphins, Irrawaddy dolphins in allopatric situations should expand their preferences to include deeper habitats in coastal waters.

10.5 Future research directions

This study has helped overcome one of the major obstacles impeding the conservation and management of coastal Irrawaddy dolphins and humpback dolphins in Australian waters: the lack of information about their behavioural ecology. Despite these advances, our understanding of the behavioural ecology of these two coastal delphinids is still in its infancy compared with some other dolphin species. In view of the concerns raised in this study about the long-term survival of these two species, future research directed at enhancing our ecological knowledge of these dolphins should inform their conservation.

Irrawaddy and humpback dolphins also provide an opportunity to study one of the central and most unresolved themes in community ecology, the coexistence of species. Although studying coexisting communities of marine mammals will be

challenging, understanding the patterns and processes structuring these communities will greatly improve our ability to predict their dynamics and thus the conservation of whole interactive communities. In this context, I have identified future research directions that should overcome some of the limitations of this study, improve conservation efforts, and help us elucidate, at least in part, the patterns and processes of their coexistence. I have divided these research directions into essential, useful and desirable, according to their conservation and management implications.

10.5.1 Research essential for conservation and management of Irrawaddy and humpback dolphins

10.5.1.1 Multi-scale approaches and ecological modelling: from local to regional patterns.

Although we have gained significant insights into the behavioural ecology of Irrawaddy and humpback dolphins, our ability to assess the impact of accelerated coastal zone development and other anthropogenic pressures (e.g., gillnetting, boat traffic) remains limited. This limitation is partly due to the localized nature of the research that I carried out. My study was limited primarily to one study area and it is clear that my research should be replicated in other areas, in order to assess the wider applicability of the patterns found here. In this context, there is a strong need to gather further data on the distribution and abundance of Irrawaddy and humpback dolphins at local and regional levels. This information will help us: 1) identify those areas that represent important habitats for both species; 2) identify areas of potential conflict with anthropogenic activities; and 3) direct conservation and management efforts efficiently towards the local populations that are most likely to contribute to the long-term survival of both species in Australian waters.

Vessel-based line transects surveys have the potential to provide information on the distribution and abundance of both species at different spatial scales. These sampling efforts, coupled with ecological modelling techniques and Geographic Information Systems (e.g., Guisan et al. 2002, Hirzel and Guisan 2002), can be used to predict the spatial distribution and density of Irrawaddy and humpback dolphins at different scales. As conservation planners and managers working with any species or system are required to make decisions at different spatial scales (e.g., Cleveland Bay, Great Barrier Reef Marine Park), future studies involving the collection and analyses of data at multiple spatial levels (ie., local and regional) will aid in these decisions.

10.5.1.2 Population structure, dispersal patterns, and social structure: the need for genetics

Management of Irrawaddy and humpback dolphins in Australian waters will vary significantly depending on the level of population structure in different populations. The site fidelity patterns and population sizes estimated for both species in Cleveland Bay suggest that populations are small and localized. However, because my study area was spatially limited, the degree of isolation or connectivity of these populations is unknown. As discussed above, populations that are small and isolated may experience accelerated inbreeding and loss of genetic diversity leading to increased risk of extinction due to environmental and demographic stochasticity (Caughley and Gunn 1996). Thus, an assessment of the level of genetic variation in Irrawaddy and humpback dolphin populations will be fundamental to define appropriate management strategies.

The social structure and dispersal behaviour of a species exerts strong influences on its population structure and therefore its persistence. Depending on the social system and dispersal behaviour of a species, different constraints are placed on

which individuals within a population breed or disperse, and thereby this can have profound effects on the distribution of genetic variation in a population (Sugg et al. 1996). Determining the sex, kinship, and dispersal distances of Irrawaddy and humpback dolphins will provide valuable data on their social and dispersal behaviour. One of the major limitations of this study was the impossibility of determining the sex and relatedness among individuals found in a school. Additionally, because my study area was finite and photo-identification does not allow continuous tracking of individuals, dispersal patterns of both species are uncertain. Molecular genetic analyses can provide all this information which otherwise is difficult or impossible to determine directly by other means with delphinids. Thus molecular studies investigating the genetic variability, social structure and dispersal patterns of Irrawaddy and humpback dolphins at a local and regional level will be fundamental in defining appropriate management strategies. Samples from live animals can be obtained by employing biopsy systems especially designed for small cetaceans which do not appear to cause any short or long term effect on the animals (Krützen et al. 2002).

10.5.1.3 The importance of photo-identification studies

Long-term monitoring of known individuals is essential for obtaining data on individual behaviour, population size, and population dynamics (e.g., survival rates, migration) that are relevant to conservation (MacGregor and Peake 1998). Photo-identification of individual dolphins from natural marks on their dorsal fin provides a non-invasive technique that has several advantages over other marking techniques that require capture and handling of individuals. Furthermore the advent of digital photography and computer assisted photo-identification software has reduced the costs and improved the collection and processing of photo-identification data, making

it more applicable and accessible (Hillman et al. 2003, Markowitz et al. 2003, Mazzoil et al. 2004). There are also disadvantages in photo-identification (see section 10.5.2.1); however, the difficulties involved in capturing wild animals still make this technique one of the most effective for collection of biological information on delphinids. For example, the possibility of using photo-identification techniques with Irrawaddy dolphins (Parra and Corkeron 2001) provided information never previously recorded for any population of these species (see Chapter 6,7, and 8).

The continuation of photo-identification studies in Cleveland Bay and extension of these to other areas along the Queensland coast will provide valuable information on the distribution, abundance, social structure, site fidelity, movement patterns, and life history parameters (e.g., survival) of Irrawaddy and humpback dolphins. All this information provides a point of comparison to this study and is valuable to the future conservation and management of Irrawaddy and humpback dolphins in Australian waters. Therefore future research efforts on Irrawaddy and humpback dolphins should include photo-identification as an integral part of their toolbox.

10.5.2 Research useful for conservation and management of Irrawaddy and humpback dolphins

10.5.2.1 Telemetry: assessing movement patterns, habitat use, and interspecific interactions in space and time

Dolphins spend most of their lives in an underwater environment, a formidable obstacle to evaluating their use of space and resource selection. The photo-identification techniques used in this study (see Chapter 6) provide a non-invasive way of obtaining such information. However photo-identification studies are limited

by inclement weather, can only be conducted during daylight hours, and depend on our capacity to find the animals and take good quality photographs. These constraints limit our ability to identify with detail the way dolphins use space, the relative importance of various habitat features, and whether the movements of individuals are influenced by conspecifics, or other species. Such information can greatly enhance conservation and management efforts by providing detailed information on the habitat use, and movement patterns of Irrawaddy and humpback dolphins,

Satellite-linked telemetry is the most direct and systematic approach for collecting data on animal movement and spatial use patterns across small and large areas and over different temporal scales (Koenig et al. 1996). A range of data loggers can be also incorporated into these tags to provide information other than location (Cooke et al. 2004). The use of satellite telemetry would greatly improve our understanding of how Irrawaddy and humpback dolphins use space, their movement patterns, habitat use, and interspecific and intraspecific interactions. Satellite telemetry has been used successfully with several species of small cetaceans (Mate et al. 1994, Mate et al. 1995, Davis et al. 1996, Westgate et al. 1998, Heide-Jorgensen et al. 2002, Corkeron and Martin 2004). Although there are concerns about the health of the animals involved in such procedures, there have been increased efforts over the last 10 years to develop remote deployment methods (Stone et al. 1994, Hanson and Baird 1998), ensure safer capture procedures (Norman et al. 2004), and smaller and more efficient tags (Hanson 1998). Trial studies involving few animals should be implemented, to assess the feasibility of using telemetry techniques with Irrawaddy and humpback dolphins.

10.5.3 Anthropogenic influences

If we are to understand the effect of human activities on Irrawaddy and humpback dolphins, studies directed at assessing these impacts should be of high priority.

10.5.3.1 Boat traffic

Boats have an effect on the behaviour and habitat use of dolphins (Janik and Thompson 1996, Wells and Scott 1997, Allen and Read 2000, Van Parijs and Corkeron 2001, Lusseau 2003, Constantine et al. 2004). Data from Cleveland Bay indicate that both species used areas with high levels of boat traffic (Chapter 5). Thus studies aimed at addressing the impact of boat traffic are needed. Comparative studies should be conducted in areas with high levels of boat-traffic (e.g., Cleveland Bay) and low levels of boat traffic (e.g., Bowling Green Bay) to assess the impact these activities can have on the behaviour, acoustic communication, and habitat use of Irrawaddy and humpback dolphins.

10.5.3.2 Gillnets

Incidental capture through entanglement in gillnets (i.e., bycatch) is one of the major threats to coastal dolphins (Reeves et al. 2003) and has been identified as the major cause of decline for riverine populations of Irrawaddy dolphins (Smith et al. 2003). Although expensive, dedicated observer monitoring programs in which trained observers onboard active fishing vessels directly record the number of marine mammals by-caught per unit of fishing effort are the most effective and reliable method to measure by-catch (IWC, 1994). In Australia, the gillnet fishery is a fishery operating out of small boats, often in remote locations, and an observer program is unlikely to be feasible for operational reasons. In this context, efforts should be

directed into assessing hotspots where the activities of humpback dolphins and gillnets overlap. Cooperation in the acquisition of gillnet fisheries effort data by government agencies will be fundamental for such a study to succeed. This information, together with abundance estimates, could be used to carry out a risk analysis of the potential impact these fisheries could have on local dolphin populations.

10.5.3.3 *Pollutants and pathogen infection*

Exposure to man-made toxic contaminants can have detrimental impacts on marine mammals (Tanabe et al. 1994, Tanabe 2002). The transport of agricultural and urban-sourced pollutants into coastal waters of the Queensland coast has been identified as a major threat to the coastal water quality in the region (Haynes and Johnson 2000, Haynes and Michalek-Wagner 2000). Toxicological studies on Irrawaddy and humpback dolphins have not been carried out in Australian waters. Analyses of blubber samples collected from stranded animals and through biopsies of free ranging individuals should help elucidate the levels of these contaminants in local populations and if they represent a risk to their health.

In addition to pollutants, the identification of infection by *Toxoplasma gondii* in humpback dolphins in Cleveland Bay is of concern. Monitoring of the incidence of this pathogen in stranded animals and studies on its potential sources are needed to determine the risks associated with *T. gondii* infection. The Queensland Marine Mammal and Turtle Strandings and Mortality Program will play a crucial role in monitoring pollutants and pathogen pollution in Irrawaddy and humpback dolphins (Kwan 2004).

10.5.4 The importance of reporting and recovering stranded animals

Carcasses and live stranded individuals provide a very important source of information for research studies on distribution, life history, taxonomy and genetic relationships, diet, toxicology, and pathology. For example, recovery and necropsy of stranded humpback dolphins in the Townsville region revealed the infection by *Toxoplasmosis gondii* as a potential threat to local populations (Bowater et al. 2003). Similarly, skin samples collected from stranded animals are helping to elucidate the taxonomy of humpback dolphins with indications that Australian populations may represent a different species (Rosenbaum et al. 2003). Collection of stomach contents has also provided the only source of information on the diet of Australian Irrawaddy and humpback dolphins (Heinsohn 1979). In addition, detailed examinations of dead or live stranded animals provide valuable information on human-related mortalities. Thus, data collection and sampling of stranded animals and subsequent analysis must be maximised and standardized.

In order to maximise the basic biological information gained from strandings and incidental captures there is a need for State and Territory authorities to coordinate and ensure that stranded specimens are examined and that important biological material (e.g., skull, skin, blubber, reproductive organs, stomach contents) is collected and made available to State museums and/or research institutions for further analysis. The existence of a marine life-stranding network along the urban coast of Queensland has the potential to provide valuable samples to be used in studies of life history, toxicology, pathology, and genetics. However, collection of samples from stranded Irrawaddy and humpback dolphins is afforded low priority in the past by local wildlife management agencies (personal observations). The success of such stranding networks depends on: 1) the fast detection and reporting of carcasses and live

stranding, 2) the standardisation of procedures for the salvage and necropsy of small cetaceans and commitment to analyse samples collected, and 3) increase in community awareness about the importance of reporting carcasses. The Queensland Marine Mammal and Turtle Strandings and Mortality Program is currently under review to try to improve procedures for the salvage, necropsy, and sampling of specimens (Kwan 2004).

10.5.5 Research desirable for conservation and management of Irrawaddy and humpback dolphins

10.5.5.1 How do prey and predation risk affect Irrawaddy and humpback dolphins habitat use and school dynamics?

Variation in school size and habitat use of delphinids is thought to be largely affected by availability of prey and risk of predation (Heithaus and Dill 2002). The influence of prey availability and predation risk on the school dynamics and habitat use of Irrawaddy and humpback dolphins is unknown but probably important (Chapter 4 and 5). The first step in discerning the influence of prey availability in the habitat use of Irrawaddy and humpback dolphins would be to determine their feeding habits as their diet in Australian waters is largely unknown.

A broad picture of the prey included in their diet can be obtained from a small sample of stomach contents available to me from animals caught in shark nets (Heinsohn 1979) and from stranded animals between 1999-2004. Based on the knowledge that fatty acids (FA) patterns in prey influence the lipid stores of their predators, FA analyses of blubber samples collected through biopsies could then be used to discern variation in prey preferences (Iverson et al. 1997, Hooker et al. 2001). This analysis coupled with studies on prey availability, predator (i.e., sharks) density

and movements, and dolphin surveys could be used to test the effect food availability and predation risk has on the habitat use and school dynamics of Irrawaddy and humpback dolphins (see Heithaus and Dill 2002 for example). This knowledge would allow us to assess the effects shift in prey and predators can have on Irrawaddy and humpback dolphins and develop conservation and management practices that would take these effects into account.

10.6 Final remarks

Given the prospects of the continuing loss of global biodiversity that will particularly affect coastal ecosystems (Hinrichsen 1996, Clark 1998, Jenkins 2003), the management and conservation of coastal dolphins will need to be intensive and adaptive. To conserve and manage coastal dolphins effectively will require a comprehensive understanding of their ecology and behaviour. This study is the first comprehensive investigation on Irrawaddy and humpback dolphins in the Australian/Papua New Guinean regions and provides a preliminary scientific basis for their future conservation and management.

My study has also produced new and interesting questions about the ecology of these two species that should serve as incentive for future research. Answering these questions will require multidisciplinary approaches and long-term painstaking studies, but should not preclude conservation actions. The results of this study indicate that Irrawaddy and humpback dolphins occur in small, localized populations close to coastal and estuarine environments. Lacking any evidence to the contrary, management actions should be based on these results and focus on developing conservation measures specifically at these two species.

The much greater challenge of conserving Irrawaddy and humpback dolphins in the highly populated developing countries within Southeast Asia demonstrates the

importance of the remote regions of tropical Australia to the conservation of these two species. In this context, Australia has the opportunity and responsibility to develop research and conservation initiatives that contribute to the conservation and long-term survival of Irrawaddy and humpback dolphins. For this to happen, the agencies responsible for environmental management throughout their range in Australian waters need to take a more, strategic, pro-active, comprehensive and coordinated approach to coastal marine mammal research and management than they have attempted to date or currently show any inclination for attempting in the near future.

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Appendix 1 List of Irrawaddy dolphin strandings and museum specimen records in Australia. The date given refers to the known date of the stranding, the date the carcass was found and reported, or the date the specimen was registered in a particular database.

Reg. No.	Date	Location	State ¹	Latitude S	Longitude E	Institution ²	Reference
284429	16-Jul-48	Melville Bay	NT	12° 00'	131° 00'	NMNH	Beasley (pers. comm., 2000)
284430	16-Jul-48	Melville Bay	NT	12° 00'	131° 00'	NMNH	Beasley (pers. comm., 2000)
M23244	14-May-65	Cable Beach, Broome	WA	17° 55'	122° 15'	WAM	Norah Cooper (pers comm., 2000)
M23242	25-Jun-65	Crab Creek Broome	WA	18° 00'	122° 24'	WAM	Norah Cooper (pers comm., 2000)
M23243	25-Jun-65	Crab Creek Broome	WA	18° 00'	122° 24'	WAM	Norah Cooper (pers comm., 2000)
JM14263	12-Jul-66	Cleveland Bay, Townsville	QLD	19° 13'	146° 55'	QM	Stephen Van Dyck (pers. comm., 2000)
M12359	1-Sep-68	Cairns	QLD	17° 00'	146° 00'	AM	Sandy Ingleby (pers. comm, 2000)
JM11343	18-Nov-68	Horseshoe Bay, Magnetic Island	QLD	19° 07'	146° 51'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4700	23-Sep-69	Pallarenda, Townsville	QLD	19° 12'	146° 46'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4705	23-Apr-70	Horseshoe Bay, Magnetic Island	QLD	19° 07'	146° 51'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4706	23-Apr-70	Horseshoe Bay, Magnetic Island	QLD	19° 07'	146° 51'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4706A	23-Apr-70	Horseshoe Bay, Magnetic Island	QLD	19° 07'	146° 51'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4714	4-Sep-70	Townsville	QLD	19° 16'	146° 48'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4707	3-Oct-70	Pallarenda, Townsville	QLD	19° 12'	146° 46'	MTQ	Arnold and Beasley (pers. comm., 2000)

Appendix 1 (Continued).

Reg. No.	Date	Location	State ¹	Latitude S	Longitude E	Institution ²	Reference
JM4708	13-Dec-70	Horseshoe Bay, Magnetic Island	QLD	19° 07'	146° 51'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4709	23-Jan-71	Horseshoe Bay, Magnetic Island	QLD	19° 07'	146° 51'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4704	23-Apr-71	Horseshoe Bay, Magnetic Island	QLD	19° 07'	146° 51'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4741	10-Jun-71	Pallarenda, Townsville	QLD	19° 12'	146° 46'	*	Jenny Haines (pers. comm., 2000)
JM4712	10-Jun-71	Pallarenda, Townsville	QLD	19° 12'	146° 46'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4720	18-Mar-72	Kissing Point, Townsville	QLD	19° 14'	146° 48'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4721	21-Apr-72	Horseshoe Bay, Magnetic Island	QLD	19° 07'	146° 51'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4722	18-Aug-74	Pallarenda, Townsville	QLD	19° 12'	146° 46'	*	Jenny Haines (pers. comm., 2000)
JM4723	18-Aug-74	Pallarenda, Townsville	QLD	19° 12'	146° 46'	*	Jenny Haines (pers. comm., 2000)
JM4725	18-Aug-74	Pallarenda, Townsville	QLD	19° 12'	146° 46'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4726	18-Aug-74	Pallarenda, Townsville	QLD	19° 12'	146° 46'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM511	27-Sep-74	Harbour Beach, Mackcay	QLD	21° 09'	149° 11'	QM	Stephen Van Dyck (pers. comm., 2000)
JM4727	28-Mar-75	The Strand, Townsville	QLD	19° 16'	146° 48'	MTQ	Arnold and Beasley (pers. comm., 2000)
MM92	24-Aug-75	Kissing Point, Townsville	QLD	19° 14'	146° 48'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4729	27-Aug-75	Kissing Point, Townsville	QLD	19° 14'	146° 48'	MTQ	Arnold and Beasley (pers. comm., 2000)

Appendix 1 (Continued).

Reg. No.	Date	Location	State ¹	Latitude S	Longitude E	Institution ²	Reference
							comm., 2000)
JM4734	30-Jul-76	Pallarenda, Townsville	QLD	19° 12'	146° 46'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4735	10-Sep-76	Rowe's Bay, Townsville	QLD	19° 13'	146° 47'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4736	4-Oct-76	Rowe's Bay, Townsville	QLD	19° 13'	146° 47'	MTQ	Arnold and Beasley (pers. comm., 2000)
NTMU249	19-Oct-83	Melville Island, off Point Jaheel	NT	11° 13'	131° 20'	MAGNT	Paul Horner (pers. comm., 2000)
M52387	3-Mar-84	Derby	WA	17° 19'	123° 38'	WAM	Norah Cooper (pers comm., 2000)
JM4739	9-Aug-84	Ross River mouth	QLD	19° 16'	146° 50'	*	Jenny Haines (pers. comm., 2000)
JM4740	30-Sep-84	Toolakea Beach, Townsville	QLD	19° 09'	146° 35'	MTQ	Arnold and Beasley (pers. comm., 2000)
NTMU532	1985	?	?	?	?	MAGNT	Paul Horner (pers. comm., 2000)
JM4937	22-Jan-85	Main Beach, Cape Hillsborough	QLD	20° 55'	149° 00'	QM	Stephen Van Dyck (pers. comm., 2000)
W539	29-Apr-85	Pallarenda Beach	QLD	19° 12'	146° 46'	QPWS	Jenny Haines (pers. comm., 2000)
W540	20-May-85	Saunders Beach	QLD	19° 11'	146° 39'	QPWS	Jenny Haines (pers. comm., 2000)
M23301	20-Oct-85	Town Beach, Broome	QLD	17° 58'	122° 14'	WAM	Norah Cooper (pers comm., 2000)
JCU1026	11-May-86	Balgol Beach	QLD	19° 02'	146° 25'	JCU	Jenny Haines (pers. comm., 2000)
JCU1027	21-Jun-86	Saunders Beach	QLD	19° 11'	146° 41'	JCU	Jenny Haines (pers. comm., 2000)

Appendix 1 (Continued).

Reg. No.	Date	Location	State ¹	Latitude S	Longitude E	Institution ²	Reference
JCU1031	12-Sep-86	Pallarenda Beach	QLD	19° 12'	146° 47'	JCU	Jenny Haines (pers. comm., 2000)
JCU1032	14-Sep-86	Ollera Creek	QLD	19° 11'	146° 41'	JCU	Jenny Haines (pers. comm., 2000)
JCU1034	1-Oct-86	Toolakea Beach	QLD	19° 11'	146° 41'	JCU	Jenny Haines (pers. comm., 2000)
W563	18-Jun-87	Saunders Beach	QLD	19° 11'	146° 40'	QPWS	Jenny Haines (pers. comm., 2000)
JCU1039	27-Jul-88	Toolakea Beach	QLD	19° 08'	146° 35'	JCU	Jenny Haines (pers. comm., 2000)
JCU1042	3-Oct-88	Saunders Beach	QLD	19° 11'	146° 40'	JCU	Jenny Haines (pers. comm., 2000)
W231	15-May-89	Horseshoe Bay	QLD	19° 07'	146° 51'	QPWS	Jenny Haines (pers. comm., 2000)
W237	10-Oct-90	Horseshoe Bay	QLD	19° 07'	146° 51'	QPWS	Jenny Haines (pers. comm., 2000)
W57	22-Jul-91	Ellis Beach, Cairns	QLD	16° 43'	145° 39'	QPWS	Jenny Haines (pers. comm., 2000)
N/A	12-Jun-92	Fog Bay	NT	12° 50'	130° 31'	PWCNT	Chatto & Warneke (2000)
W143	31-Aug-92	Bucasia, Mackay	QLD	21° 02'	149° 10'	QPWS	Jenny Haines (pers. comm., 2000)
JM10574	18-Jul-94	Moore PK Beach, Bundaberg	QLD	24° 52'	152° 21'	QM	Stephen Van Dyck (pers. comm., 2000)
W117	15-Jul-95	Ellis Beach, Cairns	QLD	16° 43'	145° 39'	QPWS	Jenny Haines (pers. comm., 2000)
W118	15-Jul-95	Ellis Beach, Cairns	QLD	16° 43'	145° 39'	QPWS	Jenny Haines (pers. comm., 2000)
W120	22-Sep-95	Ellis Beach, Cairns	QLD	16° 43'	145° 39'	QPWS	Jenny Haines (pers. comm., 2000)

Appendix 1 (Continued).

Reg. No.	Date	Location	State ¹	Latitude S	Longitude E	Institution ²	Reference
W123	20-Jul-96	Ellis Beach, Cairns	QLD	16° 43'	145° 39'	QPWS	Jenny Haines (pers. comm., 2000)
W22	5-Aug-96	Black's Beach	QLD	21° 03'	149° 11'	QPWS	Jenny Haines (pers. comm., 2000)
W25	13-Aug-96	Williamson's Beach	QLD	20° 59'	149° 06'	QPWS	Jenny Haines (pers. comm., 2000)
JM11976	20-Jul-97	Karavana Downs, Brisbane River	QLD	27° 32'	152° 49'	QM	Stephen Van Dyck (pers. comm., 2000)
W916	30-Jul-97	Sea Hill, 500m NE.Lighthouse	QLD	23° 29'	150° 59'	QPWS	Jenny Haines (pers. comm., 2000)
N/A	Aug-97	Indian Island, Bynoe Harbour	NT	12° 37'	130° 31'	PWCNT	Chatto & Warneke (2000)
W907	30-Oct-97	O'Connel River, 1 km upstream	QLD	20° 33'	148° 39'	QPWS	Jenny Haines (pers. comm., 2000)
W908	30-Oct-97	O'Connel River	QLD	20° 35'	148° 40'	QPWS	Jenny Haines (pers. comm., 2000)
M33213	6-Dec-97	Daru	PNG	09° 08'	143° 07'	AM	Sandy Ingleby (pers. comm., 2000)
W971	17-Mar-98	Pallarenda, 3 Mile Creek	QLD	19° 13'	146° 46'	QPWS	Jenny Haines (pers. comm., 2000)
W989	29-Sep-98	O'connel River, Thomson Creek	QLD	20° 23'	148° 40'	QPWS	Jenny Haines (pers. comm., 2000)
N/A	27-May-99	Northeast side of Is. of Woodah,Gulf of Carpentaria	NT	13° 22'	136° 08'	PWCNT	Chatto & Warneke (2000)
W1088	16-Sep-99	Mulambin Beach, Yeppoon	QLD	23° 12'	150° 48'	QPWS	Jenny Haines (pers. comm., 2000)
N/A	1-Oct-99	Dundee Beach, Fog Bay	NT	12° 46'	130° 22'	PWCNT	Chatto & Warneke (2000)
NTMU5079	?	?	?	?	?	MAGNT	Paul Horner (pers. comm., 2000)

Appendix 1 (Continued).

Reg. No.	Date	Location	State ¹	Latitude S	Longitude E	Institution ²	Reference
JM11342	?	Townsville	QLD	19° 16'	146° 48'	MTQ	Arnold and Beasley (pers.comm.,2000)
JM4705A	?	Horseshoe Bay, Magnetic Island	QLD	19° 07'	146° 51'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4751	?	Townsville	QLD	19° 16'	146° 48'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM4752	?	Townsville	QLD	19° 16'	146° 48'	MTQ	Arnold and Beasley (pers. comm., 2000)
MM1039	?	Townsville	QLD	19° 16'	146° 48'	MTQ	Arnold and Beasley (pers. comm., 2000)
Unregistered	?	Townsville	QLD	19° 16'	146° 48'	MTQ	Arnold and Beasley (pers. comm., 2000)
Unregistered	?	Townsville	QLD	19° 16'	146° 48'	MTQ	Arnold and Beasley (pers. comm., 2000)
JM1339	?	?	?	?	?	QM	Stephen Van Dyck (pers. comm., 2000)

¹ NSW = New South Wales, NT = Northern Territory, QLD = Queensland, WA = Western Australia, PNG = Papua New Guinea.

² AM= Australian Museum, JCU = James Cook University, MAGNT = Museum and Art Galleries of the Northern Territory, PWCNT= Parks and Wildlife commission of the Northern Territory, QPWS = Queensland Parks and Wildlife Service, QM = Queensland Museum, and WAM = Western Australian museum. Experienced personnel within these institutions were responsible for species identification and measurements.

* These specimens are not found in at MTQ or QM as their registration number indicates, however they are reported in the QPWS stranding database.

Appendix 2 List of vessel-sighting records of Irrawaddy dolphins in Australian waters.

Date	Location	Latitude S	Longitude E	School Size	Source ¹
1995	Hinchinbrook Channel	18° 18'	146° 04'	10	Preen
17-Feb-98	Tip of Cape Bowling Green	19° 18'	147° 23'	4	QPWS
26-Mar-98	Cleveland Bay	19° 17'	146° 57'	5	Preen
26-Mar-98	Cleveland Bay	19° 14'	146° 52'	6	Preen
16-Apr-98	Cleveland Bay	19° 14'	146° 50'	2	Preen
28-Sep-98	Cleveland Bay	19° 14'	146° 50'	7	QPWS
21-Aug-99	North east Bay Palm Island	18° 44'	146° 41'	1	QPWS
10-Nov-99	Townsville Port Channel	19° 14'	146° 50'	5	QPWS
20-Jan-00	Mouth of Black River	19° 10'	146° 39'	4	QPWS
20-Jan-00	Off Bushland Beach	19° 11'	146° 41'	5	QPWS

¹ Preen = Anthony Preen (unpublished data), QPWS = Queensland Parks and Wildlife Service

Appendix 3 List of aerial survey sighting records of Irrawaddy dolphins classified as "certain" in Australian waters.

Year	Survey Area	Latitude S	Longitude E	Group Size
86 (Nov.)	Repulse Bay to Bustard Head	22° 00'	149° 40'	1
86 (Oct.)	Repulse Bay-Bustard Head	21° 57'	149° 50'	5
86 (Oct.)	Repulse Bay-Bustard Head	21° 22'	149° 35'	2
86 (Sep.)	Dunk Island-Cape Cleveland	18° 08'	146° 10'	2
87 (Sept.)	Dunk Island-Cape Cleveland	19° 42'	147° 42'	1
87 (Sept.)	Dunk Island-Cape Cleveland	18° 06'	146° 03'	1
87 (Sept.)	Dunk Island-Cape Cleveland	19° 09'	146° 41'	1
94 (Nov.)	Dunk Island-Bustard Head	19° 35'	147° 44'	5
95 (Nov.)	Hunter Point-Cape Bedford	14° 16'	144° 47'	11
95 (Nov.)	Hunter Point-Cape Bedford	14° 08'	143° 58'	1
95 (Nov.)	Hunter Point-Cape Bedford	14° 08'	144° 36'	1
96 (Dec.)	Townsville-Cardwell	19° 23'	147° 24'	6
96 (Jul.)	Townsville-Cardwell	19° 06'	146° 33'	12
97 (Apr.)	Townsville-Cardwell	19° 10'	146° 46'	9
97 (Aug.)	Townsville-Cardwell	18° 59'	146° 23'	8
97 (Aug.)	Townsville-Cardwell	18° 58'	146° 22'	7
97 (Aug.)	Townsville-Cardwell	18° 55'	146° 20'	10
97 (Aug.)	Townsville-Cardwell	18° 15'	146° 02'	10
97 (Aug.)	Townsville-Cardwell	18° 11'	146° 13'	8
97 (Dec.)	Eastern Gulf of Carpentaria	12° 00'	141° 54'	2
97 (Dec.)	Mornington	17° 25'	140° 43'	1
97 (Dec.)	Mornington	16° 42'	138° 22'	7
97 (Jul.)	Townsville-Cardwell	19° 08'	146° 35'	10
97 (Oct.)	Townsville-Cardwell	19° 10'	146° 40'	10
97 (Oct.)	Townsville-Cardwell	18° 15'	146° 03'	2
97(Dec.)	Townsville-Cardwell	19° 09'	146° 38'	3
97(Dec.)	Townsville-Cardwell	19° 06'	146° 30'	4
97(May)	Townsville-Cardwell	18° 17'	146° 04'	14
98 (Apr.)	Townsville-Cardwell	18° 44'	146° 19'	3

Appendix 4 List of Indo-Pacific humpback dolphin strandings and museum specimen records in Australia. The date given refers to the known date of the stranding, the date the carcass was found and reported, or the date the specimen was registered in a particular database.

Registration No.	Date	Location	State ¹	Latitude S	Longitude E	Sex	Total Length (cm)	Est. Age (yrs) ²	Institution ³	Reference ⁴
n/a	Aug-48	Yirrkala	NT	12° 15'	136° 54'	?	?	?	?	A
J7443	31-Oct-49	Moreton Bay	QLD	27° 26'	153° 14'	?	?	?	QM	B, C, D
M12691	Jan-62	Tweed Heads Dolphinarium	NSW	?	?	?	?	?	AM	E
5452	20-Sep-62	Onslow	WA	21° 32'	115° 24'	?	?	?	WAM	F
54187	28-Jan-66	Kalumburu	WA	14° 18'	126° 38'	?	?	?	WAM	F
7683	10-Feb-68	Monte Bello Islands	WA	20° 20'	115° 30'	?	?	?	WAM	F
7899	23-Aug-68	Carbaddaman Passage	WA	22° 22'	113° 42'	?	?	?	WAM	F
JM4701	9-Oct-69	Picnic Bay	QLD	19° 11'	146° 50'	M	238	20+	QM	B, C, D
JM4703	4-Mar-70	Horseshoe Bay	QLD	19° 07'	146° 51'	M	177	3	QM	C
JM4710	4-Feb-71	Horseshoe Bay	QLD	19° 07'	146° 51'	M	143	1	QM	B,G
n/a	25-May-71	Kissing Point	QLD	19° 14'	146° 48'	M	151	1	JCU	B, C, D
J21718	14-Oct-71	North Stradbroke Island	QLD	27° 35'	153° 27'	?	?	?	QM	B, C, D
JM4717	24-Oct-71	Horseshoe Bay	QLD	19° 07'	146° 51'	M	195	5	QM	C
JM4728	16-Aug-75	Florence Bay	QLD	19° 07'	146° 53'	?	?	?	QM	B, C, D
n/a	Jan-76	Cape Cleveland	QLD	19° 21'	147° 01'	?	?	?	JCU	B,G
JM4731	19-Jan-76	Horseshoe Bay	QLD	19° 07'	146° 51'	F	?	7	QM	B,G
JM1337	15-Apr-76	Gold Coast	QLD	28° 00'	153° 26'	?	?	?	QM	B, C, D
JM2149	24-Feb-77	Gold Coast	QLD	28° 00'	153° 26'	?	?	?	QM	C

Appendix 4 (Continued).

Registration No.	Date	Location	State ¹	Latitude S		Longitude E		Sex	Total Length	Est. Age	Institution ³	Reference ⁴
									(cm)	(yrs) ²		
JM4737	5-Jul-78	Rowes Bay	QLD	19°	13'	146°	47'	M	229	12	QM	G, B
n/a	8-Oct-79	Balgol Beach	QLD	19°	02'	146°	25'	M	211	?	JCU	B,C
JM4377	19-Apr-83	Moreton Island	QLD	27°	12'	153°	22'	?	?	?	QM	B
NTM U.660	28-Nov-83	Arafura Sea	NT	09°	36'	135°	37'	M	161	?	MAGNT	H
28137	23-Mar-84	?	NT	?		?	?	M	?	?	WAM	F
JM4738	30-Jul-84	Rowes Bay	QLD	19°	13'	146°	47'	?	?	?	QM	B
W534	5-Aug-84	Bribie Island	QLD	27°	06'	153°	10'	M	260	?	QPWS	B
W536	30-Aug-84	Rowes Bay	QLD	19°	16'	146°	49'	?	236	?	QPWS	B,C
W543	23-Jun-85	Saunders Beach	QLD	19°	17'	146°	39'	M	227	?	QPWS	B
JM5333	27-Sep-85	Adder Rock,Pt Lookout,N.Strady	QLD	27°	26'	153°	32'	?	?	?	QM	B
NTM U.254	23-Nov-85	Casuarina Beach	NT	12°	21'	130°	52'	M	208	?	MAGNT	I
W552	2-Sep-86	Rowes Bay Beach	QLD	19°	14'	146°	47'	M	230	?	QPWS	B
W466	22-Sep-86	Balgol Beach	QLD	19°	02'	146°	25'	?	247	?	QPWS	B
30948	Jul-88	Cape Leveque	WA	16°	16°	122°	55'	?	?	?	WAM	F
W576	1-Oct-88	The Spit	QLD	28°	00'	153°	26'	F	260	?	QPWS	B,C
W577	3-Oct-88	Saunders Beach	QLD	19°	11'	146°	40'	M	175	?	QPWS	B,C
NTM U.528	28-Oct-88	Channel Point	NT	13°	10'	130°	07'	?	?	?	MAGNT	I
JM7678	22-Jan-90	Rowes Bay	QLD	19°	13'	146°	47'	?	?	?	QM	B
JM10416	1-Mar-94	Ayr	QLD	19°	34'	147°	24'	M	100	?	QM	B
W64	16-Oct-95	Yorkeys Knob	QLD	16°	48'	145°	43'	?	?	?	QPWS	B

Appendix 4 (Continued).

Registration No.	Date	Location	State ¹	Latitude S		Longitude E		Sex	Total Length	Est. Age	Institution ³	Reference ⁴
				(cm)	(yrs) ²							
W49	6-Feb-96	Ball Beach	QLD	20°	54'	149°	01'	M	?	?	QPWS	B
NTM U.5150	3-Mar-96	Knocker Bay	NT	11°	20'	132°	07'	?	200	?	MAGNT	I
W122	29-Jun-96	Ellis Beach	QLD	16°	43'	145°	39'	?	?	?	QPWS	B
W23	6-Aug-96	Redcliffe	QLD	27°	14'	153°	07'	F	182	?	QPWS	B
W124	11-Aug-96	Ellis Beach	QLD	16°	43'	145°	39'	?	?	?	QPWS	B
W125	14-Sep-96	Ellis Beach	QLD	16°	43'	145°	39'	?	?	?	QPWS	B
Q20248	28-Sep-96	Off Cleveland	QLD	27°	30'	153°	17'	F	226	?	QPWS	B
W41	3-Oct-96	Mon Repos	QLD	24°	48'	152°	28'	M	260	?	QPWS	B
W405	19-Feb-97	Coolangatta	QLD	28°	10'	153°	32'	?	?	?	QPWS	B
W817	10-Jun-97	Bushland Beach	QLD	19°	10'	146°	35'	F	220	?	QPWS	B
W906	9-Jul-97	Norman River, Karumba	QLD	17°	29'	140°	50'	M	262	?	QPWS	B
W865	2-Aug-97	Orchid Beach	QLD	24°	57'	153°	18'	F	?	?	QPWS	B
W863	21-Aug-97	Freshwater Pt.	QLD	21°	26'	149°	18'	?	227	?	QPWS	B
W913	3-Sep-97	Belinga	QLD	28°	09'	153°	30'	?	150	?	QPWS	B
W 76	10-Dec-97	Ellis Beach	QLD	16°	43'	145°	40'	?	260	?	QPWS	B
W896	17-Dec-97	Yorkeys Knob	QLD	16°	48'	145°	48'	F	?	?	QPWS	B
W912	23-Dec-97	Ocean Beach	QLD	26°	55'	153°	09'	?	206	?	QPWS	B
W1013	28-Jan-98	Palm Cove	QLD	16°	45'	145°	40'	M	161	?	QPWS	B
W965	24-Jun-98	Moon Point	QLD	25°	14'	153°	01'	?	232	?	QPWS	B

Appendix 4 (Continued).

Registration No.	Date	Location	State ¹	Latitude S		Longitude E		Sex	Total Length	Est. Age	Institution ³	Reference ⁴
				(cm)	(yrs) ²							
W966	28-Jul-98	Noosa	QLD	26°	23'	153°	05'	M	?	?	QPWS	B
W975	6-Aug-98	Rainbow Beach	QLD	25°	54'	153°	06'	?	?	?	QPWS	B
W1108	13-Aug-98	Maroochydore	QLD	26°	40'	153°	06'	M	?	?	QPWS	B
W992	16-Jan-99	Oaks Beach	QLD	16°	35'	145°	31'	M	?	?	QPWS	B
W1044	26-May-99	Rainbow Beach	QLD	25°	54'	153°	05'	?	?	?	QPWS	B
W1111	3-Sep-99	Bilinga	QLD	27°	55'	153°	26'	M	150	?	QPWS	B
W1106	7-Oct-99	Rowes Bay	QLD	19°	14'	146°	47'	?	210	?	QPWS	B
W1136	1-Feb-00	Pallarenda	QLD	19°	12'	146°	47'	F	200	?	QPWS	B
W1150	27-Feb-00	Haughton River	QLD	19°	25'	147°	05'	F	245	?	QPWS	B
W1161	1-Mar-00	Townsville	QLD	19°	25'	147°	07'	F	245	?	QPWS	B
W1312	17-May-00	Rainbow Beach	QLD	25°	50'	153°	04'	?	?	?	QPWS	B
W1187	17-Jun-00	Wild Cattle Ck	QLD	23°	58'	151°	24'	?	210	?	QPWS	B
W1198	7-Jul-00	Johnstone Beach	QLD	21°	14'	149°	11'	?	?	?	QPWS	B
W1215	12-Aug-00	Bohle River	QLD	19°	12'	146°	42'	F	235	?	QPWS	B
W1249	26-Sep-00	Sunrise Beach	QLD	26°	25'	153°	05'	F	240	?	QPWS	B
W1251	28-Sep-00	Crocodile Ck	QLD	19°	17'	146°	55'	F	247	?	QPWS	B
W1252	1-Oct-00	Crocodile Ck	QLD	19°	16'	146°	56'	?	270	?	QPWS	B
NTM U.5149	28-Oct-00	Lee Point Beach	NT	12°	21'	130°	53'	F	210	?	MAGNT	A
W1303	2-May-01	Sunshine Coast	QLD	?	?	?	?	?	180	?	QPWS	B
W1328	18-Jul-01	The Strand	QLD	19°	15'	146°	49'	F	232	?	QPWS	B

Appendix 4 (Continued).

Registration No.	Date	Location	State ¹	Latitude S	Longitude E	Sex	Total Length (cm)	Est. Age (yrs) ²	Institution ³	Reference ⁴
W1341	18-Jul-01	Harbour Quoin Island	QLD	23° 49'	151° 17'	M	179	?	QPWS	B
W1349	29-Jul-01	Tin Can Bay	QLD	25° 54'	153° 00'	M	?	?	QPWS	C
W1354	5-Sep-01	Yorkeys Knob	QLD	16° 46'	145° 41'	F	150	?	QPWS	C
JM5355	?	?	QLD	?	?	?	?	?	QM	B,G
JM6434	?	?	QLD	?	?	?	?	?	QM	B, C, D
1176	?	Port Headland	WA	20° 18'	118° 35'	?	?	?	WAM	F

¹ NSW = New South Wales, NT = Northern Territory, QLD = Queensland, WA = Western Australia.

² Heihnsohn (1979)

³ WAM = Western Australian museum, QPWS = Queensland Parks and Wildlife Service, QM = Queensland Museum, MAGNT = Museum and Art Galleries of the Northern Territory, JCU = James Cook University, and AM= Australian Museum. Experienced personnel within these institutions were responsible for species identification and measurements. Data from QPWS corresponds to strandings database and are not available as specimens in museums.

⁴ A = Johnson (1964), B = Jenny Haynes (QPWS, personal communication, 2002), C = Heinsohn (1979), D = Paterson (1994), E = Sandy Ingleby (AM, personal communication, 2002), F = Norah Cooper (WAM, personal communication, 2003), G = Paterson (1986), H = Gavin Dally (MAGNT, personal communication, 2002), I = Chatto and Warneke (2000).

Appendix 5 (Continued).

Irrawaddy dolphins										
Geographic Area	Proximity to coast (Km)	Water Depth (m)		School size			Abundance	95% CI	References	
		Mean	Range	Mean	SD	Range				N
Mahakam River	na	na	na	4.4	2.2	1-10	75	55 48	44-76 33-63	(Kreb 2004)
Balikpapan Bay	na	na	na	3.2	2.1	1-9	79	na	na	(Kreb 2004)
Philippines:										
Malampaya Sound	na	na	≤ 15	5.26	1.06	1-13	15	na	na	(Dolar et al. 2002)
Malampaya Sound	na	na	1.5-15.1	5.2		1-23	45	60	44-105	(Smith et al. 2002)
Australia:										
Western Gulf Of Carpentaria	na	na	2.5-18	1.63 1.93 1.77	na	na	8 27 77	1000	na	(Freeland and Bayliss 1989)

¹ na = not available

Appendix 6 (Continued).

Indo-Pacific humpback dolphins										
Geographic Area	Proximity to coast (km)	Water Depth (m)		School size			Abundance	95% CI	References	
		Mean	Range	Mean	SD	Range				n
India										
Gulf Of Kachchh	na	na	≤ 30	3.9	3.3	1-11	21	na	na	(Sutaria and Jefferson 2004)
Goa	na	na	≤ 10	6.3	7.1	1-35	135	na	na	(Sutaria and Jefferson 2004)
Cambodia										
Kompong Som Bay-Koh Kong	na	5.2	2.2-9.5	6	2.87	2-8	4	na	na	(Beasley et al. 2001)
Vietnam										
Bing Cang Bay	na	na	na	na	na	1-3	2	na	na	(Smith et al. 1997)
China										
Hong Kong	≤ 2	na	na	2.76	2.29	1-13	126	na	na	(Parsons 1998a)
Pearl River Estuary (including Hong Kong)	na	na	≤ 20	3.8	3.63	1-23	1396	1028	na	(Jefferson 2000)
Malaysia										
Jambongan	na	na	na	6	na	na	1	na	na	(Dolar et al. 1997)
Australia										
Moreton Bay	≤ 6	9	na	2.4	1.13	na	9	119 163	81-166 108-251	(Corkeron 1990, Corkeron et al. 1997)

¹na = not available

Appendix 7 Summary of prey items found in the stomachs of Irrawaddy dolphins
(modified from Heinsohn 1979, Marsh et al. 1989).

Irrawaddy dolphins					
Region	Order	Family	Species*	Habitat	
Australia	Decapoda				
	Isopoda				
	Octopoda				
	Sepioidea				
	Teuthida				
	Anguilliformes				
	Beloniformes	Hemirhamphidae	<i>Hemirhamphus sp.</i>	Pelagic. Coastal waters and estuaries	
	Clupeiformes	Chirocentridae	<i>Chirocentrus dorab</i>	Pelagic. Coastal waters, and estuaries	
		Clupeidae	<i>Sardinella albella</i>	Pelagic. Coastal waters	
		Engraulidae	<i>Stolephorus sp.</i>	Pelagic. Shallow coastal waters and estuaries	
	Aulopiformes	Synodontidae		Demersal. Coastal waters	
	Cleveland Bay	Perciformes	Apogonidae	<i>Apogonichthys sp.</i>	Pelagic. Coastal waters and estuaries
			Haemulidae	<i>Pomadasys argyreus</i>	Demersal. Coastal waters
		Perciformes	Leiognathidae	<i>Leiognathus equulus</i>	Benthopelagic. River mouths and muddy inshore areas
				<i>Secutor insidiator</i>	Demersal. Shallow coastal waters and estuaries
			<i>Leiognathus splendens</i>	Demersal. Coastal waters and estuaries	
		Nemipteridae	<i>Nemipterus sp.</i>	Demersal. Marine	
		Sciaenidae	<i>Johnius spp.</i>	Demersal. Coastal waters and estuaries	
		Sillaginidae	<i>Sillago sp.</i>	Demersal. Coastal waters and estuaries	
Terapontidae		<i>Terapon puta</i>	Benthopelagic. Coastal waters and estuaries		
Platycephalidae		<i>Platycephalus sp.</i>	Demersal. Coastal waters and estuaries		
Pleuronectiformes	Psettodidae	<i>Psettodes erumei</i>	Demersal. Coastal waters and estuaries		

Appendix 7 (Continued).

Irrawaddy dolphins				
Region	Order	Family	Species*	Habitat
Cambodia				
Mekong River	Cypriniformes	Cyprinidae	<i>Barbodes gonionotus</i>	Benthopelagic. Rivers, streams, floodplains, and occasionally in reservoirs
			<i>Cirrhinus microlepis</i>	Benthopelagic. Large rivers and lowland floodplains
			<i>Cirrhinus jullieni</i>	Benthopelagic. Rivers and floodplains
			<i>Labiobarbus siamensis</i>	Benthopelagic. Rivers and streams
			<i>Thynnichthys thynnoides</i>	Benthopelagic. Large rivers, canal, oxbows and floodplains
	Siluriformes	Pangasiidae	<i>Pangasius sanitwongsei</i>	Benthopelagic. Large rivers
			<i>Pangasius micronemus</i>	Benthopelagic. Large and medium-sized rivers

*Some species names have been changed from Marsh et al. (Marsh et al. 1989) and Heinsohn (Heinsohn 1979) to match current valid scientific names

Appendix 8 Summary of prey items found in the stomachs of Indo-Pacific humpback dolphins.

Indo-Pacific humpback dolphins						
Region	Order	Family	Species*	Habitat		
Australia						
Cleveland Bay ^a	Fish and Crustaceans					
China						
Hong Kong ^b	Crustaceans					
	Teuthida	Loliginidae	Possibly <i>Loligo sp.</i>			
	Anguilliformes	Congridae	<i>Conger sp.</i>	Marine		
	Clupeiformes	Pristigasteridae	<i>Ilisha sp.</i>		Pelagic. Coastal waters and estuaries	
		Clupeidae	<i>Sardinella sp.</i>		Pelagic. Coastal waters	
		Engraulidae	<i>Thryssa spp.</i>		Pelagic. Coastal waters and estuaries	
	Perciformes	Carangidae			Marine	
		Haemulidae	<i>Pomadasys sp.</i>			
		Leiognathidae		<i>Leiognathus sp.</i>		Benthopelagic or demersal. Coastal waters and estuaries
				<i>Leiognathus brevirostris</i>		Demersal. Coastal shallow waters
		Mugilidae	<i>Mugil sp.</i>		Benthopelagic or demersal. Coastal waters	
		Sciaenidae		<i>Collichthys lucida</i>		Demersal. Coastal waters and estuaries
				<i>Johnius spp.</i>		Demersal. Coastal waters and estuaries
				<i>Larimichthys crocea</i>		Benthopelagic. Coastal waters and estuaries
		Centrolophidae	<i>Psenopsis anomola</i>		Benthopelagic. Marine	
		Trichiuridae	<i>Trichiurus sp.</i>		Benthopelagic. Coastal waters and estuaries	
	Pleuronectiformes	Pleuronectidae			Marine and freshwater	
	Siluriformes	Ariidae	<i>Arius sp.</i>		Demersal. Coastal waters and estuaries.	
	Xiamen ^c	Beloniformes	Belonidae	<i>Tylosurus sp.</i>	Marine and freshwater	
		Clupeiformes	Clupeidae	<i>Konosirus punctatus</i>		Pelagic. Coastal waters and estuaries
<i>Sardinella lemuru</i>					Pelagic. Coastal waters.	
Pristigasteridae			<i>Ilisha elongata</i>		Pelagic. Coastal waters and estuaries	
			<i>Ilisha sp.</i>			
Engraulidae			<i>Coilia sp.</i>		Pelagic. Coastal waters and estuaries	
		<i>Setipinna taty</i> <i>Setipinna sp.</i>		Pelagic. Continental waters		
Perciformes		Carangidae	<i>Trachurus japonicus</i> <i>Trachurus sp.</i>		Pelagic.	
			Mugilidae	<i>Mugil sp.</i>	Benthopelagic or demersal. Coastal waters	
		Sciaenidae	<i>Johnius sp.</i>		Demersal. Coastal waters and estuaries	

Appendix 8 (Continue).

Indo-Pacific humpback dolphins				
Region	Order	Family	Species*	Habitat
Xiamen ^c	Perciformes	Sillaginidae	<i>Sillago sihama</i>	Demersal. Coastal waters and estuaries
		Serranidae		Marine, freshwater, and estuaries
		Sparidae		Marine, freshwater, and estuaries
		Stromateidae	<i>Pampus chinensis</i>	Benthopelagic. Coastal waters and estuaries
	Pleuronectiformes	Cynoglossidae	<i>Cynoglossus sp.</i>	Demersal. Coastal waters and estuaries
Mozambique^d				
	Albuliformes	Albulidae	<i>Alvula vulpes</i>	Pelagic. Coastal waters and estuaries
South Africa^e				
	Octopoda	Octopodidae	<i>Octopus sp.</i>	
	Teuthida	Loliginidae	<i>Loligo reynaudi</i>	
	Clupeiformes	Engraulidae	<i>Thryssa vitirostris</i>	Pelagic. Coastal waters and estuaries
		Clupeidae	<i>Hilsa kelee</i>	Pelagic. Coastal waters and estuaries
	Perciformes	Haemulidae	<i>Pomadasys olivaceus</i>	Coastal waters and estuaries
			<i>Pomadasys commersonii</i>	Demersal. Coastal waters, and estuarie.
		Mugilidae	<i>Liza richardsoni</i>	Demersal Coastal waters, and estuaries
			<i>Liza spp.</i>	Coastal waters and estuaries
			<i>Mugil Cephalus</i>	Benthopelagic. Coastal waters and estuaries
		Sciaenidae	<i>Otolithes ruber</i>	Benthopelagic. Coastal waters and estuaries
			<i>Argyrosomus thorpei</i>	Demersal. Coastal waters
		Scombridae	<i>Scomberomorus japonicus</i>	Pelagic. Coastal and offshore waters.
		Sparidae	<i>Diplodus sargus</i>	Demersal. coastal rocky reef areas
			<i>Pachymetopon aeneum</i>	Demersal. Coastal waters
	<i>Rhabdosargus sp.</i>			
	<i>Rhabdosargus thorpei</i>		Demersal Coastal waters and estuaries	

a(Heinsohn 1979, Heinsohn et al. 1980, Barros et al. 2004)

b(Parsons 1997, Jefferson 2000)

c(Wang and Sun 1982, Wang 1995)

d(Peddemors and Thompson 1994)

e(Cockcroft and Ross 1983, Ross 1984, Barros and Cockcroft 1991)

*Some species names have been changed to match current valid scientific names