SOCIO-SPATIAL ECOLOGY OF INDO-PACIFIC HUMPBACK DOLPHINS (*Sousa chinensis*) IN HONG KONG AND THE PEARL RIVER ESTUARY

by

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Abstract of thesis entitled

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The Indo-Pacific humpback dolphin (*Sousa chinensis*) in the Pearl River Estuary (PRE) is threatened by intense and ever-growing human activities. Effective conservation measures for this locally endangered species are urgently needed. This study assesses the area utilisation pattern and the social dynamics of this species in Hong Kong and the eastern section of the PRE (EPRE) and provides data that may prove fundamental in making informed conservation decisions.

Boat-based surveys were conducted in Hong Kong in 2010–2015 and throughout the EPRE in 2011–2015. Analyses of the spatial distribution of dolphin encounters and behaviours suggest that humpback dolphins in the EPRE prefer natural, undisturbed, rocky shores. Spatial modelling identified six core areas within the EPRE. Core areas of primary importance in the EPRE were located around southwest Lantau Island and Lung Kwu Chau in Hong Kong and western Neilingding Island and Sanjiao Island in mainland China waters. The other two core areas, located around eastern Qi’ao Island in China and southern Macau, appeared to be of secondary usage in this region. Foraging appeared to be the key determinant of the dolphins’ overall distribution pattern, and foraging probability was affected by distance to shore, locations, season, group size and year.

Analyses of photo-identification data collected in Hong Kong revealed that humpback dolphins form multiple, closely interacting social clusters that have different core areas but overlapping ranges. The majority of dolphins in Hong Kong belong to three social clusters. Temporal association patterns among social clusters appeared to be similar, and associations between dolphins were found to be highly fluid with various levels of temporal stability. The social and spatial segregation and variability in associations between individuals are most likely driven by the fine-scale differences in the area utilisation pattern of individuals.

To investigate the behavioural responses of humpback dolphins to anthropogenic changes in the environment, this study focused on assessing the impacts of two types of human activities: construction of large-scale infrastructure and fisheries. During the construction of the Hong Kong–Zhuhai–Macau Bridge in Hong Kong, dolphins’ core areas and ranges shifted away from the construction site and towards the south of Hong Kong; some of the responses differed between social clusters. Such changes suggest the distribution and abundance of resources are key factors shaping dolphins' social structure. Fisheries’ practices were also found to influence social dynamics and movement of humpback dolphins. After the ban on trawling in Hong Kong, trawler-associating dolphins changed their residency pattern, and associations between trawler-associating and non-trawler-associating dolphins increased. These findings highlight humpback dolphins' behavioural and social plasticity in response to environmental change.

This study demonstrates the importance of understanding animal behaviour and socio-spatial ecology in formulating effective conservation measures. It reveals that the marine protected area (MPA) coverage of behaviourally important areas in Hong Kong and the EPRE are insufficient. Such inadequacy has left critical habitats vulnerable to anthropogenic disturbances. An immediate revision to the MPA design in the EPRE is crucial for the conservation of humpback dolphins in the PRE.

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B.Sc. (Hons) The University of Hong Kong

Ph.D. Thesis

A thesis submitted in partial fulfilment of the requirement
for the degree of Doctor of Philosophy
at the University of Hong Kong
April 2017

Declaration

I declare that this thesis and the research work thereof represent my own work, except where due acknowledgement is made below and that it has not been previously included in thesis, dissertation or report submitted to this University or any other institution for a degree, diploma or other qualifications.

Signed ....

OR Ka Man

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Chapter 1 General introduction

Coastal habitats have long attracted human settlement. Rapid development along the coast and heavy human exploitation of riverine and estuarine resources have posed serious threats to the survival of numerous coastal species (Lotze et al. 2006; Lin et al. 2016). Large megafauna such as cetaceans are particularly vulnerable to intense habitat degradation, in part due to their life-history strategies that are characterised with long lives and low recruitment rates (Huang and Karczmarski 2014). In the face of human impacts, the baiji/ Yangtze River dolphins (*Lipotes vexillifer*) became the first freshwater cetacean driven to extinction (Turvey et al. 2007), and an increasing number of species and populations of coastal cetaceans are at risk and in urgent need of conservation attention (e.g. Burkhart and Slooten 2003; Jaramillo-Legorreta et al. 2007; Currey et al. 2009; Ross et al. 2010).

The humpback dolphin (genus *Sousa*) is one of the cetaceans that are at risk. They are medium-sized coastal cetaceans that inhabit shallow-water inshore habitats within the tropics and subtropics (Ross et al. 1994). The taxonomy of the genus has recently been revised, and four species are currently recognized: Atlantic humpback dolphins (*S. teuszii*) off tropical west Africa, Indian Ocean humpback dolphins (*S. plumbea*) in a narrow strip of coastal waters from South Africa to Myanmar (Burma), Indo-Pacific humpback dolphins (*S. chinensis*) ranging from east India to Southeast Asia, and Australian humpback dolphins (*S. sahulensis*) off north Australia and New Guinea (Jefferson and Rosenbaum 2014) (Fig. 1.1). Due to their preference for coastal habitats, which coincides with areas that are heavily used by humans, many populations of *Sousa* spp. are affected by multiple threats and are at risk of local extinction (Braulik et al. 2015; Collins 2015; Jefferson and Smith 2016; Parra and Cagnazzi 2016). However, only limited studies have been conducted throughout their ranges, and their biology remains not well studied (Jefferson and Curry 2015). Conservation actions are limited and restricted to areas that have conducted relevant studies. It has been suggested that more research on their population status and threats, and how to reduce the threats are required (Jefferson and Curry 2015).

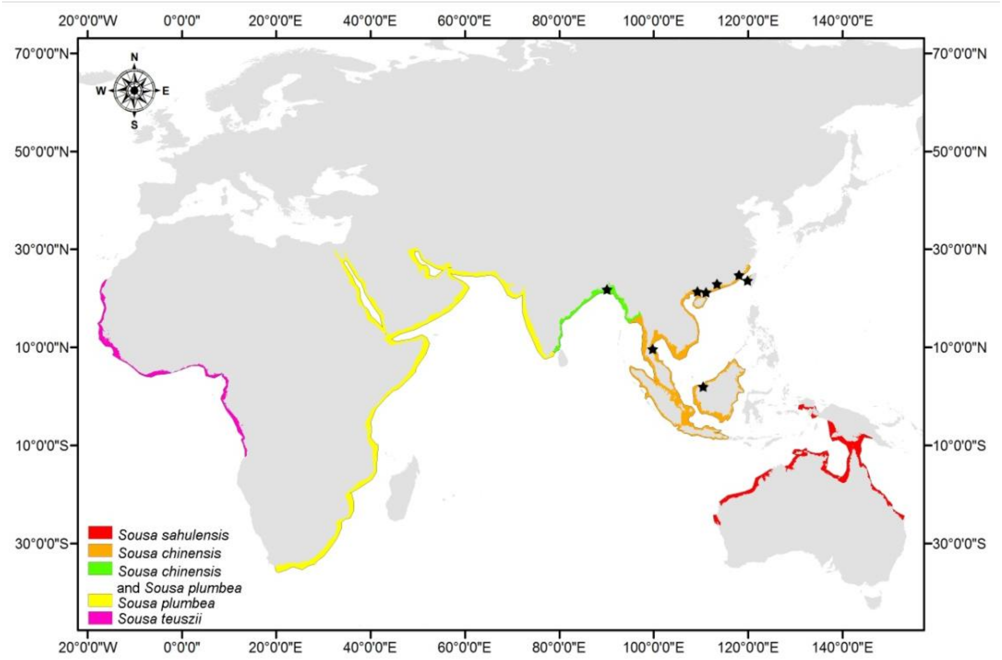

Figure 1.1 The geographic range of the currently recognised four species of the genus *Sousa* (data source: Braulit et al. 2015; Collins 2015; Jefferson and Smith 2016; Parra and Cagnazzi 2016). The localities of the previously studied populations of Indo-Pacific humpback dolphins (*Sousa chinensis*) with estimated population size are indicated with black stars.

The study presented in this thesis focuses on the Indo-Pacific humpback dolphin, a species that in the past two decades received considerably greater research attention than other species in the genus *Sousa*. This study aimed at the dolphins inhabiting coastal waters of Hong Kong and the Pearl River Delta, known to be facing particularly intense anthropogenic pressure (Karczmarski et al. 2016a, 2017).

1.1 Indo-Pacific humpback dolphins (*Sousa chinensis* Osbeck, 1765)

Indo-Pacific humpback dolphins (*Sousa chinensis*) inhabit coastal waters from China in the east and throughout Southeast Asia to either Bangladesh or eastern India in the west. Although their geographic range appears extensive, their distribution is most likely discontinuous because of their preference for estuarine habitats and gradual range reduction due to apparent habitat loss (Jefferson and Smith 2016). Throughout this range, previous studies were limited to only a few locations and mostly in Chinese waters. Off the coast of China and Taiwan, they are locally known as Chinese white dolphins. Hereafter they are referred to as 'humpback dolphins.'

There are around six to eight locations with representative records of humpback dolphins off the coast of China, which spans from southern China to the Yangtze River, and all of them centre at the mouths of large rivers (Jefferson 2000). In these areas, abundance estimates have been generated for the dolphins in waters off Xiamen (Chen et al. 2008, 2009), Zhanjiang (Zhou et al. 2007; Xu et al. 2015), in the Pearl River Estuary (Chen et al. 2010), and Beibu Gulf (Chen et al. 2009). Elsewhere in Asia, Indo-Pacific humpback dolphins are seen in waters off western Taiwan (Wang et al. 2012), Malaysia (Minton et al. 2016), Thailand (Jaroensutasinee et al. 2010; Jutapruet et al. 2015), and Bangladesh (Smith et al. 2015) (Fig. 1.1).

Similarly to other species of the genus *Sousa*, the Indo-Pacific humpback dolphins are typically found in estuarine habitats, shallow deltaic areas with mangrove vegetation, and off semi-protected natural rocky shores, in waters less than 30 m deep (Jefferson and Karczmarski 2001). They may enter rivers but are rarely found more than a few kilometres upstream (Jefferson 2000). They are considered to be opportunistic feeders that feed primarily on estuarine fish and occasionally some cephalopods (Jefferson 2000; Barros et al. 2004). There are no records of predation on Indo-Pacific humpback dolphins, likely because of the low number of large sharks and killer whales (*Orcinus orca*) in Asian estuaries (Jefferson and Smith 2016). They are usually seen in small groups with mean group size of less than eight (Jefferson 2000; Zhai 2006; Chang 2011; Jaroensutasinee et al. 2010; Xu et al. 2012; Dungan et al. 2015), except at a particular region of the Bay of Bengal, Bangladesh (Smith et al. 2015). Associations between individual group members are thought to be fluid and short-lasting. Strong bonds between individuals other than mother-calf pairs appear to be uncommon (Jefferson 2000; Chang 2011; Dungan et al. 2015).

Selected aspects of the life history of Indo-Pacific humpback dolphins have been studied only in two locations, off Taiwan and in Hong Kong waters (Wang 1995; Jefferson et al. 2000, 2012; Chang 2011; Chang et al. 2016). They appear to live up to 40 years (Jefferson et al. 2012), with gestation period lasting approximately 11 months (Jefferson 2000). The calving interval was estimated at ~3 years in waters off Taiwan (Chang et al. 2016) and ~5 years in Hong Kong (Jefferson et al. 2012). Sexual maturity is attained at 9-10 years of age for females and possibly later for males (Jefferson et al. 2012).

The species is currently listed as Near Threatened in the International Union for the Conservation of Nature (IUCN Red List), although this assessment dates back to 2008 when the currently recognised three species (*S.chinensis*, *S. plumbea*, and *S. sahulensis*) were considered as one species of *S. chinensis* (Reeves et al. 2008). A recent taxonomic revision and re-assessment of the species status suggests that the Indo-Pacific humpback dolphins should be classified as Vulnerable due to suspected population decline throughout its range, which is expected to worsen because of rapid urbanisation and a the lack of conservation measures (Jefferson and Smith 2016).

1.2 The Pearl River Estuary (PRE)

The Pearl River is the second largest river in China and the 13th largest in the world based on water discharge (Zhao 1990; Yin et al. 2004). The mean yearly discharge is 326×10^9 m^3, and 80% of the discharge occurs between April and September (Zhao 1990; Dong et al. 2006). The river consists of three main rivers: the Xi Jiang (West River), the Bei Jiang (North River), and the Dong Jiang (East River). They further branch into smaller rivers and flow into the South China Sea through eight outlets. Four outlets (Hengmen, Hongqimen, Jiaomen, and Humen) connect to the Lingding Bay where Hong Kong is situated, and another four outlets (Yamen, Hutiaomen, Jitimen, and Modaomen) connect to waters to the west of Lingding Bay (Fig. 1.2). Waters in the PRE are influenced by the Pearl River discharge, seawaters from the South China Sea, and water from South China Coastal Current (Zhao 1990). The estuary has mixed semi-diurnal tides and the tidal range is not more than 2 m (Mao et al. 2004). Nutrients are mainly from river runoff, land-based discharges and pollutants, and atmospheric deposition (Huang et al. 2003). Due to economic growth and development in the region, there has been a large increase of nutrients from anthropogenic sources in the last few decades (Yin et al. 2000). Construction of reservoirs appears to have contributed to a reduction of sediment discharge (Zhang et al. 2008). Nutrient loads, water and sediment discharge are likely to change in the coming decades (Harrison 2008; Zhang et al. 2008).

The region of the Pearl River delta has rapidly changed from an agricultural area to a developed urbanised region since the economic reform of China in 1978 (Yeh and Li 1999). Currently, it represents the world's largest urban area with a population size of about 42 million people in 2010 (World Bank 2015) and comprises of several economic centres that form the Pearl River Delta Economic Zone (Oizumi 2011).

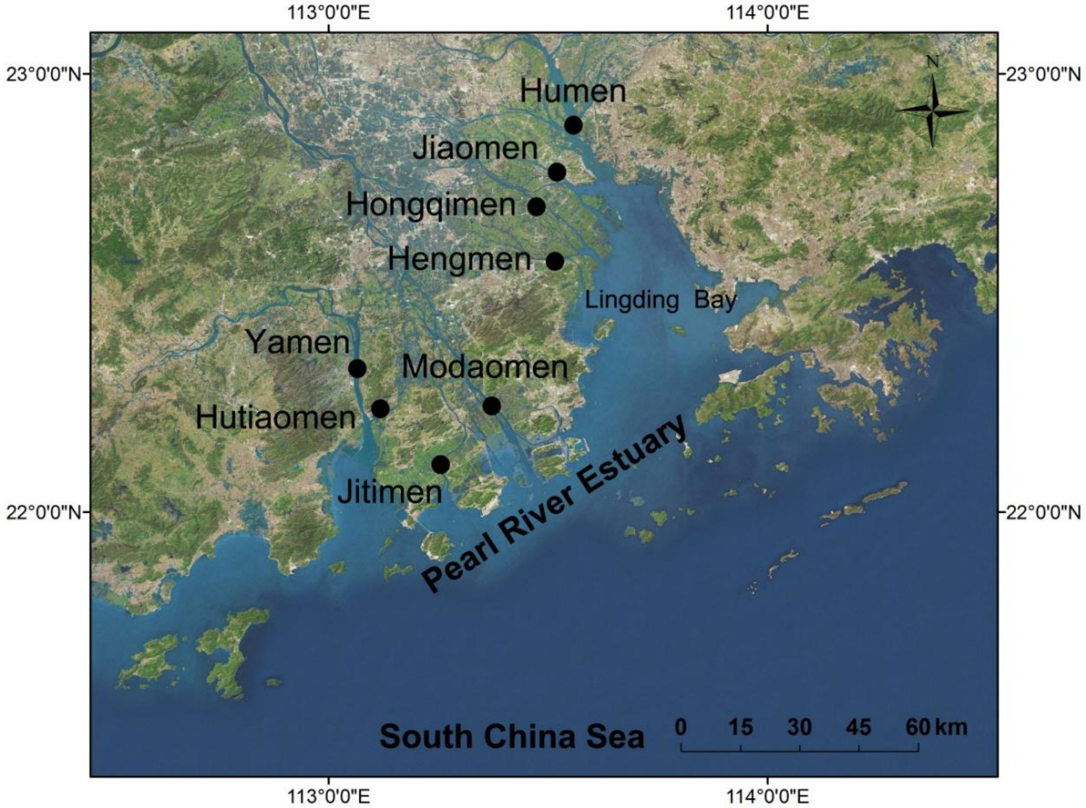

Figure 1.2 Map of the Pearl River Estuary (PRE) and the eight outlets of the Pearl River.

1.3 Humpback dolphins in the PRE

Line-transect surveys conducted in waters of the PRE in mid-2000s generated a preliminary abundance estimate of 2517-2555 dolphins (Chen et al 2010), which is substantially larger than any other population figures suggested for this species elsewhere or for any species of the genus *Sousa*. Even though this PRE estimate has to be treated cautiously, as the authors recognise (Chen et al 2010), and has been questioned because of its considerable methodological deficiencies (Karczmarski et al. 2016a; Chan and Karczmarski 2017) one could assume that the PRE population of humpback dolphins, seemingly the world's largest, may be robust enough to be long-term viable. However, the proximity to large urban and industrial centres of the Pearl River delta region, with severe anthropogenic pressures arising from coastal development and land reclamation, ever-increasing vessel traffic, pollutions, resource depletion, net entanglement and by-catch, and dredging for waste disposal and marine traffic (Jefferson 2000; Jefferson et al. 2009; Karczmarski et al. 2014; 2016a) places these dolphins at risk of local extirpation (Huang et al. 2012a; Karczmarski et al. 2017). Recent demographic analyses suggest that this population is currently declining with an annual rate of 2.46% and should be classified as Endangered, closely approaching a Critically Endangered status under the IUCN Red List criteria (Huang et al. 2012a; Karczmarski et al. 2016a). Such high risk of local extirpation highlights the urgency of conservation needs and the need for effective conservation measures.

Research of the PRE population began in the early 1990s, which was triggered by the rising concern regarding the potential impacts of coastal development projects in Hong Kong, most notably the airport reclamation project in northern Lantau Island (PADS 1989). Early studies investigated the distribution, behaviour, diet, group dynamics, and pollutant impacts on humpback dolphins in Hong Kong (Parsons 1997; Porter 1998; Jefferson 2000). At the same time, the long-term monitoring programme funded by the Hong Kong's government was initiated in 1995. The programme has continued to document the distribution and abundance of humpback dolphins in Hong Kong and is still ongoing today. Studies have extended to the mainland China part of the PRE since the mid-1990s (Jefferson 2000; Chen et al. 2010, 2011). As such, the humpback dolphin population in the PRE is the longest studied population of humpback dolphins in the world.

Previous and recent studies in Hong Kong and the PRE have provided to a varying extend information on their life history, pollutant accumulation, distribution and abundance, behaviours and social interactions (e.g. Jefferson 2000; Jefferson et al. 2012; Hung and Jefferson 2004; Hung 2008; Dungan et al.

2012; Gui et al., 2014, 2017; Zheng et al. 2016). However, population parameters and structure, social dynamics, range use patterns and habitat choice in relation to specific behaviours, and how social and spatial patterns change in response to human activities remains poorly understood; and much of the previous work has suffered from various methodological deficiencies (see Wilson et al. 2008 for a detailed critique). Moreover, the majority of previous work on population ecology was conducted in Hong Kong, while areas outside Hong Kong in the greater PRE remain largely unexplored.

1.4 Research objectives and thesis outline

This PhD study focuses on the social and spatial ecology of humpback dolphins. This includes investigation of the relationships between individuals, within and between groups, and relates these patterns to ecological processes. It also includes investigations on the spatial dynamics of the dolphin groups and their relationships with the natural environment.

Attempts have recently been made to define the social structure of humpback dolphins in Hong Kong (Dungan et al. 2012). However, it was based on the association pattern of a small proportion of dolphins recorded in Hong Kong. It is, therefore, worthwhile to revisit the structure and the group dynamics with the inclusion of more individuals in a substantially larger dataset. Besides, while there is a vast amount of coastal development and human activities in the PRE, their impacts on the social dynamics of humpback dolphins have never been empirically documented. Between 2011 and 2013, a large-scale construction project commenced and fisheries practices changed in Hong Kong, which provided a valuable opportunity to study the response of humpback dolphins to abrupt environmental changes. Such information may prove informative, perhaps even essential to the development of effective conservation measures for this heavily anthropogenically affected population.

Aiming to protect the habitats of humpback dolphins, marine protected areas (MPAs) have been established in Hong Kong since 1997 and in mainland China waters since 1999. However, their effectiveness have yet to be assessed. Moreover, given the rapid urban expansion in the eastern PRE (EPRE), particularly in Hong

Kong, there is a need to identify biologically important areas of humpback dolphins and prioritise the areas for further protection.

By addressing these knowledge gaps, the study presented in this thesis aims to advance the understanding of the area utilisation pattern and the social dynamics of humpback dolphins in Hong Kong and the EPRE in relation to a changing environment and provides management recommendations for conservation of humpback dolphins in this region. To fulfil these aims, there are four main objectives in this study and the thesis is structured as follows:

Objective 1. Advance the understanding of humpback dolphins' distribution pattern in Hong Kong and identify priority areas for protection based on their spatio-behavioural dynamics and pattern of habitat selection (**Chapter 2**).

Objective 2. Investigate and quantify the social structure, group dynamics, and range use patterns of humpback dolphins in Hong Kong (**Chapter 3**).

Objective 3. Investigate anthropogenic impacts on the social dynamics and movement of humpback dolphins in Hong Kong (**Chapter 4**).

Objective 4. Investigate and quantify the area use pattern of humpback dolphins in the EPRE and assess the adequacy of the current MPAs in protecting important habitats in the region (**Chapter 5**).

The final chapter (**Chapter 6**) summarises the key findings of this study, synthesises the factors that drive the socio-spatial dynamics of humpback dolphins, discusses their conservation implications, and provides suggestions for future research.

Chapter 2 Priority sites for Marine Protected Area designation for Indo-Pacific humpback dolphins in Hong Kong [1]

2.1 Introduction

Resources are naturally patchy in occurrence, which leads to a differential usage of available habitats by animals across their range. Determining the area utilisation pattern of animals, especially their spatio-behavioural use of the environment and the factors that affect the occurrence and distribution of biologically important behaviours, can facilitate the identification of ecologically important areas (Hastie et al. 2004; Ashe et al. 2010). This in turn can provide scientific basis for prioritising and zoning areas for conservation and management (Hooker & Gerber 2004; e.g. Karczmarski et al. 1998; Lusseau and Higham 2004; Cañadas et al. 2005).

The concept of Marine Protected Area (MPA) is a widely adopted conservation tool to protect marine ecosystems and species of concern. The commonly adopted definition is the same as for a terrestrial protected area. According to the International Union for the Conservation of Nature (IUCN), it is ‘a clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values’ (Dudley 2008). In practice, MPAs are areas in which anthropogenic activities that threaten the population either directly or indirectly are prohibited or considerably controlled (Carr 2000). In a coastal environment, habitats are often intensively modified by humans, and coastal species can be under constant multiple threats (Gray 1997). Protecting ecologically important sites for the target species becomes critical in relieving some of the pressure caused by habitat loss, and this is generally a fundamental objective of MPAs.

For animals inhabiting marine environments, distant locations are more likely to be functionally connected than in terrestrial environments (Jones 2002; Carr et al.

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[1] This chapter is currently submitted to Journal of Applied Ecology and under peer-review as follows: Or, C.K.M. and Karczmarski, L. Marine Protected Area designation based on behavioural ecology: The case of Indo-Pacific humpback dolphins in Hong Kong.

2003). This increases the vulnerability of an area to distant ecological changes and human disturbances, and increases the difficulty of setting up robust MPAs. Added to the challenge is the pattern of spatial ranging of many marine species (Carr et al. 2003), which lowers the feasibility of achieving MPAs that have sufficient coverage on the animals' range. The prevalent pattern among existing MPAs is that of a frequent failure to safeguard the species they are meant to protect (see examples in Agardy et al. 2011) and the reasons are manifold, especially in the case of marine mammals (Agardy et al. 2011). There are also cases, however, of MPAs that are indeed effective in conserving marine mammals (e.g. Gormley et al. 2012) as long as their design and designation are based on sound scientific evidence.

To create effective MPAs for cetaceans, their design has to be based on the area utilisation pattern of the target species to preserve their core areas and critical habitats (Ross et al. 2011). These critical areas and habitats are the locations used regularly by animals for essential daily activities needed for their well-being and survival, and for sustaining the health of the population (Hoyt 2011; Ross et al. 2011). In order to identify these important areas, studies have to investigate not only the distribution of a species but also the spatial pattern of the species' behaviour. Despite this being fundamentally challenging for wide-ranging species living in marine environments, identification of critical habitats with the incorporation of behaviour data has been applied in marine mammals living in some restricted habitats. This includes identification of critical habitats such as resting grounds of spinner dolphins *Stenella longirostris* in the main Hawaiian Islands (Thorne et al. 2012), resting and socialising areas of bottlenose dolphins *Tursiops* spp. in Doubtful Sound (Lusseau and Higham 2004), foraging grounds of southern resident killer whales *Orcinus orca* in the north-east Pacific (Ashe et al. 2010) and nursery areas of dusky dolphins *Lagenorhynchus obscurus* in Kaikoura, New Zealand (Weir et al. 2008).

In Hong Kong, MPAs are designated and managed under the Marine Parks Ordinance and its Regulations, which were enacted in 1995 (Morton 1998). The Ordinance provides the legal framework for designating, controlling and managing two types of MPAs: marine parks and marine reserves. Both types of

MPAs prohibit trawling and limit boat speed to 10 knots but marine parks are established for conservation and recreation, in which multiple use is allowed and only destructive activities are prohibited or controlled. Marine reserves are considerably more restrictive and allow only activities related to conservation and scientific research.

The first and to date the only protected area for humpback dolphins in Hong Kong waters was designated in 1996 (Liu and Hills 1997). This MPA, the Sha Chau and Lung Kwu Chau Marine Park, covers a sea area of 12 km^2 and is managed similarly as other marine parks in Hong Kong over which the boat speed is limited to 10 knots, and bottom trawling is prohibited. The bottom trawling was banned in the waters of the Sha Chau – Lung Kwu Chau Marine Park since its establishment, prior to the territory-wide trawl ban introduced in Hong Kong in December 2012; although various other forms of fishing have always been allowed, on permit basis, within the park boundary.

Numerous concerns regarding the viability and effectiveness of this marine park have been expressed since early stages of its planning and implementation, as it was seen to be far too small to maintain sufficient quantity of habitat to support the needs of humpback dolphins inhabiting the vastly degraded coastal environment of Hong Kong (Hoffman 1995; Liu and Hills 1997). Furthermore, the park is in close proximity to a high-speed ferry route and has an aviation fuel receiving facility that is in operation within the park boundary since 1997.

Over the past two decades, a number of protected areas for humpback dolphins in Hong Kong have been proposed, based on the dolphin distribution data available at that time (Morton 1998; Porter 1998; Tsang and Milicich 1999; Morton 2000; Hung 2008). Early recommendations by Morton (1998) stated that a marine park covering northern, western and southern Lantau Island is needed (see Appendix 1). Porter (1998) proposed a marine reserve that covered western to southern Lantau Island and a marine park that enveloped the marine reserve and extended to southern mainland China’s waters (see Appendix 1). It was further revised by Morton (2000) and a large marine reserve covering western Lantau Island to the Soko Islands was suggested (see Appendix 1). Feasibility study conducted in

1998-1999 proposed two marine parks; one located off southwest Lantau Island and another at Soko Islands (Tsang and Milicich 1999; see Appendix 3). Hung (2008) evaluated these recommendations and, using dolphin distribution data collected in 1996-2005, proposed establishing a small marine reserve off central-west Lantau Island, near Tai O village, an area known to be frequented by the dolphins; and two other marine parks, one off southwest Lantau and another around Brothers Islands off north Lantau (see Appendix 3). Hung (2008) also suggested protecting habitats that were used by both humpback dolphins and finless porpoise (*Neophocaena phocaenoides*) and proposed establishing a Site of Special Scientific Interest (SSSI) around southern Lantau Island (see Appendix 3). In Hong Kong, SSSIs are generally set up to ensure that scientifically important areas are given consideration when development projects are proposed nearby and no active management is required. More recently, in 2014, a new protected area was suggested to compensate for a newly proposed construction of a third runway of the Hong Kong International Airport (Airport Authority Hong Kong 2014). This newly proposed MPA was suggested to cover waters off north Lantau Island and connect the existing Sha Chau – Lung Kwu Chau Marine Park with the proposed marine park at Brothers Islands.

Of those various past and recently suggested MPAs, four are currently under official consideration, namely: the The Brothers Marine Park, Southwest Lantau Marine Park, Soko Islands Marine Park, and the third runway’s "compensatory" marine park off north Lantau Island (see the Discussion section for further details). The Brothers Islands Marine Park is planned to be established on 30 December 2016. The Southwest Lantau Marine Park and Soko Islands Marine Park are both tentatively planned to be designated in early 2017. The “compensatory” marine park is to be designated upon the completion of the reclamation work of the third runway project (the 3rd runway of the Hong Kong International Airport), which is currently estimated to be in 2023.

Similarly as in the past case of the Sha Chau – Lung Kwu Chau Marine Park, concerns have been voiced regarding the abovementioned MPAs, pointing out the superficiality of the designs and insufficient considerations of the available scientific evidence during the process that has led to the MPAs' designation (e.g.

Or et al. 2013; CEL 2014; Or and Karczmarski 2015a; 2015b; Karczmarski et al. 2016a). Some of the proposed conservation areas are close to major construction sites and intended to function as a “compensation” measure for large-scale construction projects in Hong Kong. This on its own account faces criticisms (e.g. WWF-Hong Kong 2014; Karczmarski 2015; Karczmarski et al. 2016a) as the habitats will already be largely degraded by the extensive construction projects before the MPAs come to existence. Moreover, these MPAs may not necessarily cover the prime habitats of the dolphins they are meant to protect, and little attention has been given to identify what constitutes primary habitats for these animals on Hong Kong waters. This conundrum of issues reflects a considerable misconception and evident lack of prioritisation in the MPA designation that should be, but currently is not based on area utilisation patterns and behaviour of humpback dolphins in Hong Kong. Such omission of critical habitats in MPA is a severe failure in the designation process. This contrasts with the general guidance in MPA designation given by the IUCN (Dudley 2008) and Hoyt (2011), which recommend stricter protection for critical habitats.

The study presented in this chapter investigates spatio-behavioural dynamics of humpback dolphins in Hong Kong waters. It examines factors that influence dolphins' daily behaviours and quantifies their spatial distribution patterns by constructing area utilisation models with data on site-specific behaviours. With the application of mixed effect models and Geographic Information System (GIS), this study identifies the pattern of habitat use and preferences of humpback dolphins in Hong Kong waters, the factors affecting their foraging behaviour, and proposes a framework for local MPA designation that is based on the spatio-behavioural dynamics of the animals at the centre of the long ongoing conservation debate. The chapter concludes with a suggestion of a conservation framework that may well be the last chance to secure the continuous presence of these animals in Hong Kong waters.

2.2 Methods

2.2.1 Study area

The territorial waters of Hong Kong (HK), formerly a British colony and currently the Hong Kong Special Administrative Region (HKSAR) of the People’s

Republic of China, represent the easternmost reaches of the Pearl River Estuary (PRE). This study focuses on western HK waters (Fig. 2.1), which is the only region within HK territorial waters known to be frequented by humpback dolphins (Hung 2008). The hydrography in the area is strongly influenced by the outflow of the Pearl River. In the summer months, the salinity decreases from 29.3-32.3 psu to 21.7-25.8 psu (Data summarized from EDP HKSAR, 2015) and the turbidity increases because of the increased rainfall and freshwater outflow (Morton 1990). The surrounding shores are primarily rocky or have been anthropogenically altered (through land reclamation) with enforced concrete structures, with occasional stretches of sandy shores or embayments. Despite its limited size, this area is intersected by a major cargo shipping lane and criss-crossed by several high-speed ferry lanes connecting HKSAR with seven ports in mainland China. During the study period, the region experienced large coastal infrastructure construction, the Hong Kong–Zhuhai–Macau Bridge (HKZMB), which started in December 2009 in mainland China and was followed in November 2011 by similar coastal construction work in HK waters.

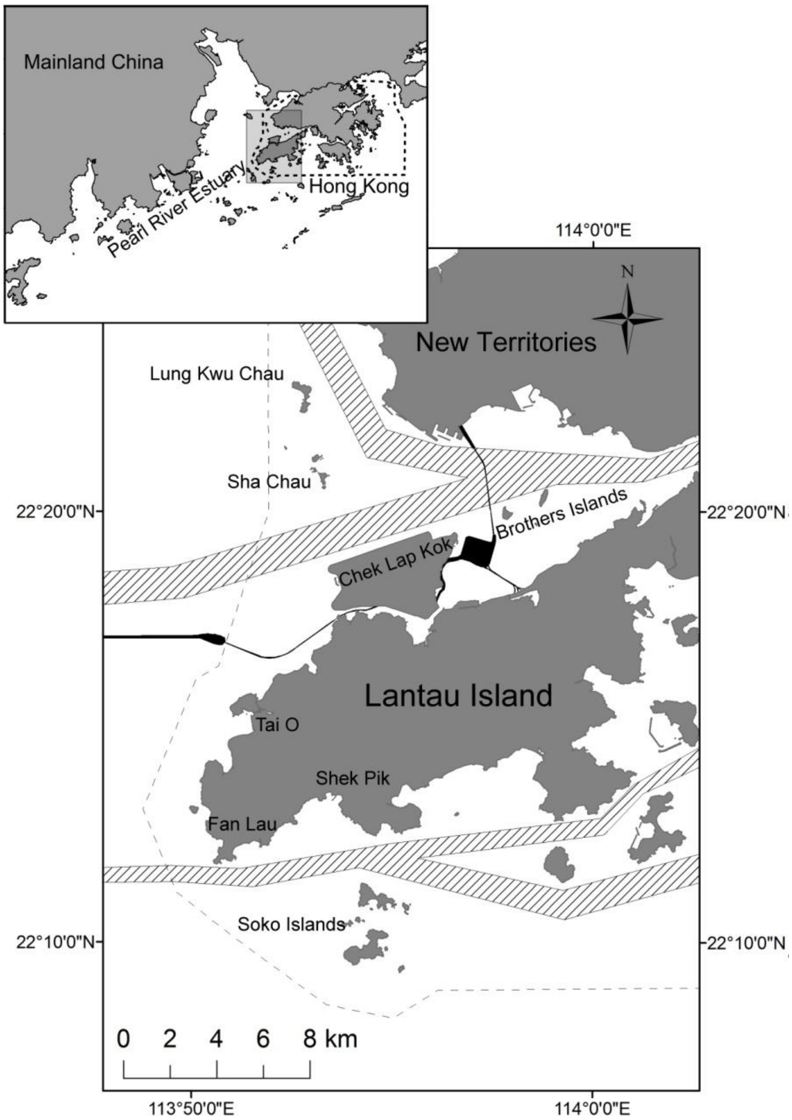


Figure 2.1 Western Hong Kong waters, the study area, represent the eastern reaches of the Pearl River Estuary (PRE). Whenever sea conditions permitted, the boat-based surveys covered the entire study area in a survey-day. Frequently, however, surveys had to be limited to either the northern section (from Tai O peninsula to Chek Lap Kok, Sha Chau – Lung Kwu Chau, New Territories and the Brothers Islands) or the southern section (from Tai O peninsula to Fan Lau, Shek Pik peninsula and Soko Islands) of the study area. The administrative boundary of the Hong Kong Special Administrative Region (HKSAR) is denoted by the dotted black line. A large-scale coastal infrastructure, the Hong Kong–Zhuhai–Macau Bridge (HKZMB), and its associated facilities (under construction during the study period) are indicated as black polygons. Shipping channels are denoted as hatched areas.

2.2.2 Field data collection

Field surveys were conducted using an 8-m boat powered with a 140-HP 4-stroke outboard engine from October 2011 to December 2014, with sea state ≤ 3 in Beaufort scale. Surveys did not follow predetermined routes but searched for dolphins as part of an ongoing photo-ID research. A dedicated effort was made to cover the surveyed area as uniformly as possible, and whenever sea conditions permitted, surveys covered the entire study area in one survey-day. At times, however, surveys had to be limited to either the northern or southern section of the study area (see Fig. 2.1).

Once dolphins were sighted, the initial behaviour of the animals was noted and, subsequently, environmental data, geographic location and animal behaviour were recorded at the start and end of the encounter and in 10-minute intervals throughout the encounter. Environmental data included water depth and sea surface temperature, both measured with a hand-held Hawkeye H22PX depth finder, which delivered measurements with a precision of 1/10 unit (0.1m and 0.1 °C). Geographic locations were recorded with Garmin Geographic Positioning System units GPSMAP 78S and 62X. The distance to the nearest shore was initially visually estimated and subsequently confirmed by plotting the geographic coordinates of each encounter on a map using ESRI ArcMap 9.3.1 and calculating the distance to the nearest shore.

As sampling could not always be performed at exact 10 minutes intervals, data collected within +/- 2 minutes of the 10 minutes interval were used for that particular interval.

Dolphin behaviour was recorded as the predominant behaviour of the majority of group members, following Karczmarski and Cockcroft (1999) and Karczmarski et al. (2000), which corresponds to the definition of predominant behaviour by Mann (2000), i.e. over half of the individuals in the group engaged simultaneously in the same specific behaviour. Definitions of behavioural states were adopted from Karczmarski and Cockcroft (1999) and Karczmarski et al. (2000), as well as other recent studies (e.g. Keith et al. 2013; Koper et al. 2016) and they closely resemble several similar studies conducted elsewhere (e.g. Lusseau and Higham 2004; Parra 2006; Degrati et al. 2008). These behavioural states are as follows:

Foraging: irregular, often steep and/or fast dives, including rapid accelerations, in varying directions with short swimming distances between dives; frequently accompanied by fish seen at the surface, seemingly escaping the dolphins' pursuit.

Travelling: movement in one persistent direction with relatively regular surfacing pattern and breathing intervals.

Milling: localised movements of individuals with relaxed asynchronous surfacing in relatively close but varied proximity of one another and frequent changes in direction.

Socialising: active and often vigorous interaction with other dolphins, involving body touching and chasing and frequent energetic displays, with irregular distances between individuals and irregular dive durations.

Resting: low-energy activity, usually relatively motionless at the surface with limited movement.

Undetermined: activities that could not be assigned to any of the above categories, or when the animals were lost from sight.

2.2.3 Utilisation distribution analyses

Geographic coordinates (GPS positions) of dolphin sightings, along with associated behavioural data were used to investigate spatio-behavioural patterns with the application of ESRI ArcMap 9.3.1 as analytical tool. The overall and behaviour-specific utilisation distribution, which refers to the relative frequency distribution for the recorded positions of the animals over time (Van Winkle 1975), were quantified with the application of Local Convex Hulls (LoCoH) models (Getz and Wilmers 2004; Getz et al. 2007). Different from analysis of sighting density using grid and directly calculating sighting density within grids (where the grid sizes by itself may affect the results; Vandermeer 1981), analyses of utilisation distribution does not produce space use pattern confined by pre-set grids and thus is not affected by grid size or placement (Silverman 1986). Instead, irregular contours (isopleths) are constructed that indicate the probability of area/habitat use by the animals. Since it is a quantification of a relative spatial use, such probability contours are often applied in the identification of critical areas and 50% and 95% isopleths are commonly used to delineate core areas and overall range estimations (Powell 2000; Laver and Kelly 2008).

Fixed k-Local Convex Hulls (k-LoCoH; Getz and Wilmers 2004; Getz et al. 2007) were calculated to estimate utilisation distributions (UDs), with 95% and 50% isopleths for the overall occurrence and core area estimations, respectively, using the adehabitat package (v 1.8.6; Calenge 2006) in R (v 2.1.3; R Development Core Team 2011). The symbol k refers to the number of nearest neighbour points from which convex hulls were created. Calculations of k followed Getz et al. (2007), in which $\mathrm{k} = \sqrt{\mathrm{n}}$ and n is the total number of points. The calculation of area size was based on projected coordinates in the Hong Kong 1980 Grid coordinates system. To test for independence of spatial data, significance of autocorrelation was calculated as Swihart & Slade Index and Schoener Index in ArcGIS 9.3.1 (ESRI 2008) through Home Range Tools (Rodgers et al. 2007). When significant autocorrelation of data is found, it is indicated by the Swihart & Slade Index > 0.6 (Swihart and Slade 1985) or the Schoener Index <1.6 or >2.4 (Schoener 1981).

2.2.4 Factors influencing foraging probability

After determining the most frequently displayed behaviour (which was foraging; see Results), to investigate the influence of environmental variables on foraging, the response variable (foraging *vs*. other) was defined as a binary factor, with the presence of foraging as 1 and all other behaviours as 0. Undetermined and mixed foraging behaviours were discarded as they could not be categorised as either 1 or 0.

The fixed variables used in the generalised linear mixed models were latitude (N), longitude (E), year, group size, depth (metres), sea surface temperature (SST,

°C), tidal state and distance from shore (metres). Latitude and longitude standing alone represent the locations and a measurement of proximity to the estuary. Geographic coordinates were projected in the Hong Kong 1980 Grid system. The year was incorporated to detect any potential annual fluctuation. Gregariousness, denoted as group size, was used to represent the group dynamics. Sea surface temperature was taken as a proxy for seasonal influence. As indicated by several studies of humpback dolphins elsewhere (Karczmarski et al. 2000a; Parra et al. 2006; Keith et al. 2013; Lin et al. 2013), depth, distance to shore and tides are all parameters likely to influence the dolphins' behaviour. Consequently, depth was collected in the field and distance to shore was calculated in ArcMap 9.3.1 (as described above). Tidal states were defined as 'High' and 'Low' for the time period of 1-hour before and after high and low tides. 'Flood' and 'Ebb' were defined as the periods in between High and Low. The tide data were obtained from the tide tables published by the Hong Kong Observatory. Two-way interactions between latitude, longitude and distance to shore were included. As data were collected by the means of boat-based group follows, the 'Group' value was set as the random factor in order to account for a nested data structure. Sightings with missing data in the fixed variables were removed from the analysis.

All continuous variables were standardised to a mean of 0 and standard deviation of 1 to facilitate comparison between coefficients. Collinearity among predictors was examined using variance inflation factors (VIF) and using the 'vif.mer' function (downloaded from https://github.com/aufrank/R-hacks/blob/master/mer-utils.R) in R. A predictor with a VIF higher than 3 is considered collinear and shall be removed from the analysis (Zuur et al. 2009).

All analyses were performed in R (v.3.1.2; R Development Core Team). A generalised linear mixed model with the maximum likelihood approximated by an adaptive Gauss-Hermite quadrature was constructed in the lme4 package (v 1.1-7; Bates et al. 2014). The Akaike Information Criterion (AIC) was used to compare the fit of alternative models. Interaction terms that improved the model fit compared to the global model were incorporated for further modelling. After ranking by the AIC, models with differences in AIC values (Δ AIC) < 10 from the most parsimonious model underwent model averaging to account for model uncertainty in the R package MuMln (v1.12.1; Bartoń 2014). Models with Δ AIC ≥ 10 are generally seen as not well supported to be a candidate model (Burnham and Anderson 2004; Burnham et al. 2011). The relative importance of variables was calculated as a sum of the Akaike weight (w_i) of all the models for which a particular variable was found.

The predictive power of the averaged model was assessed using the receiver operating characteristic (ROC) approach through k-fold cross validation (Boyce et al. 2002). The whole data set was divided randomly into 5 subsets. In each round of the cross-validation process, 4 out of the 5 subsets were taken to train the model as the training data, followed by validation using the remaining subset as the testing data. ROC curve was constructed by plotting the probability of a positive prediction of presence (sensitivity) against 1-probability of positive prediction of absence (1-specificity). The model's predictive power was measured using the area under the curve (AUC), with 1 referring to a perfect model performance and 0.5 as no predictive power (Boyce et al. 2002). The process was repeated until each of the divided data was used as the testing data. The ROC analysis was performed by R package pROC (v1.8; Robin et al. 2011).

As humpback dolphins in Hong Kong are known to follow fishing boats, especially trawlers, to forage (Jefferson 2000; Hung 2008), to eliminate any possible influence of fishing boats on the occurrence of foraging, the procedure of mixed modelling was repeated for a dataset that excluded sightings of dolphins associated with fishing boat(s).

2.3 Results

2.3.1 Database

During the 38 months of field data collection, 226 surveys were completed, with 1037.3 hours spent at sea, a total of 1133 dolphin encounters, and 445.4 hours of collecting environmental data and recording dolphin behaviour.

To minimise spatial bias between years, the data were subsampled to achieve equal survey effort, which was defined as an equal number of survey days across the entire study area each year. This resulted in a total of 112 surveys that were used for further analyses. Of these, 48 surveys covered the whole study area and 64 surveys covered either the northern or southern part of the area (Table 2.1, Fig. 2.2). Combining the data across years, the whole study area was surveyed 80 times during the study period.

Table 2.1 Survey effort in Hong Kong waters (2011-2014) after subsampling that equalised the number of survey days across the whole study area in each year.

	Number of survey days				
	2011	2012	2013	2014	Total
Full area coverage	0	4	21	23	48
North only	2	11	11	8	32
South only	2	11	11	8	32
Total	4	26	43	39	112

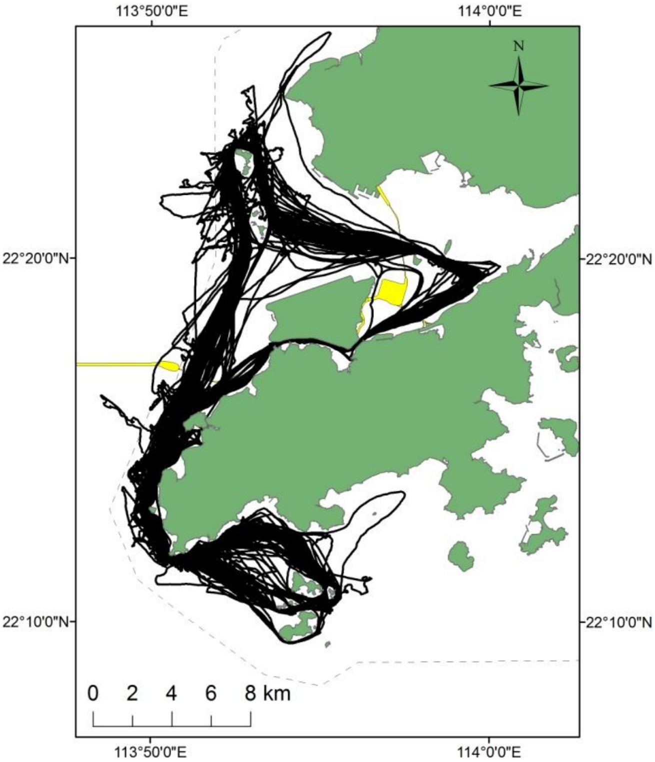


Figure 2.2 Survey tracks in western Hong Kong waters conducted between September 2012 and December 2014, displayed after sub-sampling that equalised the number of survey days across the whole study area in each year. The track records are not available prior to September 2012, but survey protocol was consistent throughout the study period.

2.3.2 Spatial pattern of range use

Area utilisation pattern derived from the full subsampled dataset was well-defined, with core areas (50% isopleth) clustered around southwest Lantau Island and northern Lung Kwu Chau, while the overall range (95% isopeth) expanded to southern Lantau Island and Soko Islands in the south and northern Lantau, Sha Chau and the Brothers Islands in the north (Fig. 2.3).

The most frequently seen behaviour was foraging (~46%), followed by travelling (~28%) and milling (~12%), while socialising and resting were rarely seen (cumulatively ~2%). Behaviour classified as ‘undetermined’ and cases of ‘mixed’ behaviour, in which two behaviours were equally dominant, were not used in further spatial and temporal analyses; see Table 2.2 for details.

The exclusion of mixed and undetermined behaviours had a minimal impact on the overall estimate of the area utilisation pattern, and there was no indication of autocorrelation (Swihart & Slade Index < 0.6; Schoener Index >1.6 or <2.4); see Table 2.3. The k-LoCoH utilisation distributions (UD) for different behaviours showed a substantial overlap of the utilisation range and core areas of different behaviours, but produced different spatial estimates, especially for the 50% isopleth core areas (Fig. 2.4, Table 2.3). The 50% UD for foraging was distinctly clustered close inshore off southwest Lantau Island and east off Lung Kwu Chau (Fig. 2.4), with an overall area approximately half the size of the 50% UD for travelling (Table 2.3), which extended further and considerably broader than any other behaviour. The UD for milling was notably small, with few discontinuous core areas scattered across the utilisation range, including inshore waters east of Brothers Islands. Socialising and resting were too infrequent to calculate k-LoCoH UDs, but 87% (*n*=20) of the records of socialising were within the foraging range, and 17.3% were within foraging cores.

The majority (>80%) of the utilisation range and dolphin core areas (95% and 50% UD, respectively) were outside the waters protected by the Sha Chau – Lung Kwu Chau Marine Park, and only a small fraction (~6%) of foraging cores were within the park boundary (Table 2.4).

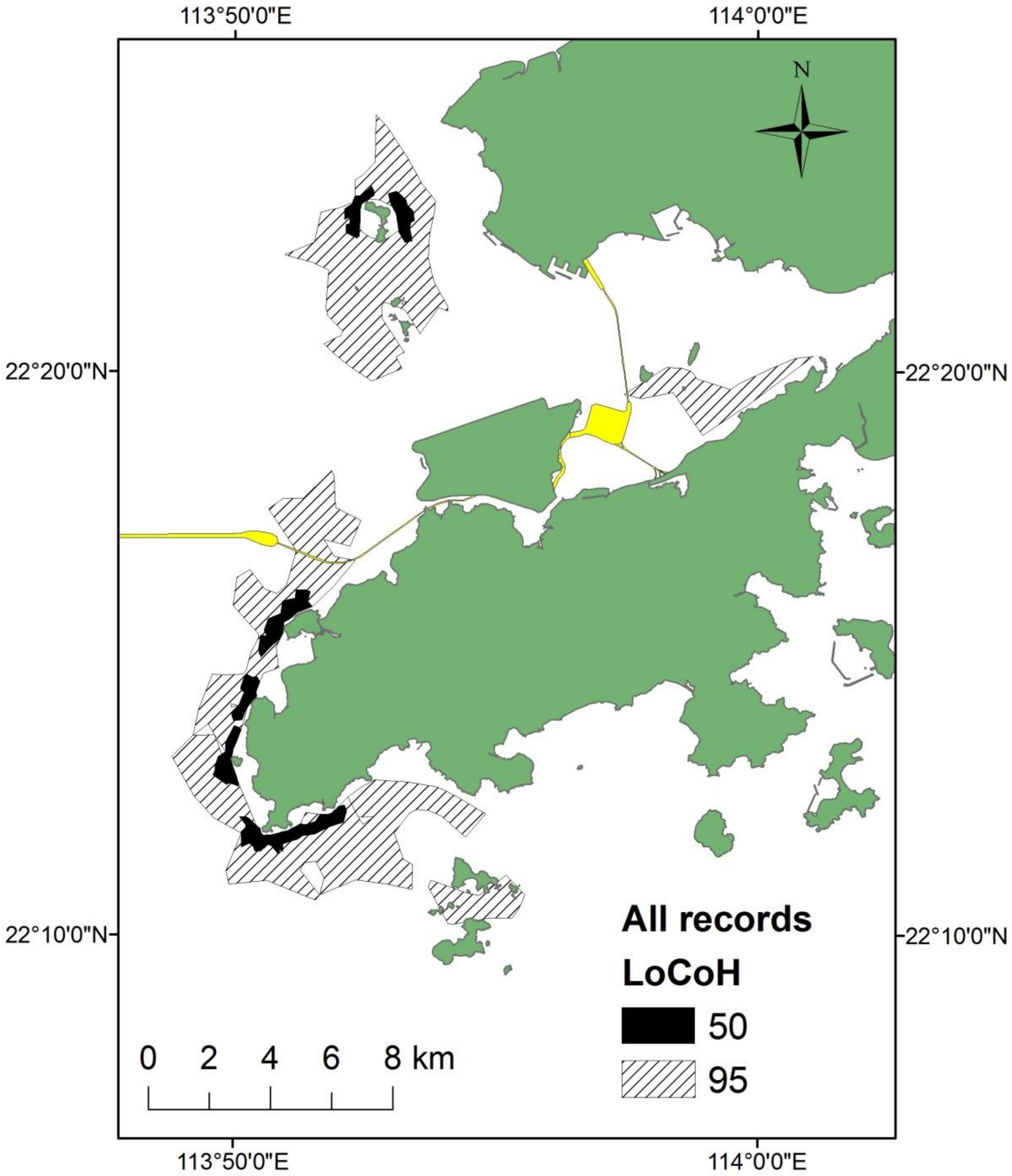


Figure 2.3 Area utilisation pattern of Indo-Pacific humpback dolphins in Hong Kong waters estimated with 50% and 95% isopleths of Local Convex Hull (LoCoH) for all sightings recorded in Hong Kong during 2011-2014.

Table 2.2 Number of GPS points of the behaviour of Indo-Pacific humpback dolphins recorded in Hong Kong waters during 2011–2014.

	Total	Percentage (%)
Foraging	614	46.1
Travelling	367	27.6
Milling	162	12.2
Socialising	23	1.7
Resting	5	0.4
Foraging-Socialising	3	0.2
Foraging-Milling	34	2.6
Foraging-Travelling	21	1.6
Milling-Resting	2	0.2
Milling-Socialising	5	0.4
Travelling-Milling	22	1.7
Undetermined	74	5.6
Total	1332	100

Table 2.3 Calculated areas (in km^2) of Local Convex Hull (LoCoH) estimates at 95% and 50% utilisation distributions for all sightings recorded during 2011-2014 in Hong Kong waters. There was no indication of significant spatial autocorrelation; none of the calculated values of Swihart & Slade Index (Swihart and Slade 1985) was > 0.6 and none of the values of Schoener Index (Schoener 1981) was < 1.6 or > 2.4. Sample sizes of socialising, resting and mixed behaviours were too small to generate estimates.

	LoCoH 50%	LoCoH 95%	Swihart & Slade Index	Schoener Index	*n*
All records	6.10	62.41	0.30	1.80	1332
Foraging	3.12	35.13	0.27	1.90	614
Travelling	6.15	49.69	0.22	1.82	367
Milling	1.86	19.45	0.53	1.64	162

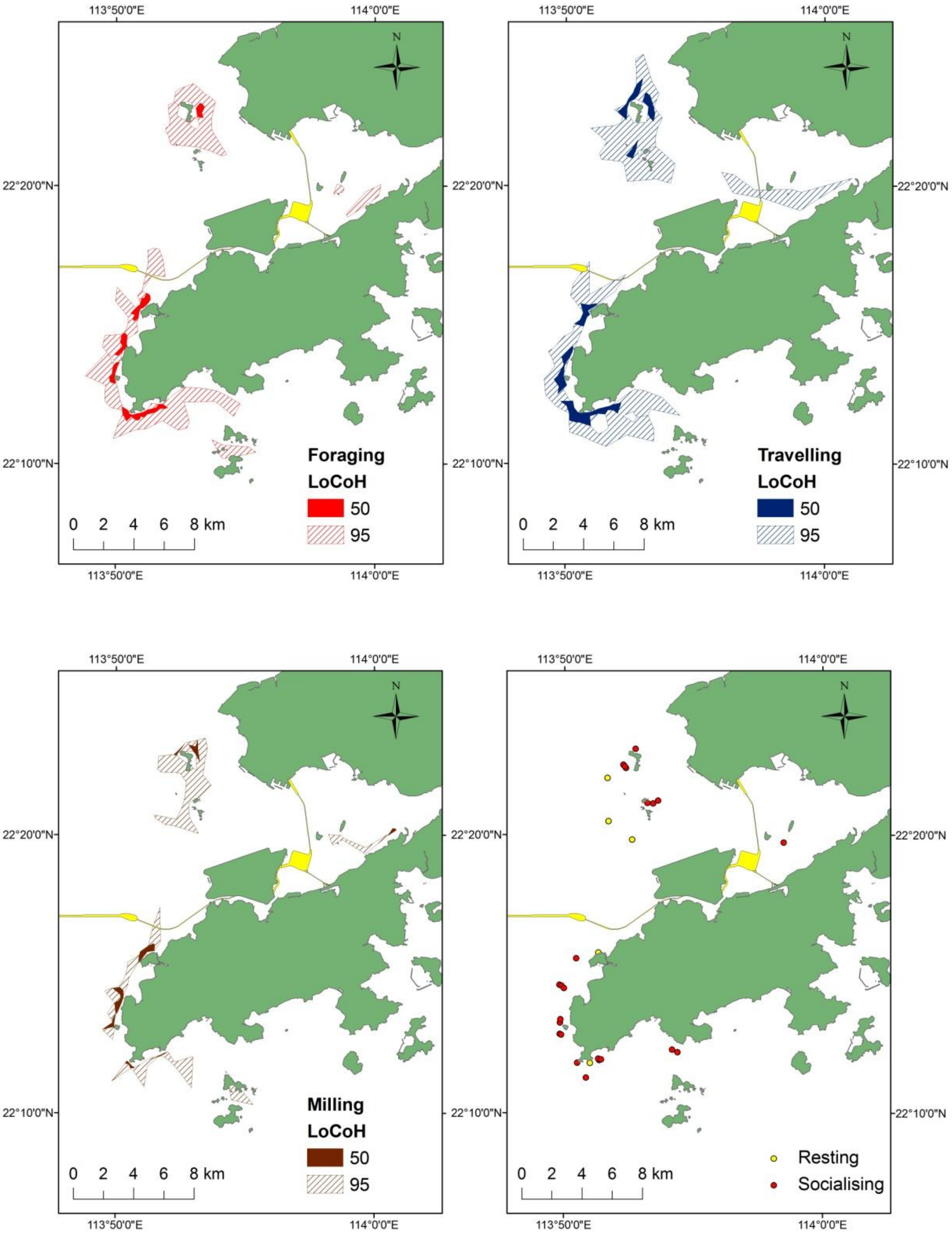


Figure 2.4 Local Convex Hull (LoCoH) estimates of 95% (hatched polygons) and 50% isopleths (filled polygons) utilisation distributions for foraging, travelling and milling, and records of socialising and resting of Indo-Pacific humpback dolphins in Hong Kong waters during 2011-2014.

Table 2.4 Percentage of Local Convex Hull (LoCoH) estimates at 95% and 50% utilisation distributions for all humpback dolphin sightings recorded in Hong Kong waters during 2011-2014 that were within the boundary of the existing marine protected area.

	LoCoH 50%	LoCoH 95%
All records	18.65	17.97
Foraging	6.13	17.75
Travelling	22.76	22.17
Milling	18.24	32.90

2.3.3 Factors influencing foraging probability

Fixed variables of humpback dolphin sightings recorded during 2011-2014 and used for logistic regression analysis are given in Table 2.5. None of the variables displayed collinearity (VIF < 3; Table 2.5) and, consequently, no variables were removed from further analysis. Interaction term that reduced AIC of the global model was latitude × distance to shore and was incorporated in model averaging. The Akaike weight of the top model was small (0.14) and 63 models were within the limit of Δ AIC values < 10, indicating high model uncertainty. Variables such as distance to shore, year, group size and latitude were found in more than half of the models with Δ AIC values < 10. The Akaike weight indicated that they have a greater influence on foraging probability than other fixed variables, such as tidal state, sea surface temperature, depth and longitude (Table 2.6).

Negative values of model-averaged coefficient estimates in the distance to shore and latitude and their interaction indicated a higher foraging probability when dolphins were closer to shore and in the southern section of the research area (Table 2.6, see also Fig. 2.4). Group size had a positive influence on foraging probability and high importance measured by the Akaike weight. The relative importance of year was accompanied by large standard errors, either close to the coefficient estimate (in 2012) or larger (in 2011), except in 2014, which had significantly higher foraging probability compared to the reference level (in 2013). The relationship between foraging probability and variables such as tidal state, sea surface temperature, depth and longitude were tenuous, with standard errors larger than coefficient estimates and low relative importance measured with the Akaike weight. Good predictive power of the averaged model was indicated by area under the ROC curve of all testing data based on 5-fold cross validation (AUCs were 0.86 to 0.89).

The exclusion of data collected during the presence of fishing boats had a minimal effect on the modelling outcome. All 91 models with Δ AIC < 10 demonstrated consistent results, and model averaging identified the same ranking of variables (Table 2.6).

Table 2.5 Summary and variance inflation factors (VIF) of fixed variables of humpback dolphin sightings recorded in Hong Kong waters during 2011-2014. Geographic coordinates were projected in the Hong Kong 1980 Grid Coordinates system. Categorical data such as Year and Tidal state do not produce mean and range. Year 2013 and Tidal state Ebb were taken as reference levels of the two categorical variables in the calculation of variance inflation factors.

	Mean (±SD)	Range	VIF	*n*
Latitude	22.26819 (0.07)	22.170006-22.412252	1.27	996
Longitude	113.86473 (0.03)	113.813723-113.986298	1.20	996
Group size	4.11 (3.24)	1-25	1.08	996
Depth (m)	11.48 (4.13)	4.2-26.8	1.04	996
Sea surface temperature (℃)	27.45 (4.10)	13-35	1.10	996
Distance to shore (m)	694.16 (602.79)	23.59-3532.18	1.22	996
Year 2011	-	-	1.08	46
Year 2012	-	-	1.14	145
Year 2013	-	-	-	410
Year 2014	-	-	1.22	395
Tidal state Ebb	-	-	-	330
Tidal state Flood	-	-	1.36	296
Tidal state High	-	-	1.30	254
Tidal state Low	-	-	1.15	116
Latitude: Distance to shore	-	-	1.13	-

Table 2.6 Model averaged coefficients and the relative importance of variables ($\sum w_i$) from generalised linear mixed effect models with AIC difference (Δ AIC) less than 10 for foraging probabilities of Indo-Pacific humpback dolphins with and without the presence of fishing boats in Hong Kong waters during 2011-2014. Year and tidal state were treated as categorical variables, with 2011 and ebb tide as the reference level. The interaction term is indicated with a colon. Pr(>|*z*|) < 0.05 are in bold.

	All sighting data					Sightings without fishing boats				
	Estimate	Std. Error	*z* value	Pr(>|*z*|)	$\sum w_i$	Estimate	Std. Error	*z* value	Pr(>|*z*|)	$\sum w_i$
(Intercept)	-0.389	0.468	0.830	0.407		-0.591	0.514	1.149	0.251	
Distance to shore	-0.912	0.237	3.840	**0.000**	1.00	-0.858	0.251	3.416	**0.001**	1.00
Year					1.00					1.00
2011	1.240	1.675	0.740	0.460		0.599	1.799	0.333	0.739	
2012	-1.338	0.934	1.431	0.152		-1.606	1.001	1.602	0.109	
2014	1.969	0.662	2.972	**0.003**		2.002	0.716	2.791	**0.005**	
Group size	0.561	0.209	2.679	**0.007**	0.96	0.462	0.217	2.130	**0.033**	0.82
Latitude	-0.469	0.296	1.581	0.114	0.78	-0.452	0.319	1.415	0.157	0.74
Latitude: Distance to shore	0.380	0.232	1.631	0.103	0.46	0.407	0.247	1.647	0.100	0.44
Sea surface temperature	-0.234	0.297	0.786	0.432	0.33	-0.268	0.320	0.836	0.403	0.34
Depth	-0.079	0.186	0.424	0.672	0.28	-0.099	0.195	0.507	0.612	0.29
Longitude	-0.060	0.314	0.189	0.850	0.28	-0.070	0.333	0.209	0.834	0.28
Tidal state					0.12					0.22

Table 2.6 continued

	All sighting data					Sightings without fishing boats				
	Estimate	Std. Error	*z* value	Pr(>|*z*|)	$\sum w_i$	Estimate	Std. Error	*z* value	Pr(>|*z*|)	$\sum w_i$
Flood	-0.120	0.640	0.188	0.851		0.268	0.692	0.386	0.699	
High	-0.656	0.550	1.191	0.234		-0.534	0.586	0.910	0.363	
Low	0.434	0.742	0.585	0.559		1.094	0.838	1.304	0.192	

2.4 Discussion

2.4.1 Spatio-behavioural dynamics

In this study, Indo-Pacific humpback dolphins were seen predominantly in close proximity to the shore, usually foraging in shallow waters alongshore natural coastlines in the westernmost part of Hong Kong territorial waters. They were highly selective in their use of the area. Spatially separated utilisation cores followed closely the pattern of distribution of core foraging grounds. While the general gradient of area utilisation conforms to the previously reported dolphin density distribution in Hong Kong (Hung 2008; 2014), the spatio-behavioural models indicate extensive overlaps of travelling and milling with core foraging areas, suggesting that foraging, the most frequently seen behaviour in HK waters, represents the key determinant of the dolphins' overall diurnal distribution pattern.

Further examination of the spatial distribution of humpback dolphin behaviours indicates that in certain sections of the study area, travelling extended further from the shore, such as in between southern Lantau Island and the Soko Islands and between Sha Chau and Tai O. This likely represents an optimal route choice, the shortest travel distance between core areas/habitats, an equivalent of a "corridor" used for a quick transition through areas poor in resources to resource-abundant destinations, as suggested by Karczmarski et al. (2000).

The application of mixed effect models revealed that foraging probability was higher in the southern part of the study area and closer to shore, indicating that the long stretch of natural rocky shoreline of southern Lantau Island, with several embayments and small river outlets (e.g. Tai O area), harbours suitable habitat for dolphin prey species and represents their key foraging grounds. Dolphins foraging and capturing prey, and shoals of fish actively escaping their pursuit were frequently seen during field surveys off Lung Kwu Chau and southern Lantau. This resembles the pattern described by Karczmarski et al. (2000a) for the Indian Ocean humpback dolphins, *S. plumbea*, in Algoa Bay, South Africa, where inshore rocky reefs in the south-western part of the bay constitute the dolphin's primary foraging ground and, despite their limited size, a focal point of the dolphins' use of a much larger coastal zone of the bay.

In the PRE, humpback dolphins prey on both benthic and epipelagic estuarine reef-associated fish, with Belanger's croaker, *Johnius belangerii*, lionhead croaker, *Collichthys lucida,* largehead hairtail, *Trichiurus lepturus,* and anchovies, *Thryssa* spp. representing the most common prey species (Barros et al. 2004; W. Lin et al., Sun Yat-sen University, unpublished data; W. Lin, L. Karczmarski and Y. Wu, study in progress). Most of these species peak in abundance during summer months, between May and October (as reviewed in Chan and Karczmarski 2017), but their spatial distribution in Hong Kong and PRE remains poorly known. Although by inference, higher foraging frequency can be reasonably assumed to be indicative of greater prey abundance in an area, hence likely greater net prey intake and, consequently, indicative of the likely location of the dominant prey items. However, with no fisheries data available and nocturnal behaviour of the dolphins unknown, such conclusion, although logical and reasonable, remains somewhat fragmentary and further investigations are needed. For that purpose, acoustic monitoring of the occurrences of humpback dolphins and their sonically active prey species (e.g. Lin et al. 2013) should be encouraged.

Although humpback dolphins are generally known for their restricted inshore distribution and narrow habitat selectivity (e.g. Karczmarski et al. 2000a; Parra 2006; Stensland et al. 2006; Weir and Collins 2016), they are also thought to be opportunistic-generalist predators (Barros et al. 2004; Parra 2006) that maximise their use of shallow-water habitats in areas with diverse physiographic features that facilitate natural aggregation of their inshore prey (e.g. estuaries, rocky shores, coastal lagoons and reefs; as discussed in Karczmarski, 2000). In Hong Kong, which represents the eastern-most reaches of a large estuarine system of the PRE, the occurrence of humpback dolphins exclusively in HK western waters is thought to be due to the estuarine influence of the Pearl River (Hung 2008; Jefferson 2000), while their selective use of specific locations as core foraging areas (namely: Lung Kwu Chau, Tai O, southern Lantau) concurs with the general pattern observed elsewhere (e.g. Karczmarski et al. 2000a; Parra 2006; Keith et al. 2013; Xu et al. 2015).

The results of mixed effect models showed increased gregariousness during foraging, unrelated to the presence or absence of fishing boats. While the mean group size was < 5 individuals (see Chapter 3), similarly as in other known humpback dolphin (*Sousa* spp.) populations elsewhere (e.g. Karczmarski 1999; Parra et al. 2011; Jutapruet et al. 2015) the foraging group size exceeded at times 20 individuals. This pattern differs from that observed in Australian humpback dolphins, *S. sahulensis*, off northeast Queensland (Parra et al. 2011) and *S. plumbea* off South Africa (Keith et al. 2013), where the dolphins were seen forming smaller groups when foraging; but it is similar to that of *S. plumbea* in Maputo Bay, southern Mozambique, where the foraging groups frequently exceed the mean group size (Guissamulo 2008). Such differences between sites are likely related to differences in prey distribution and abundance, with larger foraging aggregations formed in response to larger and denser prey patches (Gowans et al. 2008). In the PRE, 93% of humpback dolphin prey species are from the fish families of Sciaenidae, Engraulidae, Trichiuridae and Clupeidae which frequently form large shoals (Barros et al. 2004). Consequently, the spatial distribution of foraging behaviour and large foraging groups are both likely indicative of the relative importance of those locations to the daily nutritional needs of the dolphins.

Hung (2008) suggested foraging to occur in deeper waters as the dolphins were seen frequenting dredged shipping lanes off northern Lung Kwu Chau. However, this was not supported by the results of mixed effect models examining foraging probability in our study. In fact to the contrary, all identified core foraging areas are in close proximity to the shore and in waters 7-15m deep. Foraging probability did not vary longitudinally (east to west), implying limited heterogeneity of environmental conditions along this spatial axis of the narrow stretch of western HK waters.

The notable influence of year on foraging probability is likely a result of a high variability in the number of dolphin encounters between years. Except for a higher foraging probability in 2014, no clear pattern of variation could be inferred. In other words, the annual variation appears random. All other temporal variables had negligible influence on foraging probabilities. There was no evidence for the influence of season, measured by the sea surface temperature, suggesting that the seasonal movement in and out of HK waters (Chan and Karczmarski 2017) and seasonally varying dolphin densities (Jefferson 2000; Hung 2008) have no significant effect on foraging probability. In other words, even if the number of humpback dolphins that use HK waters as part of their range may differ between summer and winter (Chan and Karczmarski 2017), the area that function as they core foraging grounds remain so throughout the year.

Foraging was not influenced by the tide, perhaps because the foraging grounds are sufficiently far from the river mouth to limit tidal impacts on prey movement (Lin et al. 2013). Furthermore, due to the depth gradient, most of the coastal area of HK western waters remains accessible to the dolphins even during spring low tides. By comparison, foraging of Indian Ocean humpback dolphins seems similarly unaffected by tidal cycle in the exposed to oceanic elements coastal waters of Algoa Bay, South Africa (Karczmarski and Cockcroft 1999; Karczmarski et al. 2000b), but is greatly tide-dependent in shallow coastal lagoons of Maputo Bay, Mozambique (Guissamulo 2008), where the dolphins were seen using different foraging sites depending on the tide (L. Karczmarski, personal comm.).

Interestingly, previous observational study by Parson (1998), conducted from two land-based platforms in western Hong Kong, reported increased sightings and higher dolphin abundance at ebbing tide, although no indication of the observed behaviours was given. While the cause of this considerable difference between the two studies remains unclear; the importance of environmental variables is known to be scale-dependent (Elith and Leathwick 2009). Perhaps tidal influence may not be detectable at the spatial scale used in the current study. Alternatively, perhaps some level of observational bias has not been accounted for in the earlier work by Parsons (1998). Consequently, follow-up observations investigating the tidal effect at different core foraging areas should be considered in future studies.

2.4.2 Conservation implications

The findings indicate a considerable disparity between the daily pattern of range use displayed by humpback dolphins and the current management approach in Hong Kong. While the majority of the dolphins' foraging cores and core utilisation areas are off southwest Lantau Island, the Hong Kong's only MPA specifically intended for humpback dolphin conservation is located around the islands of Sha Chau and Lung Kwu Chau (Fig. 2.4), encompassing < 17% of the dolphins' core areas and < 7% of their core foraging grounds. Furthermore, of all the MPAs currently under consideration by Hong Kong authorities (Fig. 2.4), only the smallest, off west Lantau, encompasses some of the critically important core foraging grounds. In contrast, the newly designated and proposed MPAs, around Brothers Islands and off north Lantau, both intended as "compensation" measures in response to large coastal construction projects, do not harbour a single core foraging area and encompass < 5% of foraging range. This calls into question their usefulness for the conservation of the dolphin species they are meant to protect (for detailed discussion see Karczmarski et al. 2016a).

To address this obvious dilemma and current conservation needs, and to facilitate the development of informed management strategy, this study proposes a hierarchical approach to habitat protection based on the level of utilisation and the pattern of spatio-behavioural usage of coastal waters displayed by humpback dolphins in Hong Kong. In this approach, the 1st tier of habitat protection involves the identification of the core areas and habitats that are critical to long-term presence of humpback dolphins in Hong Kong waters. This is an equivalent of delineating key conservation sites and securing their protection. The 2nd tier of the hierarchical conservation approach focuses on securing habitat continuity and connectivity. This involves implementation of a functional structure, such as designation of marine park that provides buffer zones and moderates anthropogenic impact through managing human activities within the park boundary.

Given that foraging appears to be the key determinant of humpback dolphins' overall distribution pattern in Hong Kong, and that core utilisation areas centre around their core foraging grounds (50% isopeths in Fig. 2.3 and 2.4), these locations are of particular importance for the dolphins' daily nutritional needs and should be given a high level of protection. This 1st tier of habitat protection should be in a form of marine reserves, nested within a larger development-free conservation area. The reserves should function as no-take zones, with no coastal development, limited boat traffic and restricted human activities within the designated reserves.

To date, no marine reserve has yet been designated for dolphin conservation in Hong Kong, although there is adequate legislation to do so (ie. the Marine Parks Ordinance; Whitford et al. 2013). This study indicates that marine reserves with strict conservation measures are needed to safeguard the few remaining core areas of humpback dolphins in HK waters.

The next step in the hierarchical approach, the 2nd tier, involves securing a maximum connectivity and habitat continuity between cores areas, to minimise the process of habitat partitioning. There is a growing body of evidence that habitat fragmentation and loss may have detrimental effect on population structure and long-term persistence, and a recent study off Taiwan's west coast (Karczmarski et al. 2016b) provides one such explicit example. In Hong Kong, establishment of development-free conservation area off west/southwest Lantau and Soko Islands (2nd tier conservation), with several specific sites within this area designated as marine reserves (1st tier conservation), should be seen as top priority conservation action (Karczmarski et al. 2014).

While non-destructive activities could be allowed within the 2nd tier conservation area, in order to minimise behavioural disturbance (e.g. Ng and Leung 2003; Sims et al. 2012) and direct injuries (e.g. Jefferson 2000; Chan and Karczmarski 2015) vessel speed limits should be adopted (a speed limit of 10 knots is frequently recommended elsewhere; e.g. Vanderlaan and Taggart 2007; Hoyt 2011) and some high-speed ferry lines may have to be re-routed.

Following such development and relevant requirements, and to enhance conservation measures, a marine park connecting all the core areas and enveloping most of the dolphins' range (i.e. 95% isopeths in Fig. 2.3 and 2.4) should be designated (2nd tier conservation). This include connecting the core areas in the north to the south as dolphins frequently move between the two areas and social communities closely interact with each other (see Chapter 3). Under the Marine Parks Ordinance in Hong Kong, marine parks function as multiple use areas (e.g. allowing fishing, dolphin watching and other human activities within the park boundary), hence the implementation of the 2nd tier conservation over a larger spatial scale will help to effectively control, but not strictly eliminate or overly compromise the human usage of the area. The resulting MPA, as proposed here (see Fig. 2.4) would be large and rooted in the increasing body of evidence that for mobile marine species, to be effective, MPAs need to be large in size (Slooten 2013; Edgar et al. 2014) and, especially in coastal regions, protect habitat integrity and connectivity (Karczmarski 2000a; Karczmarski et al. 2016b). This contrasts with the MPA framework that is currently promoted by the Hong Kong authorities (Agriculture, Fisheries and Conservation Department, AFCD and the Airport Authority) and which comprises segmented and small protected areas, much of them outside the dolphin core areas and habitats.

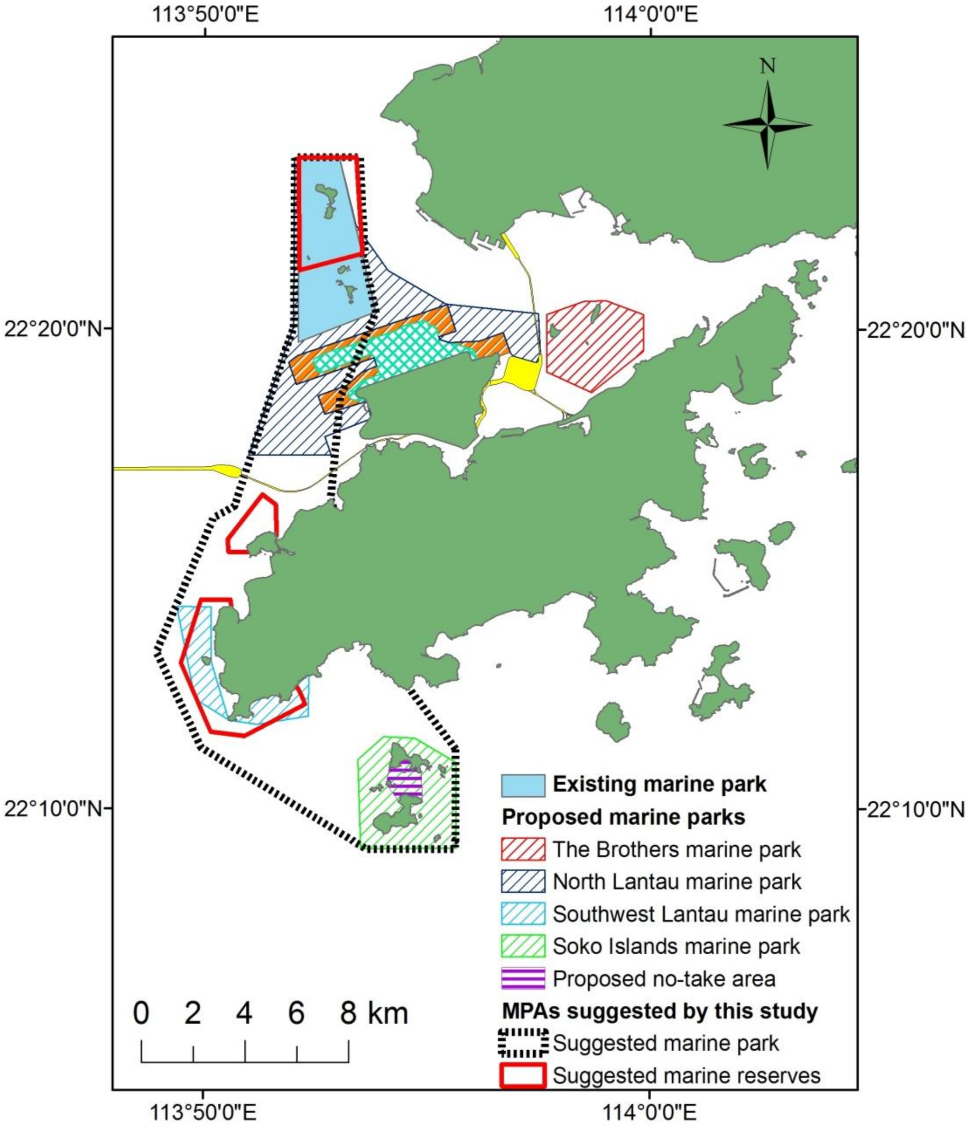


Figure 2.5 Suggested MPAs based on the current study include a marine park, indicated as an enclosure by the black dotted line, and marine reserves in red. The existing Sha Chau and Lung Kwu Chau Marine Park (12km^2) is denoted by the blue coarse background. Proposed marine parks under consideration are in hatched lines. These include the Brothers Islands (as compensation after the completion of the Hong Kong-Zhuhai -Macau Bridge, HKZMB; denoted in red), north Lantau Island (as compensation for the proposed expansion of the Hong Kong International Airport; denoted in dark blue), southwest Lantau Island (illustrated in light blue) and the Soko Islands (indicated in green). The proposed area of reclamation due to the expansion of the Hong Kong International Airport is denoted in green cross-hatched lines and its associated expansion of the approach area, which has prohibited entry, is denoted by the orange hatched lines.

2.4.3 Historic perspective

There are indications that the distribution of humpback dolphins in Hong Kong waters may have changed over the course of the past two decades. A comparison of early sightings (Jefferson and Leatherwood 1997) and more recent records (Jefferson 2007; Hung 2008; 2014) indicates a substantial shift in dolphin distribution from the waters off north Lantau and west New Territories in the late 1990s to the region of west–southwest Lantau at present. This distribution shift seemingly coincides with the onset and since ever-increasing levels of anthropogenic impacts in north–northwest HK territorial waters.

Dolphin densities off Brothers Islands had been reported to be comparatively high during 1990s through early 2000s (Jefferson and Leatherwood 1997; Hung 2008) when the Brothers Islands MPA was first proposed. Since then, however, dolphin densities decreased in waters off northeast and west Lantau and the dolphins have almost completely ceased to be seen off east Lantau (Jefferson 2007). As the anthropogenic impacts accumulate and behavioural disturbances kept increasing, the dolphin usage of that area decreased (e.g. Marcotte et al. 2015). Currently, as shown by the study presented here, waters off north Lantau and east of Lung Kwu Chau Islands represent peripheries of dolphin use with not a single foraging core area. This is likely due to the combined impacts of reclamation, marine traffic, ongoing construction and underwater piling works of HKZMB (see Chapter 4), all of which have severely compromised any potential usefulness of the Brothers Islands MPA in contributing to dolphin conservation. This situation is unlikely to change in a foreseeable future as large-scale construction projects (e.g. the 3rd runway of the Hong Kong International Airport) are tabled to continue in adjacent waters (for a detailed discussion see Karczmarski et al. 2016a).

Even more striking case of management misconception is the recently proposed North Lantau marine park, intended as "compensation" measure for the upcoming expansion of the Hong Kong International Airport. The proponents of this MPA argue that it will connect the Sha Chau–Lung Kwu Chau with Brothers Islands marine park; but this argument omits an important fact that, according to the current development plans in Hong Kong, both Sha Chau–Lung Kwu Chau and Brothers Islands areas will already be severely compromised by large-scale construction works well before the proposed North Lantau marine park would come to existence. First of all, however, as pointed out in Karczmarski et al. (2016a), the fundamental question to be answered is "why designate a marine park for the protection of a species/population in an area that is neither their core range nor frequently used, and is directly adjacent to an area of projected major ecological devastation, instead of conserving areas that account for the predominant core of the distribution, daily behaviour and the critical habitats of the animals that are meant to be protected" (Karczmnarski et al. 2016a, page 53, line 1-9). The study presented in this chapter offers precisely such an alternative along with the scientific evidence needed to effectively guide the MPA designation process that is currently lacking in Hong Kong.

The hierarchical approach to habitat protection proposed by the current study should be implemented prior to any upcoming coastal construction project in the area as it could offer a habitat refuge for the dolphins during environmental disturbance elsewhere in western HK waters (Karczmarski et al. 2014; Karczmarski and Or 2016). However, the MPA system proposed here is not without limits. While it is expected to reduce the loss of critical habitats and limit the impacts of marine traffic and fishery, the area remains vulnerable to water pollution. To tackle the potential risk of harmful pollutants, other means of controlling these pollutants are required (Karczmarski et al. 2016a). Moreover, the suggested MPA covers only part of the dolphins' population range (see Chapter 5), and, although much needed, it is unlikely to suffice as the only functional conservation measure of the PRE dolphin population.

The survey period of this study has overlapped with large-scale construction in Hong Kong and China. While impacts on distribution can be anticipated, the core areas from the spatial analysis are considerably large in size and overlap with the high density dolphin areas that have been reported in the course of the past two decades. This denotes the high likelihood of these areas persisting as critical habitat, and their suitability for long-term protection. To cope with distributional shifts in the future, it is recommended to adopt adaptive management of protected areas (Hooker et al. 2011; Hoyt 2011; Ross et al. 2011) and allow boundaries to be periodically reviewed and adjusted when changes are detected to ensure that the level and extent of protection responds to the changing environment.

2.5 Conclusion

Incorporating biologically important behaviours to spatial analyses enhances the understanding on how the animals utilise their core areas. In Hong Kong, foraging appears to be the key determinant of the humpback dolphins’ overall distribution pattern. Distance to shore, location and group size are also important predictors of foraging probability. In Hong Kong, two spatially segregated key foraging grounds were identified, but conservation efforts have to go beyond a site-specific approach and protect habitat integrity and connectivity. A hierarchical model of MPA design was developed based on the spatio-behavioural pattern of range use by the animals the MPA is meant to protect. Such an approach can be applied across species and habitats, facilitating empirically guided conservation framework. The incorporation of behaviour into spatial analyses offers a powerful tool in conservation zoning and development of management measures that approach the MPA designation from the animal's point of view, which is likely to serve better the animals and habitats that the MPAs are meant to protect.

Chapter 3 Social dynamics of Indo-Pacific humpback dolphins in Hong Kong

3.1 Introduction

Social structure is generally understood to represent a composite of the nature, quality and pattern of relationships between individuals (Hinde 1976). To study social structure, a bottom-up approach is often adopted by quantifying interactions between identifiable individuals and synthesising them into relationships between individuals over time (Hinde 1976; Whitehead 2008). As interactions between individuals vary in space and time, different types of social structures may arise.

Among social mammals, a wide range of intraspecific and interspecific social patterns have been observed (e.g. Mann et al. 2000; Mitani et al. 2012) and variations in physical and social environments seem to play a pivotal role in promoting such diversity in social organisations (e.g. Gowans et al. 2008). It is currently thought that different social strategies evolve to maximise fitness under particular environmental conditions through balancing the costs of group living, such as resource competition and disease transmission, with the benefits of group living, such as, among other, lowering predation risk, facilitating cooperative foraging, mate finding, and social learning (Krause and Ruxton 2002). Studying grouping patterns at ecologically differing sites provides valuable insights into the ecological influences on social structures.

While associations between individuals define the social structure, the resultant pattern may constrain individuals’ behaviours and create a feedback loop that influences animal interactions (Kappeler and Van Schaik 2002; Gowans et al. 2008). Moreover, social structure has a profound influence on population processes, such as gene flow and reproductive success (Sugg et al. 1996; Storz 1999; Silk 2007; Silk et al. 2010) and may affect population structure across larger spatio-geographic scales (Lusseau et al. 2006; Hoelzel et al. 2007; Andrews et al. 2010). Association patterns can also determine the rate and pattern of disease transmission and social information transfer (Corner et al. 2003; Lusseau 2003; Cross et al. 2004; Cantor and Whitehead 2013). Given the variability of social patterns and their strong relationships to demographic processes, understanding social structures at specific locations is an important aspect of local conservation and species management (Whitehead et al. 2004; Yamagiwa and Karczmarski, 2014).

Humpback dolphins' social dynamics have been studied across several species and populations of the genus *Sousa*, including Indian Ocean humpback dolphins (*S. plumbea*) in South Africa (Karczmarski 1996; 1999) and Mozambique (Guissamulo 2008), Australian humpback dolphins (*S. sahulensis*) off northeast Australia (Cagnazzi et al. 2009; Parra et al. 2011), and Indo-Pacific humpback dolphins (*S. chinensis*) in Hong Kong (Jefferson 2000; Dungan et al. 2012), Taiwan (Chang 2011; Dungan et al. 2015) and China (Zhai 2006; Chen et al. 2011; Xu et al. 2012). Groups of humpback dolphins are generally small, with mean group sizes ranging from 2.4 individuals in Moreton Bay, Australia (Corkeron 1990), to 14.9 in Maputo Bay, Mozambique (Guissamulo 2008). Unusually large groups have been reported in the Arabian region (ranging from 30 to 100 individuals; Baldwin et al. 2004) and in the Bay of Bengal, Bangladesh (19 - 205 individuals; Smith et al. 2015), which is considered exceptional for humpback dolphins. In general, across the humpback dolphin species and populations studied to date, their social structure follows a dynamic fission-fusion pattern, with mostly short-term associations and fluid groupings, and mother–calf associations often described as the only strong social bond between individuals (Jefferson and Karczmarski 2001). The only exception has been found in Maputo Bay, Mozambique, where humpback dolphins exhibit relatively stronger associations (Guissamulo and Cockcroft 2004; Guissamulo 2008). This suggests that variations in association patterns exist and appear to be influenced by local environmental and social factors.

In the region of the Pearl River Estuary (PRE), studies of humpback dolphin social structure remain preliminary and recent (Jefferson 2000; Dungan et al. 2012), and have been focused primarily on the animals inhabiting Hong Kong waters. Jefferson (2000) noted the lack of stable associations among individuals and suggested that their social system is likely similar to the fission-fusion pattern described earlier for humpback dolphins off the South African coast (Karczmarski

1999). More recently, analyses of a 10-year dataset collected in Hong Kong between 2000 and 2009 have suggested that there may be two communities inhabiting waters north and south off Lantau Island, with overlapping ranges in coastal waters off northwest Lantau Island (Dungan et al. 2012). Association patterns were reported to differ between these two communities, albeit only slightly, with more short-term associations in the northern community (Dungan et al. 2012). This is the first and to date the only quantitative study that has described the social structure of humpback dolphins in the PRE region. Dungan et al. (2012) also attempted to evaluate the influence of calf and the presence of fishing vessel on association patterns and speculated that kinship, resource partitioning and habitat degradation may have contributed to the observed social structure. Beyond that, the driving factors that shape the social patterns of these animals remain unknown.

Although Dungan et al. (2012) attempted to determine whether and how the dolphins in Hong Kong exhibit social segregation, the conclusion was drawn from analyses of a very small proportion (*n*=88) of a considerably larger number of dolphins known to use Hong Kong waters as part of their range. Recent photo-identification study indicates that at least 368 humpback dolphins frequent Hong Kong waters (Chan and Karczmarski 2017) and the number of individuals photo-catalogued in Hong Kong in < 5 years (L. Karczmarski, University of Hong Kong, study in progress) quadruples the 10-year sample size used by Dungan et al. (2012). It seems apparent therefore that analyses performed on a considerably larger sample size (more individuals) may prove informative, perhaps necessary, in gaining greater insights into the socio-dynamics of humpback dolphins and test the previously suggested social community structure in Hong Kong waters.

In Chapter 2, the pattern of area utilisation by humpback dolphins in Hong Kong was quantified and modelled. Two major foraging areas were identified and the distribution of foraging grounds was suggested to be the key factor determining the pattern how dolphins use Hong Kong coastal waters. The current chapter focuses on the population-wide social structure in Hong Kong by analysing the dyadic relations between individuals and their patterns of area use, and discusses the likely factors affecting the dolphins' socio-spatial dynamics. Based on the associations between photographically-identified individuals, this chapter investigates temporal patterning in associations, examines the societal structure and tests community division, and relates the observed social dynamics to the pattern of area utilization and potential social and ecological factors.

3.2 Methods

3.2.1 Field surveys

Boat-based surveys were conducted using an 8-m boat powered by a 140-HP 4-stroke outboard engine, from May 2010 to December 2014, at sea state ≤ 3 in the Beaufort scale. Surveys were conducted without predetermined routes, as described in Chapter 2. To maximise the area covered at each survey day, up to two research boats were in operation in different areas at the same time.

Photographs of dorsal fins and upper bodies of dolphins were taken using digital cameras Canon EOS 1D Mark III/IV with a 100–400 mm f/4.5–5.6 variable lens. A dedicated effort was made to photograph both sides of the dorsal fin of each dolphin during each encounter. Animals engaging in similar behaviours and interacting with each other in close proximity were defined as a ‘group’ (Whitehead and Dufault 1999). Behaviours of the groups were determined following the definitions of the behavioural categories used in Chapter 2.

3.2.2 Photo identification

All ID-images along with relevant observations and environmental data were input into program DISCOVERY, a photo identification data management system for individually recognisable animals (Gailey and Karczmarski 2012). Age class was assigned based on the individual’s external appearance, colouration and body size (Chang et al. 2016). Calves could be distinguished by their dark grey to light grey colour, approximately two-thirds or less the length of an adult, and their constant close proximity to an adult. Individuals approximately 2 m in length, light grey in colour and visibly less robust than adults were classified as juveniles; while those with a body length similar to that of adults but still less robust and mostly grey on the dorsal side were termed subadults. Individuals classified as adults were 2.5 m or more in length, with robust bodies and mostly or entirely pink in colour. As younger dolphins (newborn and calves) may follow the association pattern of their mothers, all analyses performed in this study included only adults in order to avoid replicating associations brought by younger individuals (Gero et al. 2005; Elliser and Herzing 2014).

All ID-images were graded for their quality, on a scale of 1–100 (Karczmarski et al. 2005) and all individuals captured on those images were graded for their distinctiveness, on a scale of 0–5 (Friday et al. 2000). To ensure a reliable identification of individuals, only images that scored ≥ 70 for their quality were use for further analyses, which ensured that all images were well-exposed, in focus, without (or with only moderate) parallax, and with the upper body of the dolphin well above the water. This strict quality control allowed for inclusion in the analyses of all individuals with distinctiveness above 0.

3.2.3 Data analysis

3.2.3.1 Grouping pattern and associations

To determine whether group sizes varied with behaviours, Kruskal–Wallis test with Dunn's post hoc test was used to examine the significance of different group sizes (Zar 2010). All analyses were performed in R (v 2.1.3; R Development Core Team 2011).

All social analyses were performed in MATLAB R2013b using SOCPROG 2.6 (Whitehead 2015). The sampling interval was defined as one day. Under the assumption that dolphins in the same group were associated as 'the gambit of the group' (Whitehead and Dufault 1999), the strength of the dyadic relationship among individuals in the same group was measured by an association index, which is defined as the rate of association between two individuals (Whitehead 2008). In this study, group members were observed to change frequently and the photo-ID coverage of a group was variable, depending on the group size. It was common not being able to photograph all individuals in the group and this could potentially produce a downward bias in the association index (Gowans et al. 2001). To minimise such bias, only groups in which 70% or more of the individuals were photographed with acceptable image quality (referred further to as photo-coverage ≥ 70%) were used for further analyses.

The half-weight association index (HWI, Cairns and Schwager 1987) was applied to minimise the bias where two individuals are more likely to be recorded separately rather than together (Cairns and Schwager 1987), which is a common scenario in field studies of cetaceans (Slooten et al. 1993; Whitehead 2008). HWI was defined as:

$$\text{HWI}=\frac{X}{X+\frac{Y_a+Y_b}{2}}$$

where X = number of groups with both dolphins a and b, Y_a= number of groups with dolphin a but not dolphin b, and Y_b = number of groups with dolphin b but not dolphin a. HWI ranges between 0 (a and b were never seen together) and 1 (a and b were always observed together). Standard deviation and coefficient of variation (CV) of the HWI were also calculated.

To assess if the data possessed enough power to provide a representative social structure, the accuracy of association was measured by the correlation coefficient (r), which is:

$$r = \frac{S}{CV_{est}}$$

where S is social differentiation, a measure of variation in the association data, and $CV_{est}$is the CV of the observed HWIs (Whitehead 2008).

Values of $S < \sim 0.3$ indicate low social differentiation and values $\geq \sim 0.5$ indicate a well-differentiated social structure. For a dataset with a moderate representation of social structure, r shall approximately be ≥ 0.4 (Whitehead 2008). To achieve an acceptable r, only individuals sighted more than four times were included in further social analysis.

3.2.3.2 Test of preferred association

To test if the associations were random in relation to the existence of long-term preferred/avoided relationships, permutation tests were performed following the method proposed by Bejder et al. (1998), with modification by Whitehead (2008). The permutation was carried out among associations within samples. In each step, the test involved a flip of two randomly chosen rows and columns within the same sampling period (i.e. same day) from the association matrix, thus producing a new association matrix. As the new association matrices produced were not independent, the number of required permutations was determined by increasing the number of permutations until the *p*-value stabilised (Manly 1995). The *p*-value stabilised at 20,000 permutations, with 1000 trials per permutation. The presence of preferred associations over sampling periods was indicated by a significantly higher standard deviation of the observed association indices than that generated from random data ($p < 0.05$) (Whitehead 2009).

3.2.3.3 Network analysis

To further examine the associations between individuals, a network analysis was performed. In networks, individuals were represented by nodes and connections between them were represented by edges. Parameters that measured different aspects of connectivity between individuals were calculated. These parameters included strength, reach and clustering coefficient. Strength is the sum of the association indices of an individual with all other individuals (Barrat et al. 2004), which is a measurement of gregariousness; higher strength indicates higher tendency of an individual to form associations with others. Reach is the overall strength of the associates of an individual (Whitehead 2008), which measures indirect connectedness. Higher values indicate individuals are more strongly associated with other individuals indirectly. Clustering coefficient is the level of association between the associates of an individual (Holme et al. 2007). Higher values indicate a stronger association between associates of an individual and a tighter, more homogeneous society. To compare the parameters of observed network with a random network (i.e., when associations between individuals are random), a permutation test was performed. 5000 random networks were generated by permuting the associations within the sampling period.

3.2.3.4 Social cluster analyses

To examine social clustering among individuals, the modularity (Q) was calculated, which refers to the difference between the proportion of total associations within clusters and the expected proportion for random associations (Newman 2004). A modularity of 0 indicates random association, whereas a modularity of 1 indicates no association between clusters. Modularity values of

0.3 or above indicate social differentiation between clusters of individuals (Newman 2004). Two methods were used to examine the community structure.

(1) An eigenvector-based method using a divisive algorithm developed by Newman (2006) and modularity calculated under the control on gregariousness (Newman 2004). As a divisive method, the population was progressively divided and adjusted to increase modularity. The clusters were displayed as a social network diagram drawn in NETDRAW 2.097 (Borgatti 2002) with the application of a spring-embedded algorithm (Kamada and Kawai 1989). The algorithm places nodes randomly and arranges them in an iterative process that aims to place nodes with higher associations closer to one another while minimising node overlap (Gajer and Kobourov, 2002). The resultant network displays nodes with higher links at the centre and isolated nodes at the periphery.

(2) A dendrogram-based method using average-linkage hierarchical cluster analysis (Morgan et al.1976; Milligan and Cooper 1987) with modularity calculated under the control on gregariousness (Newman 2004). As an agglomerative method, individuals were clustered progressively to maximise modularity. The representativeness of the resultant dendrogram was determined by a cophenetic correlation coefficient (Bridge 1993), which ranges from 0 to 1, with 1 indicating a perfect fit. Values greater than 0.8 indicate that the dendrogram is reasonably representative of the data (Bridge 1993).

A Mantel test was further applied to test the null hypothesis that associations were similar between and within clusters.

3.2.3.5 Temporal association pattern

Temporal stability of associations was quantified by calculating the standardised lagged association rate (SLAR), which is an estimation of the probability that two individuals associated at a time remain still associated after a time lag *t* (Whitehead 1995). The standardised lagged association rates were used, which are calculated by dividing the lagged association rate by the number of associations recorded on each occasion (Whitehead 1995), performed when photographing all individuals at each encounter in the field is not always possible. The null SLAR, representative of the pattern when the associations are by chance alone, was also calculated. Standard errors were obtained by jackknife procedure. Models of different social patterns, developed by Whitehead (1995), were fitted to the observed data and their fit performance was compared. Model fit was determined by quasi-Akaike Information Criterion (QAIC). The best model is represented by the smallest QAIC and the level of model fit is measured by the difference between the QAIC of the models (ΔQAIC). Models with less than two QAIC units difference from the best model are considered equally representative, while ΔQAIC greater than 10 indicate no support for those models (Burnham and Anderson 2002).

3.2.3.6 Spatial distribution

To examine the spatial pattern of social clusters, area utilisation maps of each cluster were generated using kernel density estimation. The locations of individual sightings were pooled from the survey track by matching the time that the photograph was taken with the nearest time that a geographic location was recorded. Probability contours (i.e. kernel) was allocated around data points in accordance to the intensity of usage (Worton 1989; Seaman and Powell 1996). Adaptive kernel density estimates with least-squares cross-validation (LSCV) for calculating kernel smoothing parameter were calculated using the Home Range Estimate extension tool (Rodgers et al. 2005) in ArcGIS 9.3.1 (ESRI 2008). Contours of 50% and 95% were used to indicate the core and range use of each social cluster.

3.2.3.7 Movement pattern

Movement analyses were performed in MATLAB R2013b using SOCPROG 2.6 (Whitehead 2015). Same as social analyses, the sampling interval was defined as one day. Since movement analyses based on photo-identification data are less sensitive to heterogeneity in photo quality, the analyses were repeated with the inclusion of lower quality photos (ie. images quality ≥ 60) in order to test if the results would be distinctively different from the results generated from higher quality photos (ie. image quality ≥ 70).

The study area was broadly divided into two regions, the northern region and the southern region, based on the pattern of area use (utilisation distribution) exhibited by the dolphins (see Chapter 2). The division was placed at 22°18' 00" N because of the fewest sightings recorded at this latitude (Fig. 3.1). Movement within and between these two areas was quantified and modelled using lagged identification rates (LIR), which represent the probability that an individual seen at a time in a particular location will be identified again in the same area after time lag *t* (Whitehead 2001).

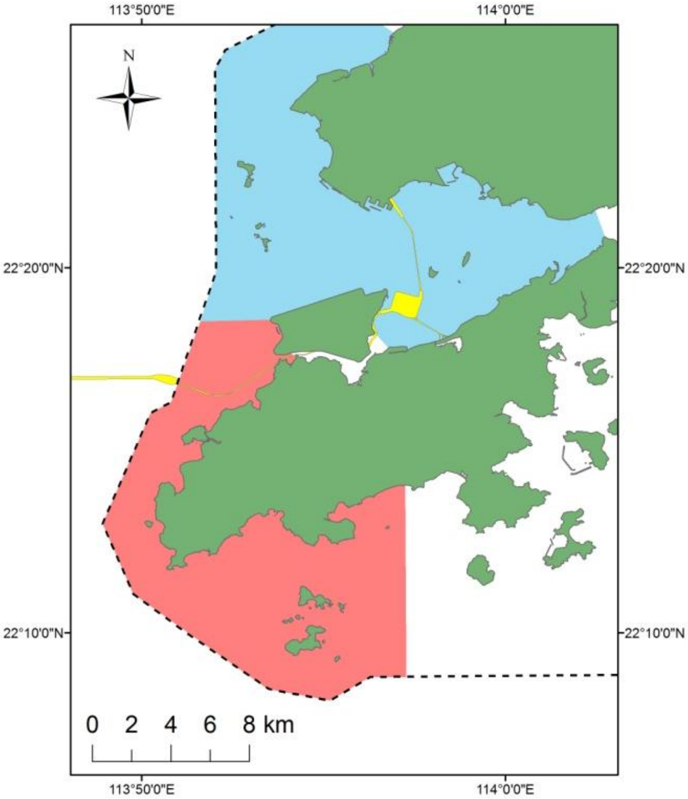


Figure 3.1 Northern region (blue) and southern region (red) of the study area defined based on area utilisation of Indo-Pacific humpback dolphins in Hong Kong. Hong Kong's administrative border is denoted as dotted line.

Using individual identifications as a measure of sampling effort, LIR representing residence in one area and movement from one area to another can be calculated using a modified maximum-likelihood method based on Hilborn (1990) and Turchin (1998). The site fidelity of individuals was illustrated by plotting LIR against the time lag. The decline in LIR over the time lag indicates emigration and the levelling off suggests that either the animals remained in the area or moved back again (Whitehead 2001). For movement between two areas, the rise in LIR over the time lag indicates animals leaving one area and entering another specified area. Standard errors of LIR were calculated by bootstrapping (Whitehead 2008). Different models of residency, as described by Whitehead (2001), were fitted to the observed data. Model fit was determined by QAIC, where models with the lowest QAIC are considered best-fit models. The difference between QAIC of models (ΔQAIC) indicates the level of model fit, with ΔQAIC > 10 indicating no support for the model with larger QAIC (Burnham and Anderson 2002).

3.2.3.8 Testing the existence of two communities in Hong Kong

The hypothesis by Dungan et al. (2012) suggesting two social communities of humpback dolphins in Hong Kong waters was tested by sub-sampling the dataset to simulate that of Dungan et al. (2012). By selecting all individuals seen > 14 times across the 4.5-year study period, a sub-set of 88 individuals was generated, which corresponds to the dataset of 88 individuals seen > 10 times across the 10-year period in Dungan et al. (2012). A full suite of cluster and spatial analyses were repeated on this subset of data.

3.3 Results

3.3.1 Dataset summary

From 18 May 2010 to 31 December 2014, a total of 295 survey-days were spent out at sea in the study area. A total of 1362 dolphin groups were seen, which resulted with 428 dolphins photo-identified, of which 337 (78.7%) were adults. Under the restrictions on photographic quality criteria (i.e. Quality ≥ 70), photographic coverage of the group (≥ 70%), and individual sightings frequency of more than four times, a subset of 202 adults was used for further analyses. For movement analysis, photo-ID data of all adults that met the photographic quality criteria of Quality ≥ 70 was used (329 individuals). Movement analysis was repeated with the inclusion of lower quality photos (Q ≥60) and the dataset included 336 individuals.

3.3.1.1 Grouping pattern

Groups ranged in size from 1 to 30 individuals (Fig. 3.2), with mean size of 4.58 (SD ± 3.65). Focal samples of behaviour were obtained for 1285 groups. The overall mean group size across all behavioural categories seen was 4.67 (SD ± 3.66) individuals, and the median value was 4 with the majority of groups (60%) numbering ≤ 4 individuals (Fig. 3.3). Group size varied significantly with dolphin behaviour (Kruskal–Wallis test: $X^2 = 32.3$, $P < 0.001$; Dunn's test: $P < 0.001$). On average, group sizes during socialising were significantly larger than during other behaviours (Dunn's test: $P < 0.001$). However, the largest groups, reaching up to 30 individuals, were seen during foraging.

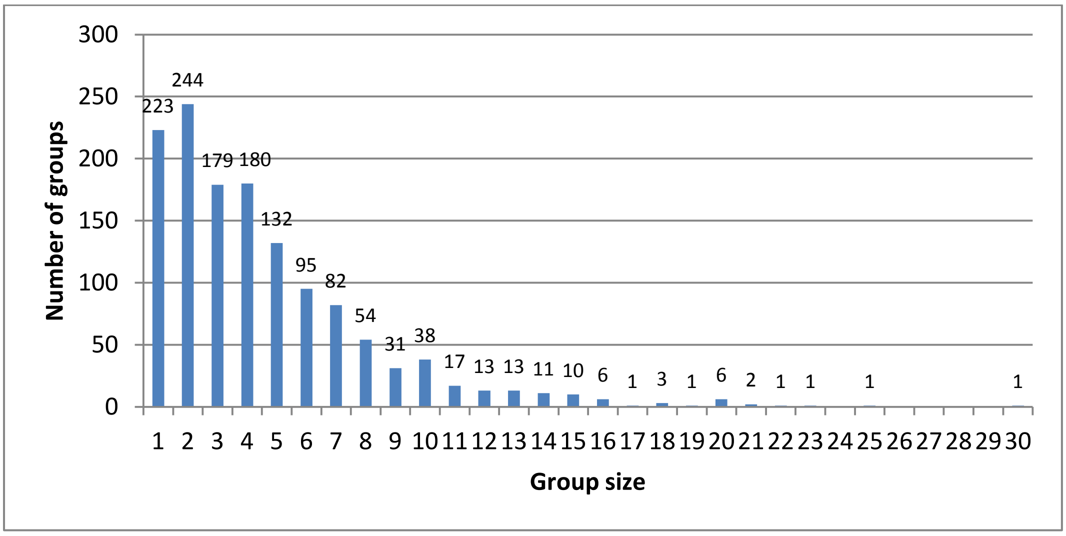


Figure 3.2 Group sizes of Indo-Pacific humpback dolphins seen in Hong Kong waters between May 2010 and December 2014.

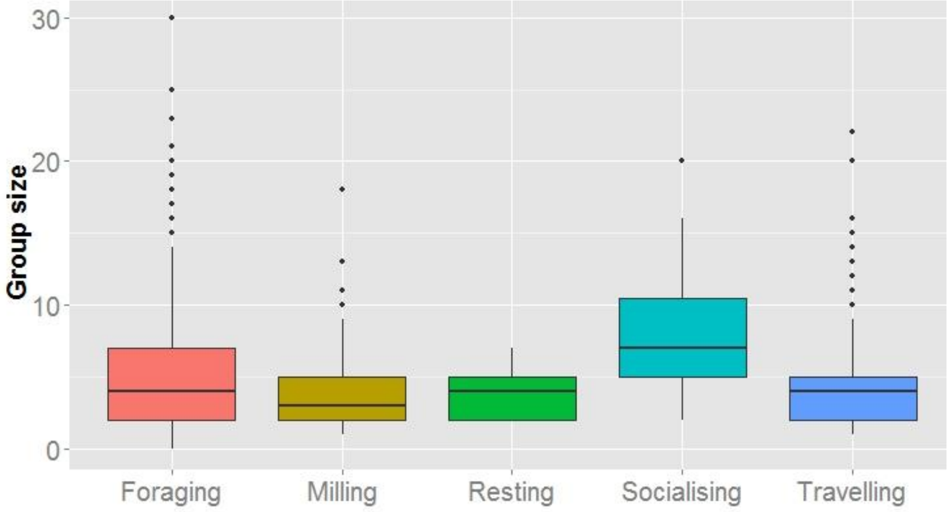


Figure 3.3 Group size by behaviour of Indo-Pacific humpback dolphins seen in Hong Kong waters between May 2010 and December 2014. Medians are represented by thick horizontal lines. The 25th percentiles and 75th percentiles are represented by the bottom and top of the boxes and data within 1.5 times of the interquartile ranges are shown as whiskers extending from the boxes. Outliers are indicated as black dots.

3.3.1.2 Associations

The correlation between true and estimated association indices in this dataset indicated the dataset had a moderate power to detect the true social structure (r = 0.443±0.019) and high social differentiation (S = 0.876 ±0.024) was detected. Associations were generally weak, with mean individual HWI of 0.03±0.01 and maximum individual HWI of 0.33±0.12. The standard deviation of observed HWI was significantly higher than that of randomly permuted data (Table 3.1), indicating preferred associations among individuals. Two network parameters, strength and reach, were higher than those of random data (Table 3.2).

Table 3.1 Results of permutation test of preferred association of Indo-Pacific humpback dolphins with more than four sightings between May 2010 and December 2014 in Hong Kong. Strength of associations were measured by half-weight association index (HWI). p-value < 0.05 indicates that SD of observed data was significantly higher than that of random data.

Parameter	Observed data	Random data	*p*-value
Mean HWI± Standard deviation	0.029±0.057	0.029±0.050	0.000

Table 3.2 Results of network analysis of Indo-Pacific humpback dolphins with more than four sightings between May 2010 and December 2014 in Hong Kong.

Parameters	Observed data	Random data	*p*-value
Strength	5.81±2.46	5.77±2.51	1.00
Reach	39.79±19.44	39.50±19.11	1.00
Clustering coefficient	0.09±0.03	0.10±0.02	0.18

3.3.1.3 Community structure

Using the eigenvector method of Newman (2006) with modularity calculated under the control on gregariousness, five broadly interacting clusters were identified (Fig. 3.4). Modularity was 0.344, suggesting the division was meaningful. The Mantel test confirmed that associations within clusters were higher than among clusters (*t* = 47.0521, *p* = 1).

Average-linkage hierarchical cluster analysis with modularity calculated under the control on gregariousness suggested a similar pattern, with a weak division between the clusters (Fig. 3.5). The maximum modularity was 0.32373 at an HWI of 0.0227; while the cophonetic correlation coefficient (CCC) was less than 0.8 (CCC = 0.6942).

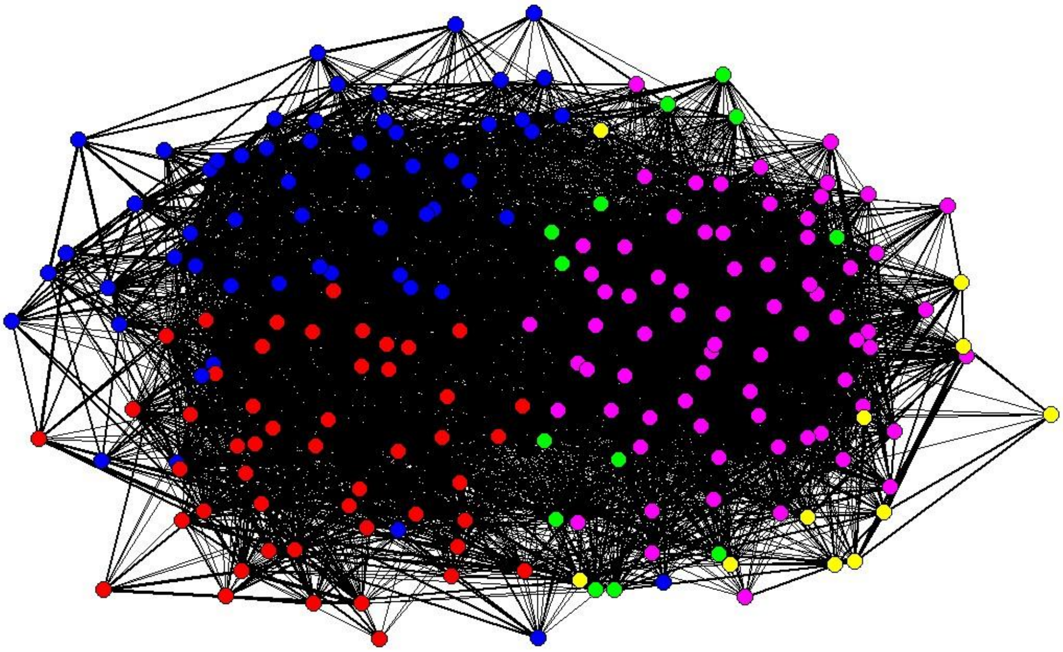


Figure 3.4 Network diagram of Indo-Pacific humpback dolphins seen in Hong Kong waters more than four times between May 2010 and December 2014. Individuals are shown as nodes. Line thickness indicates the strength of associations. Individuals in Cluster 1 (*n*=49) are denoted as red nodes, in Cluster 2 (*n*=11) as yellow, Cluster 3 (*n*=57) as blue, Cluster 4 (*n*=13) as green, and Cluster 5 (*n*=72) as pink nodes.

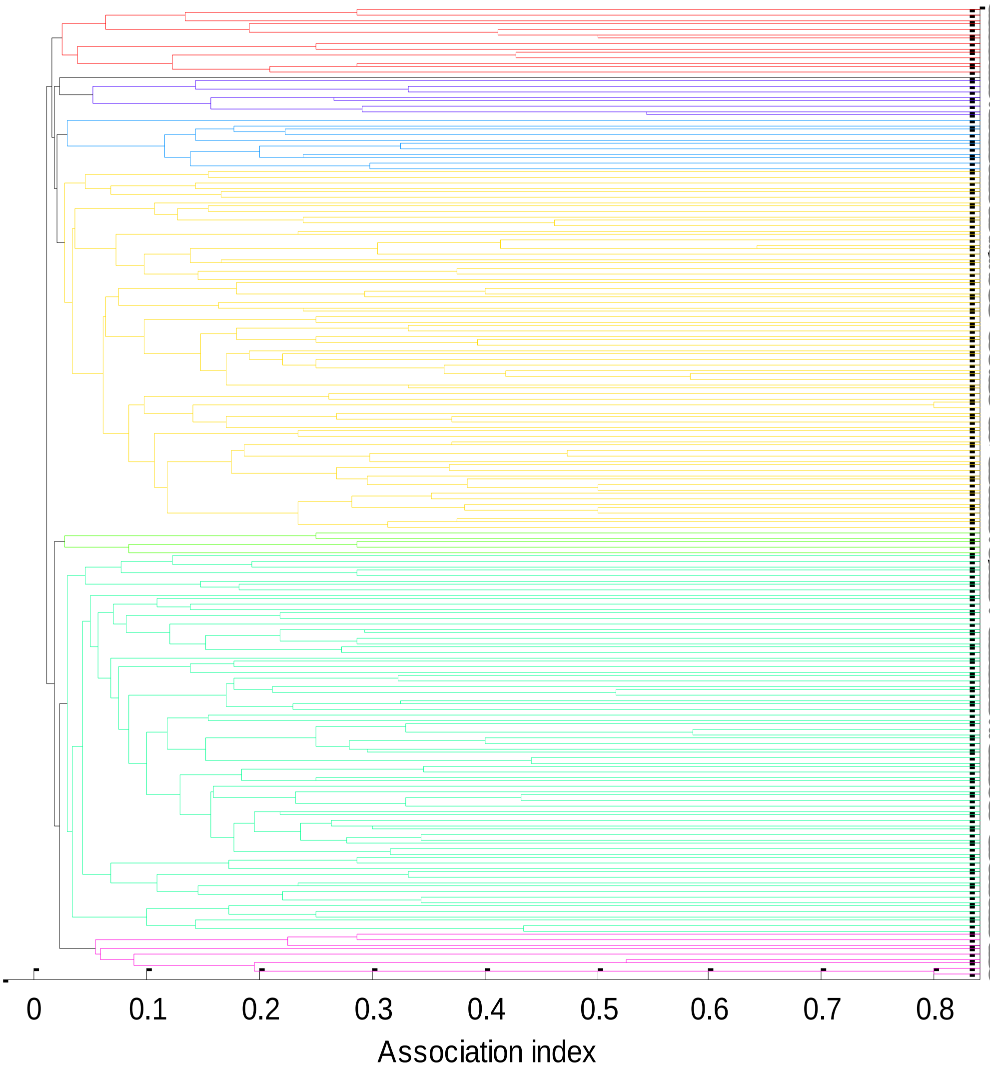


Figure 3.5 Dendrogram of hierarchical cluster analysis of Indo-Pacific humpback dolphins seen in Hong Kong waters more than four times between May 2010 and December 2014.

3.3.1.4 Temporal pattern of associations

Standardised Lagged Association Rates (SLARs) were calculated for all individuals (the whole dataset) and individual clusters, and in all cases SLARs were higher than the random association rates indicated by the null models (Figs. 3.6 and 3.7). SLAR of all individuals (Fig. 3.6) dropped sharply within approximately 100 days and, subsequently, continued to gradually decrease through the study period. Temporal models of group dynamics that best fit the observed data were ‘casual acquaintances’ and ‘two levels of casual acquaintances’ (Table 3.3; *sensu* Whitehead 2008), suggesting considerable variability in temporal associations among humpback dolphins in Hong Kong.

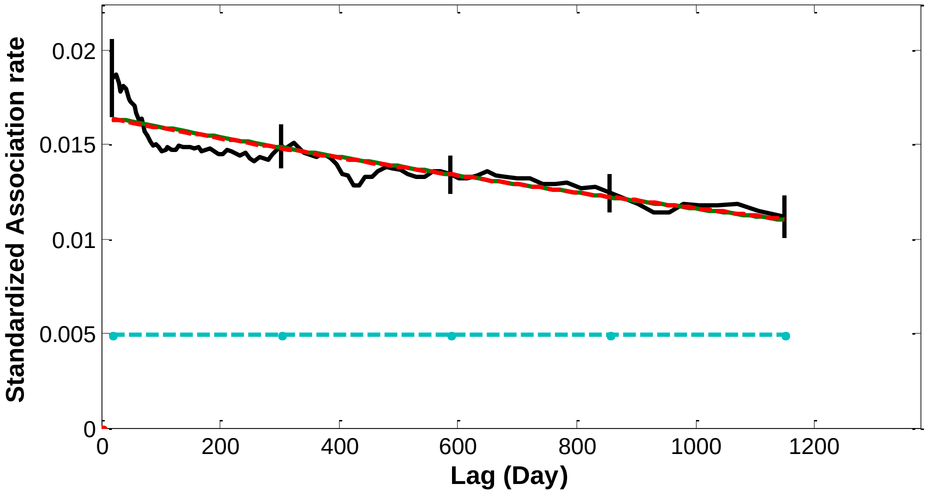


Figure 3.6 Standardised lagged association rates of all Indo-Pacific humpback dolphins seen in Hong Kong waters > 4 times between May 2010 and December 2014. Jackknife error bars are indicated with vertical lines. Null model is shown as straight broken blue line. The best fit models, ‘casual acquaintances’ and ‘two levels of casual acquaintances’ are denoted as green solid line and red broken lines, respectively (the two lines overlap).

Table 3.3 Models of temporal group dynamics fitted to standardised lagged association rates of Indo-Pacific humpback dolphins seen in Hong Kong waters more than four times between May 2010 and December 2014. ΔQAIC of 0-2 are in bold.

Models	QAIC	ΔQAIC
Preferred companions	84395	118
Casual acquaintances	**84277**	**0**
Preferred companions + Casual acquaintances	84390	113
Two levels of casual acquaintances	**84279**	**2**

Similar pattern was seen in each subset of the data representing the clusters (Fig. 3.7), except cluster 3, where two contradictory models ('preferred companions' and 'casual acquaintances'; Table 3.4) had equally good fit, which should be viewed cautiously. The error bars of SLARs were generally small for cluster 1 and 5, indicating considerable reliability of the estimates. Clusters 2 and 4, both of which consisted of a small number (n = 11 and 13, respectively) of loosely grouped individuals (see Fig. 3.4), had insufficient data to generate SLARs.

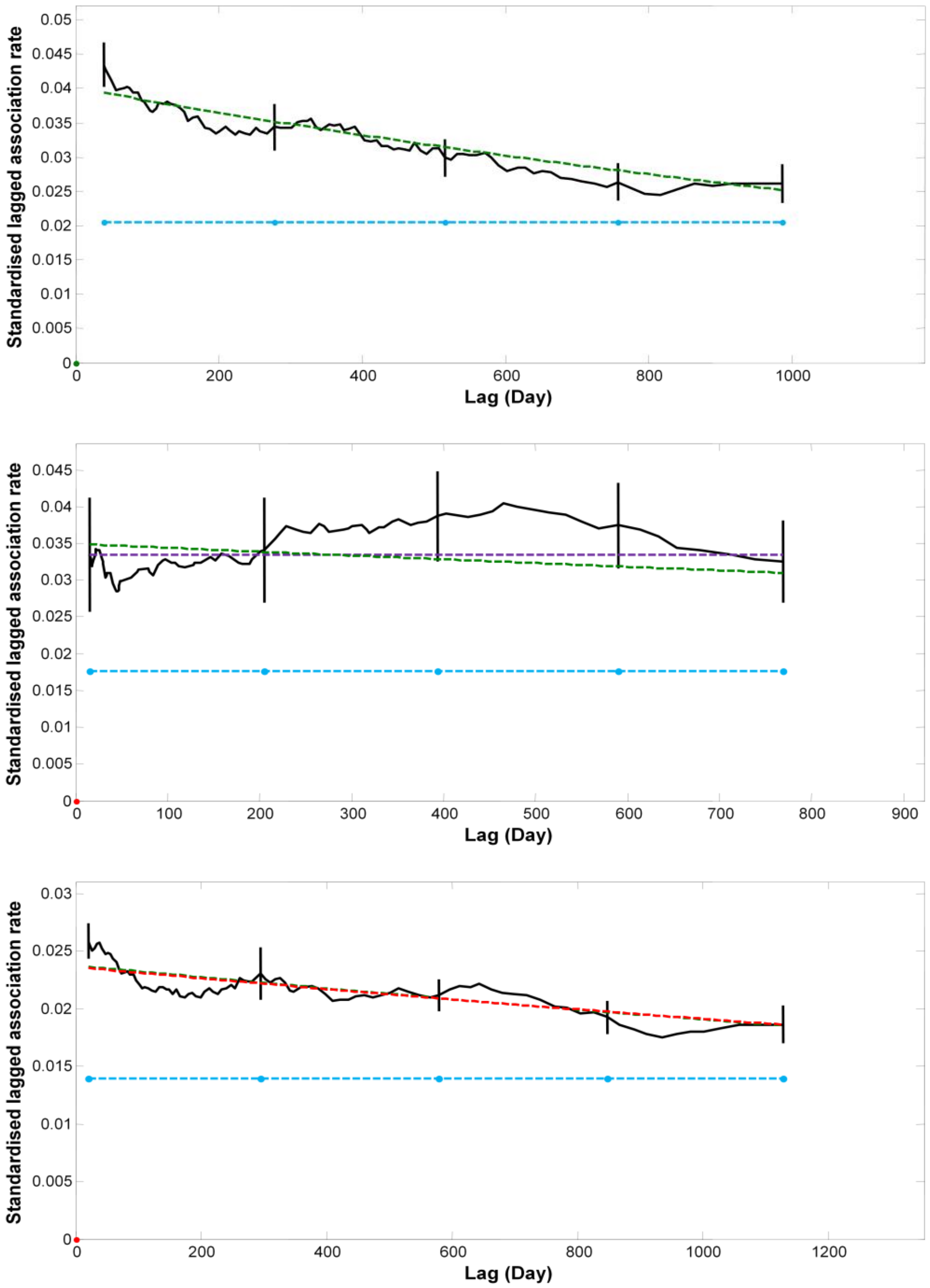


Figure 3.7 Standardised lagged association rates of Indo-Pacific humpback dolphins seen in Hong Kong waters > 4 times between May 2010 and December 2014 and grouped into five social clusters following the eigenvector method of Newman (2006). Jackknife error bars are indicated with vertical lines. Null models are shown as straight broken blue line. Best-fit models are as follows, Cluster 1 (top): ‘casual acquaintances’ denoted as green broken line; Cluster 3 (middle): ‘preferred companions’ in purple, and ‘casual acquaintances’ in green; Cluster 5 (bottom): ‘casual acquaintances’ in green and ‘two levels of casual acquaintances’ in red. Clusters 2 and 4 had insufficient data to generate SLARs.

Table 3.4 Models of temporal group dynamics fitted to standardised lagged association rates of Indo-Pacific humpback dolphins seen in Hong Kong waters > 4 times between May 2010 and December 2014 and grouped into five social clusters following the eigenvector method of Newman (2006). ΔQAIC of 0-2 are in bold. Clusters 2 and 4 had insufficient data to generate SLARs and models were not fitted.

(A) Cluster 1

Models	QAIC	ΔQAIC
Preferred companions	25324	58
Casual acquaintances	**25266**	**0**
Preferred companions + Casual acquaintances	25324	58
Two levels of casual acquaintances	25270	4

(B) Cluster 3

Models	QAIC	ΔQAIC
Preferred companions	**5373**	**0**
Casual acquaintances	**5373**	**0**
Preferred companions + Casual acquaintances	5377	4
Two levels of casual acquaintances	5377	4

(C) Cluster 5

Models	QAIC	ΔQAIC
Preferred companions	65741	40
Casual acquaintances	**65702**	**1**
Preferred companions + Casual acquaintances	65737	36
Two levels of casual acquaintances	**65701**	**0**

3.3.1.5 Socio-spatial pattern

The five social clusters, as suggested by the eigenvector method of Newman (2006), differed in their spatial pattern of range use. Their spatial pattern could be broadly categorised into three types (as indicated by kernel density utilisation distributions, UDs):

1. Ranging throughout the species' known home range in Hong Kong waters, with 50% UD clustering around Lung Kwu Chau and, more sparsely, off the west coast of Lantau Island. This spatial pattern is represented by Cluster 1 (Fig. 3.8); the only cluster that displayed small kernels of 50% UD in the region of the Brothers Islands.
2. Utilising the westernmost Hong Kong waters, both Lung Kwu Chau and west coast of Lantau Island, but with 50% UD predominantly off the west coast of Lantau Island (Cluster 3; Fig. 3.8).
3. Utilisation distribution (50% UD) centred exclusively off southwest Lantau Island (Cluster 5; Fig. 3.9).

The remaining two smallest clusters, Clusters 2 and 4, displayed a pattern intermediate between Type 2 and Type 3, but spatially more akin to Type 3, with 50% UD off west and southwest Lantau (Figs. 3.8, 3.9), similarly as Cluster 5 with was their closest social intermix (see Fig. 3.4).

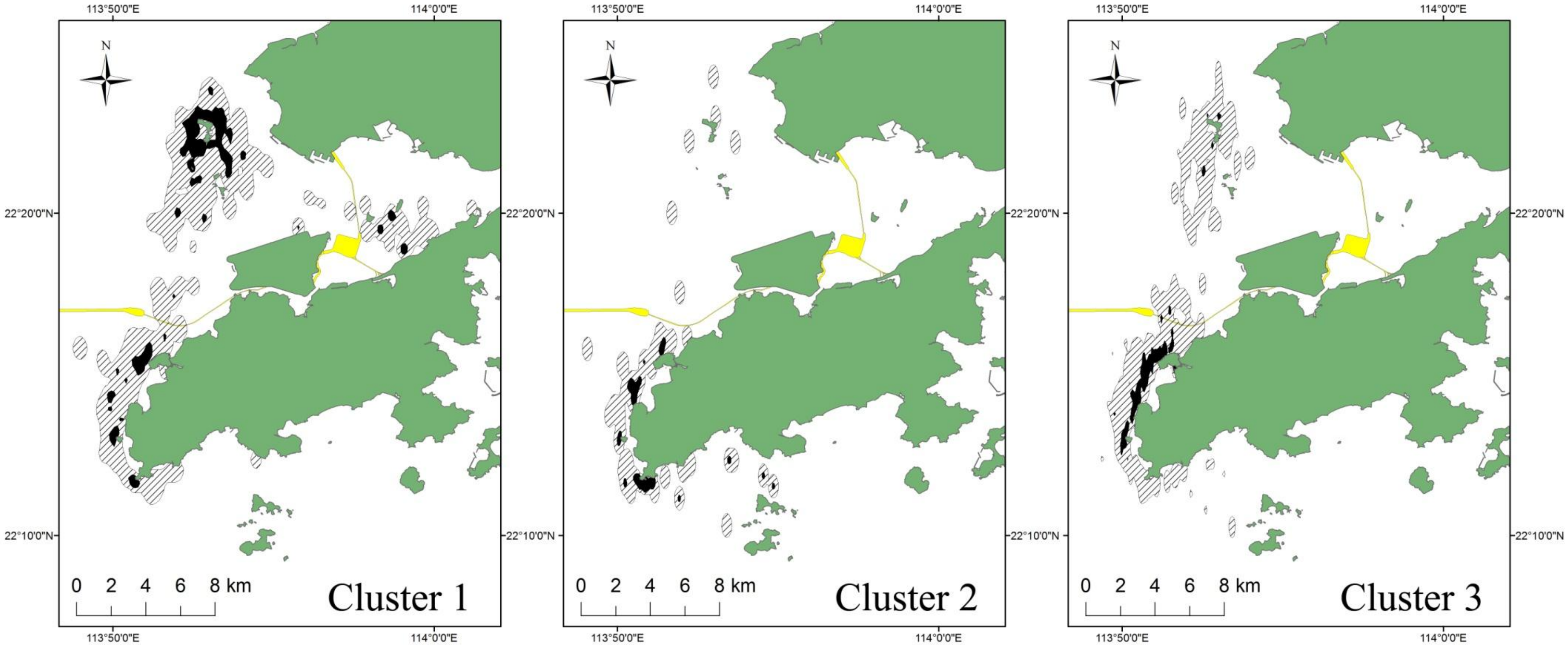


Figure 3.8 Kernel density estimates of 95% (hatched polygons) and 50% volumes (filled polygons) of area utilisation of Cluster 1, 2, and 3 of Indo-Pacific humpback dolphins seen in Hong Kong waters > 4 times between May 2010 and December 2014. Grouping into social clusters followed the eigenvector method of Newman (2006).

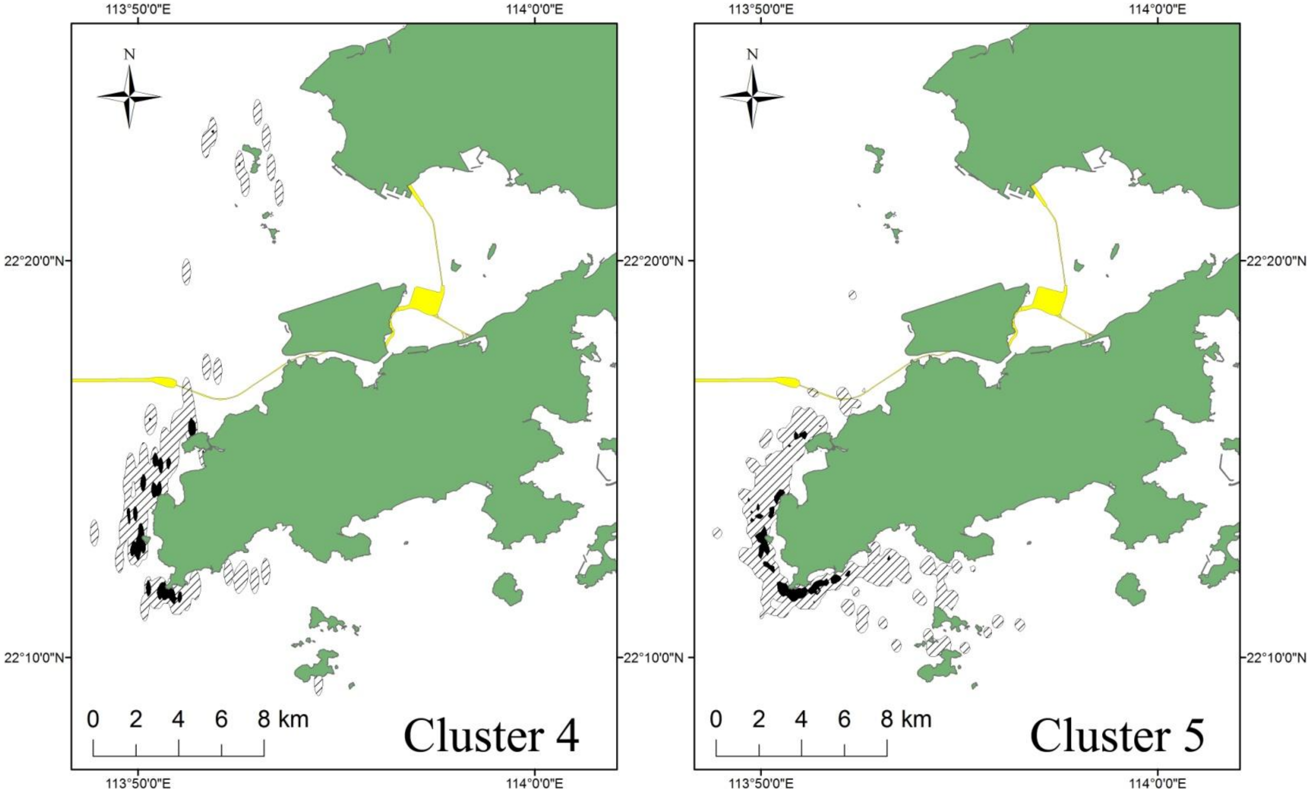


Figure 3.9 Kernel density estimates of 95% (hatched polygons) and 50% volumes (filled polygons) of area utilisation of Clusters 4 and 5 of Indo-Pacific humpback dolphins seen in Hong Kong waters > 4 times between May 2010 and December 2014. Grouping into social clusters followed the eigenvector method of Newman (2006).

3.3.1.6 Movement pattern

Dolphin movement, quantified with lagged identification rates (LIR), was broadly comparable across the study area. In both north and south section of western Hong Kong waters, initial values of LIR dropped sharply in a short period of time (several days to couple of weeks) and, subsequently, continued to gradually decline over time (Fig.3.10). In the north section, models that best described the pattern of dolphin movement were 'emigration' and 'emigration + re-immigration + mortality', while in the south section it was 'emigration + re-immigration + mortality' (Table. 3.5).

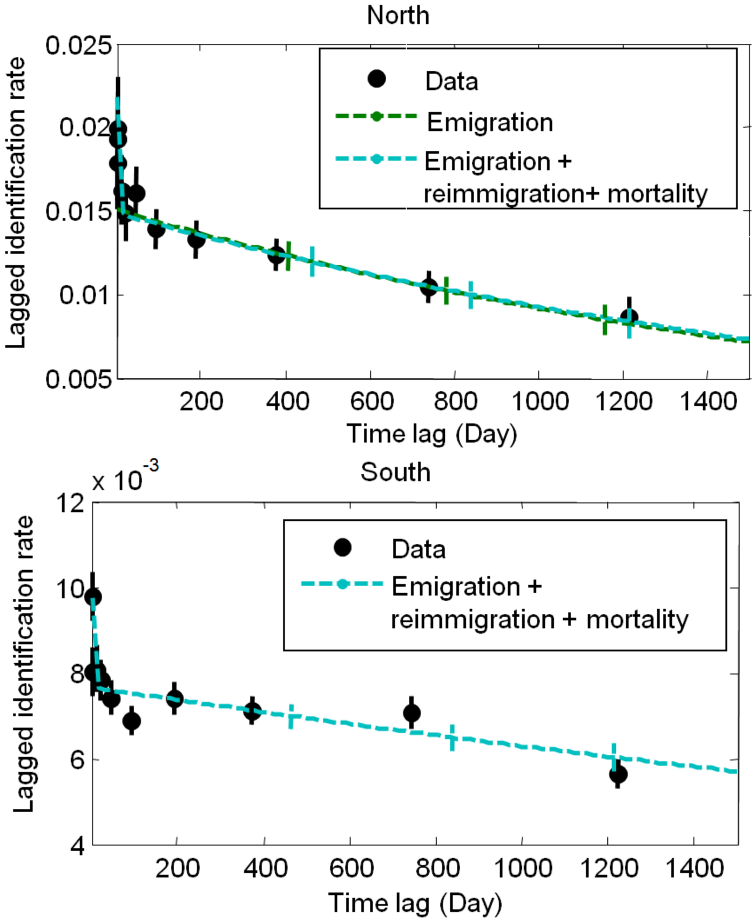


Figure 3.10 Lagged identification rates of Indo-Pacific humpback dolphins seen in the north and south of the study area (western Hong Kong waters) between May 2010 and December 2014. Broken lines represent the best fit models with ΔQAIC within 2 units. Vertical lines indicate bootstrap estimates of SE.

Table 3.5 Movement models fitted to lagged identification rates of Indo-Pacific humpback dolphins seen in the north and south of the study area (western Hong Kong waters) between May 2010 and December 2014. ΔQAIC of 0–2 are in bold.

Model	QAIC	ΔQAIC	Maximum-likelihood value for parameters	Bootstrapped SEs
North				
Closed	54113.5	144.7	*N* = 83.6	6.3
Emigration	**53970.8**	**1.9**	*N* = 66.2	6.2
			Mean residence = 2013.6	583.7
Emigration + re-immigration	53971.7	2.9	*N* = 64.6	6.3
			Residence time in = 1554.4	581.1
			Residence time out = 2629.8	4437068986737.4
Emigration + re-immigration + mortality	**53968.9**	**0**	*N* = 41.7	6.6
			Residence time in = 9.7	100.8
			Residence time out =5.9	41.0
			Mortality = 0.00047574	0.0

Table 3.5 continue

Model	QAIC	ΔQAIC	Maximum-likelihood value for parameters	Bootstrapped SEs
South				
Closed	291381	167.6	*N* = 143.1	6.1
Emigration	291222	9.1	*N* = 129.8	6.4
			Mean residence = 4888.0	1668.6
Emigration + re-immigration	291325	111.7	*N* = 117.158	34.0
			Residence time in = 220.2936	1976.4
			Residence time out = 54.7425	1640934020558.2
Emigration + re-immigration + mortality	**291213**	**0**	*N* = 45.9	10.1
			Residence time in = 0.81	9.0
			Residence time out = 1.5	1.8
			Mortality = 0.00019751	0.0

Lagged identification rates representing the movement of Indo-Pacific humpback dolphins between north and south of the study area are shown in Fig. 3.11. Both movement models representing interchange between areas fit well the observed data (Table 3.7). The low residence estimate produced by the ‘migration-full interchange’ model suggests that the interchange of individuals between areas occurs frequently. Among individuals seen more than once during the study period, most dolphins (47%; n = 131) were seen in both north and south of Hong Kong western waters, 45% (n = 124) were seen only in the south and 8% (n = 22) were seen only in the north (Fig. 3.12).

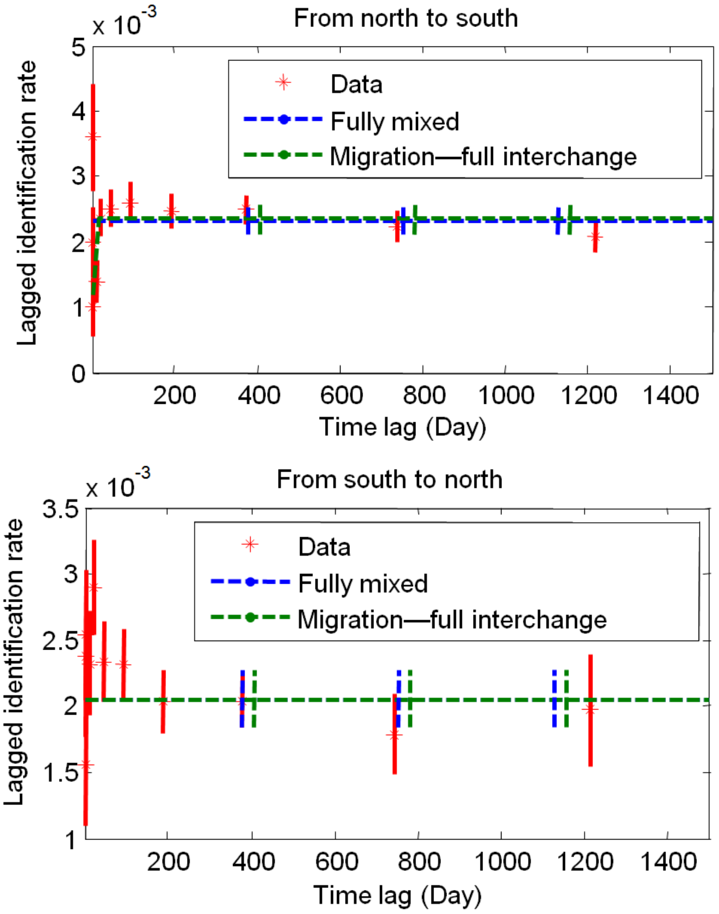


Figure 3.11 Lagged identification rates indicating movement of Indo-Pacific humpback dolphins between north and south of the study area (western Hong Kong waters) between May 2010 and December 2014. Broken lines represent the best-fit models with ΔQAIC within 2 units. Vertical lines indicate bootstrap estimates of SE.

Table 3.6 Movement models fitted to lagged identification rates for within- and between-area movement of Indo-Pacific humpback dolphins between May 2010 and December 2014 in Hong Kong. ΔQAIC of 0–2 are in bold.

Model	QAIC	ΔQAIC	Maximum-likelihood value for parameters	Bootstrapped SEs
From north to south				
Fully mixed	**35849.3**	**1.2**	*N* = 428.9	39.7
Migration–full interchange	**35848.1**	**0**	*N* = 427.9	39.7
			Mean residence = 1.4	0.6
From south to north				
Fully mixed	**17902.5**	**0**	*N* = 486.9	48.3
Migration–full interchange	**17904.5**	**2**	*N* = 486.9	48.3
			Mean residence = 0.03	0.2

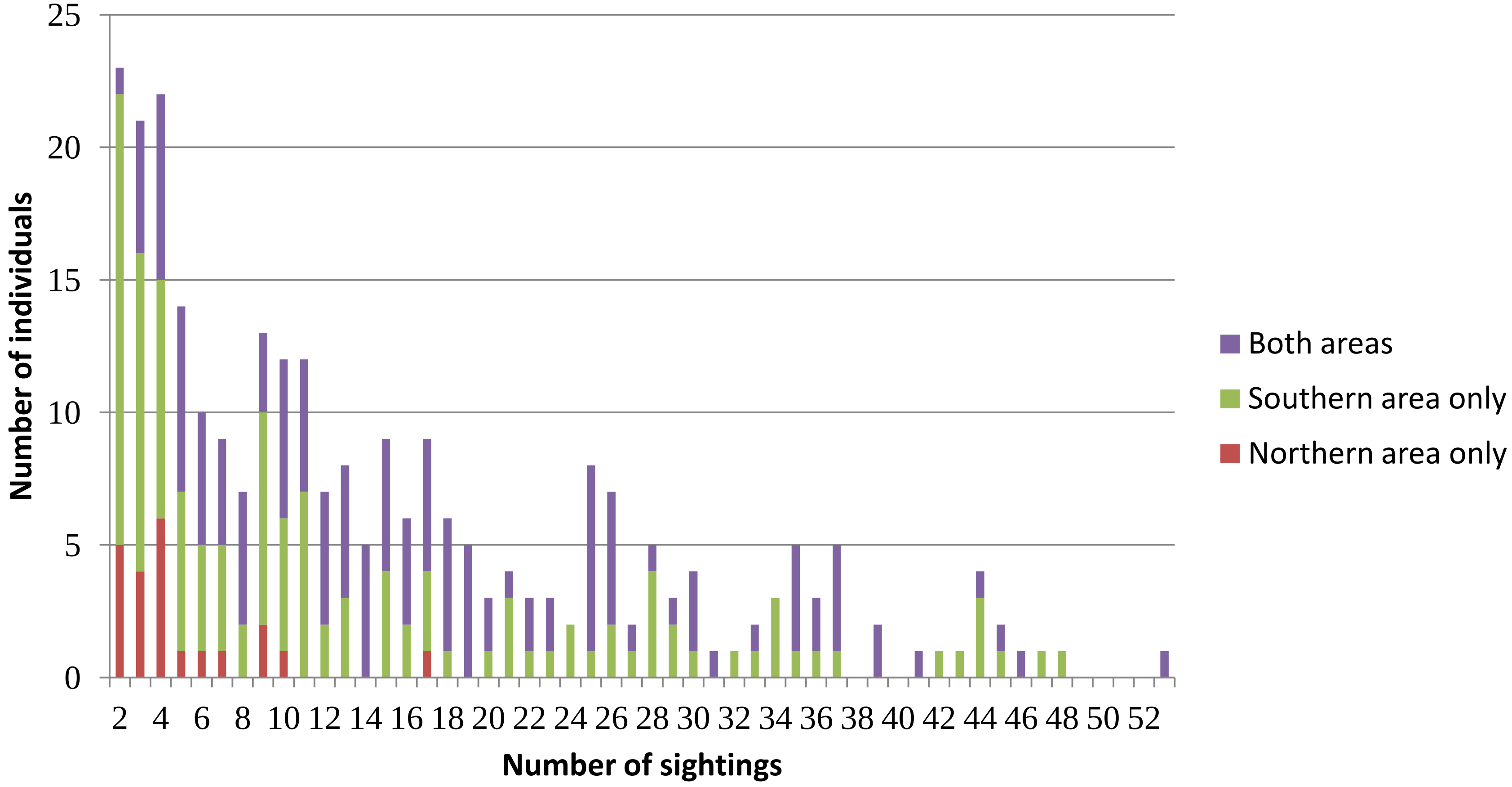


Figure 3.12 Sighting frequency of Indo-Pacific humpback dolphins that were seen either only in the north or south, or both north and south of the study area (western Hong Kong waters) between May 2010 and December 2014.

Results generated from the dataset with lower quality photos (ie. image quality ≥ 60) consistently presented similar movement patterns within and between north and south of the study area. LIR reduced sharply in a short period of time (several days to couple of weeks) and continued to drop gradually over time (Fig.3.13). In the north section, models that best described the pattern of dolphin movement were ‘emigration + re-immigration’ and ‘emigration + re-immigration + mortality’, while in the south section it was ‘emigration + re-immigration + mortality’ (Table. 3.7).

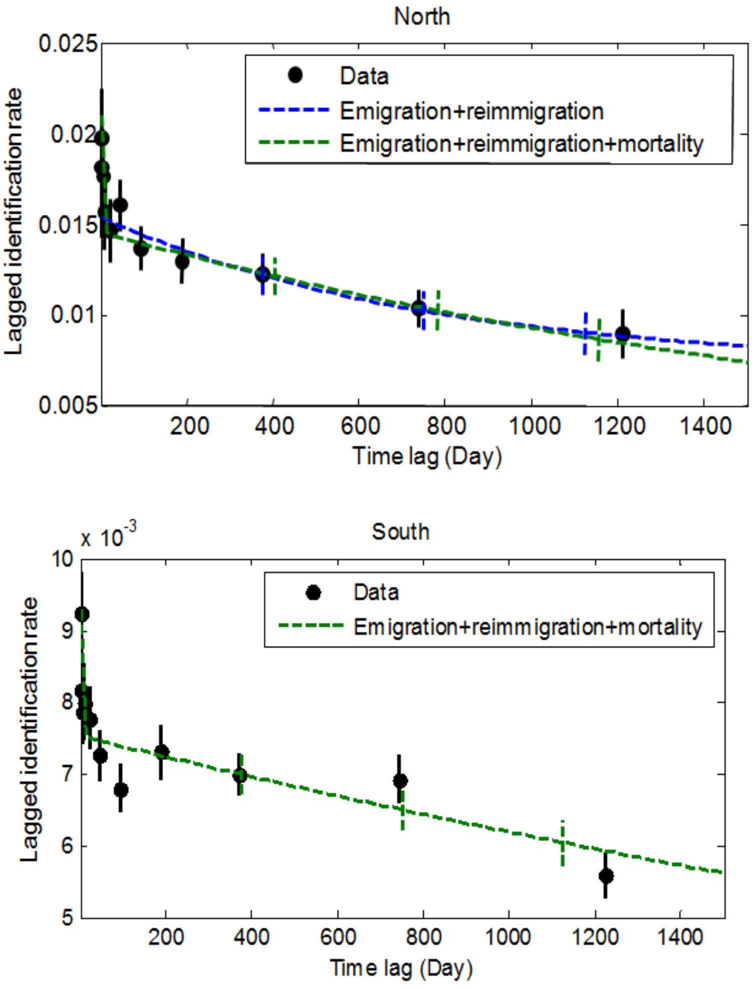


Figure 3.13 Lagged identification rates of Indo-Pacific humpback dolphins seen in the north and south of the study area (western Hong Kong waters) with image quality ≥ 60 between May 2010 and December 2014. Broken lines represent the best fit models with ΔQAIC within 2 units. Vertical lines indicate bootstrap estimates of SE.

Table 3.7 Movement models fitted to lagged identification rates of Indo-Pacific humpback dolphins seen in the north and south of the study area (western Hong Kong waters) with image quality ≥ 60 recorded between May 2010 and December 2014. ΔQAIC of 0–2 are in bold.

Model	QAIC	ΔQAIC	Maximum-likelihood value for parameters	Bootstrapped SEs
North				
Closed	61383.6	151	*N* = 84.5	6.5
Emigration	61235.2	2.6	*N* = 67.7	5.2
			Mean residence = 2112.4	518.5
Emigration + re-immigration	61234.3	**1.7**	*N* = 65.0	5.4
			Residence time in = 1400.7	538.4
			Residence time out = 1627.8	2548268142668.8
Emigration + re-immigration + mortality	61232.6	**0**	*N* = 43.4	7.1
			Residence time in = 10.6	109.8
			Residence time out = 6.1	50.4
			Mortality = 0.00045232	0.0

Table 3.7 continue

Model	QAIC	ΔQAIC	Maximum-likelihood value for parameters	Bootstrapped SEs
South				
Closed	325400.0	174.3	*N* = 145.5	6.6
Emigration	325232.0	6.3	*N* = 132.3	7.1
			Mean residence = 4962.5	1373.1
Emigration + re-immigration	325234.0	8.3	*N* = 132.3	13.9
			Residence time in = 4962.8	2184.1
			Residence time out = 5286602398.5	1367394702577.2
Emigration + re-immigration + mortality	325225.7	**0**	*N* = 40.3	15.5
			Residence time in = 0.6	20.7
			Residence time out = 1.4	1.6
			Mortality = 0.00019556	0.0

Same as the results from the dataset with only images of quality ≥ 70, both movement models representing interchange between areas fit well to the dataset with lower quality images (Table 3.8). Among individuals seen more than once during the study period, similar percentages of dolphins were recorded in either one of the areas or both areas compared with the dataset with only high quality photos. Most dolphins (48%; n = 136) were seen in both north and south of Hong Kong western waters, 45% (n = 129) were seen only in the south and 7% (n = 20) were seen only in the north (Fig. 3.15).

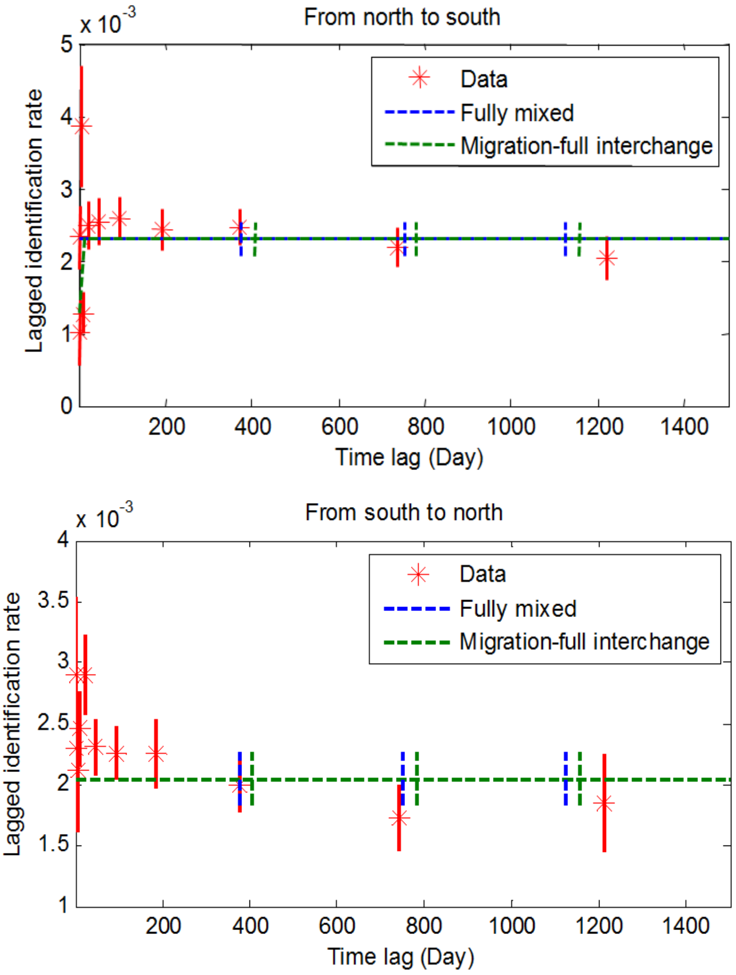


Figure 3.14 Lagged identification rates indicating movement of Indo-Pacific humpback dolphins between north and south of the study area (western Hong Kong waters) with image quality ≥ 60 recorded between May 2010 and December 2014. Broken lines represent the best-fit models with ΔQAIC within 2 units. Vertical lines indicate bootstrap estimates of SE.

Table 3.8 Movement models fitted to lagged identification rates for within- and between-area movement of Indo-Pacific humpback dolphins with image quality ≥ 60 recorded between May 2010 and December 2014 in Hong Kong. ΔQAIC of 0–2 are in bold.

Model	QAIC	ΔQAIC	Maximum-likelihood value for parameters	Bootstrapped SEs
From north to south				
Fully mixed	40623.4	**1.1**	*N* = 434.3	45.2
Migration–full interchange	40622.3	**0**	*N* = 433.5	45.2
			Mean residence = 1.2	0.4
From south to north				
Fully mixed	19505.2	**0**	*N* = 488.4	54.3
Migration–full interchange	19507.2	**2.0**	*N* = 488.4	54.3
			Mean residence = 0.04	0.1

3.3.2 Testing previously suggested community structure

Restricting the dataset to individuals seen > 14 times limited the analysis to 88 adults. In this restricted dataset, the correlation between true and estimated association indices was good (r = 0.708±0.022) and social differentiation was high (S = 0.926 ±0.020). Associations were generally weak, with a mean and maximum HWI of 0.06±0.02 and 0.32±0.10, respectively.

3.3.2.1 Community structure

Using the eigenvector method of Newman (2006) with modularity calculated under the control on gregariousness, four clusters were identified (Fig. 3.13). Such division between clusters was useful (modularity = 0.341) and the Mantel test indicated that associations within clusters were higher than among clusters (t = 28.124, p = 1).

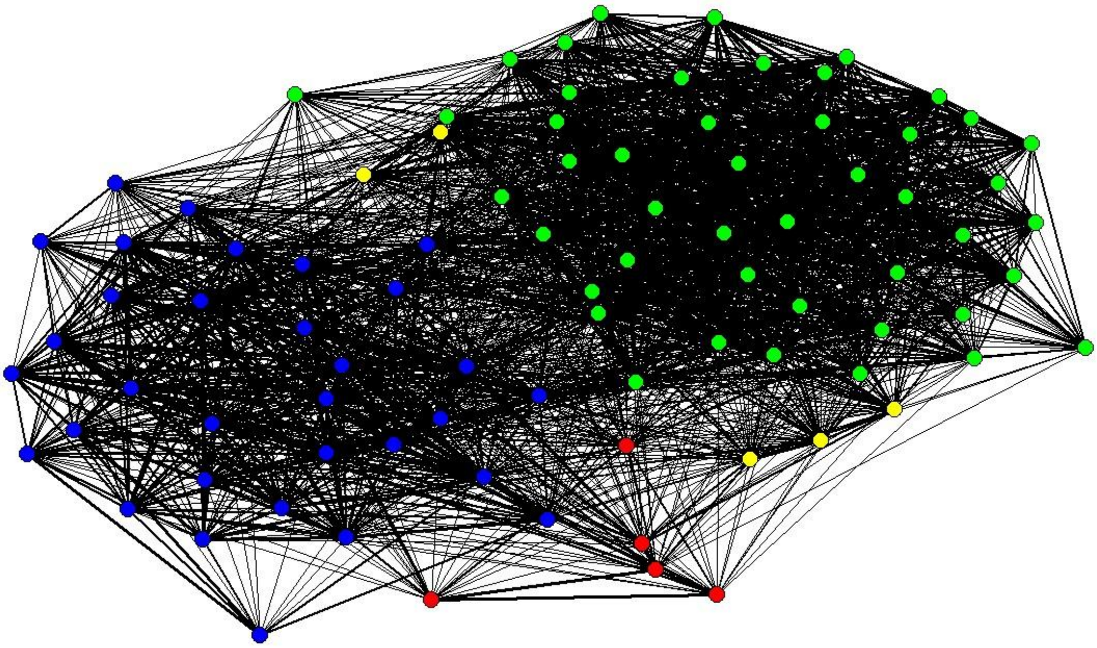


Figure 3.15 Network diagram of Indo-Pacific humpback dolphins seen in western Hong Kong waters > 14 times between May 2010 and December 2014. Individuals are shown as nodes. The thickness of lines indicates the strength of association. Individuals in Cluster 1 (n=5) are denoted as red nodes, Cluster 2 (n=5) as yellow, Cluster 3 (n=32) as blue and Cluster 4 (n=46) as green nodes.

Average-linkage hierarchical cluster analysis with modularity calculated under the control on gregariousness identified three clusters (Fig. 3.14). The Cophenetic Correlation Coefficient of the constructed dendrogram was 0.7981 and maximum modularity was 0.3425 at an HWI of 0.0339, both considered close to representative.

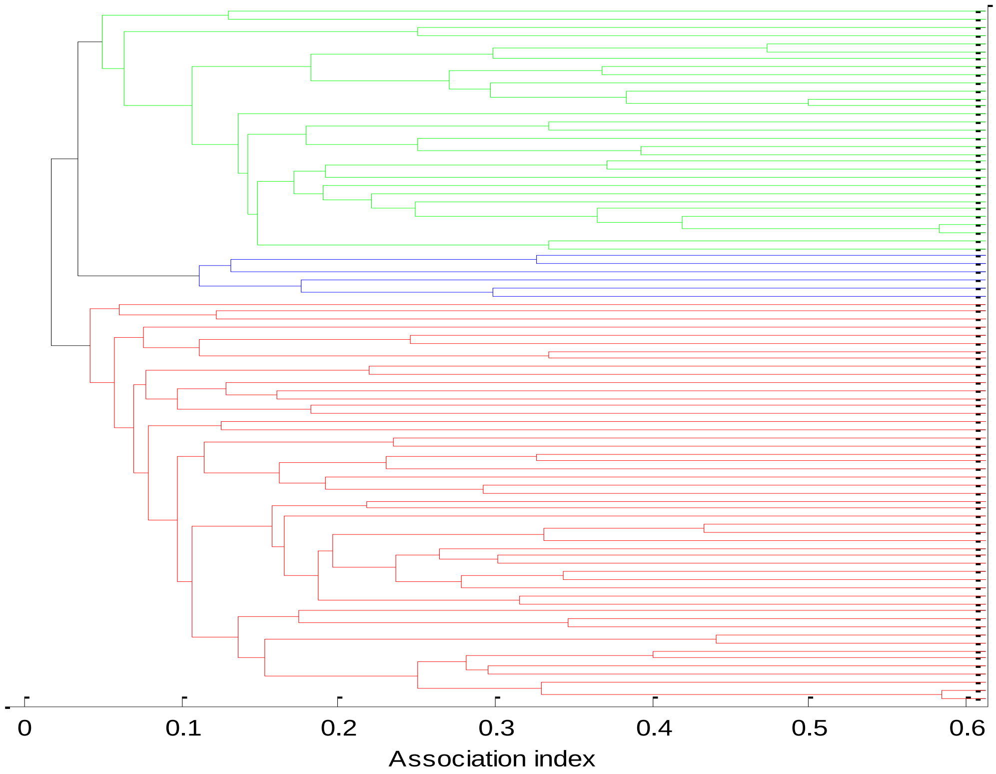


Figure 3.16 Dendrogram of hierarchical cluster analysis of Indo-Pacific humpback dolphins seen > 14 times in western Hong Kong waters between May 2010 and December 2014.

3.3.2.2 Socio-spatial pattern

The restricted dataset has shown a spatial pattern similar to that of individuals seen > 4 times (Fig. 3.15). Cluster 3 displayed Type 1 distribution (see page 58), Cluster 1 displayed Type 2 distribution and Cluster 4 displayed Type 3 distribution. Cluster 2 displayed an intermediate pattern between Type 2 and Type 3 distribution.

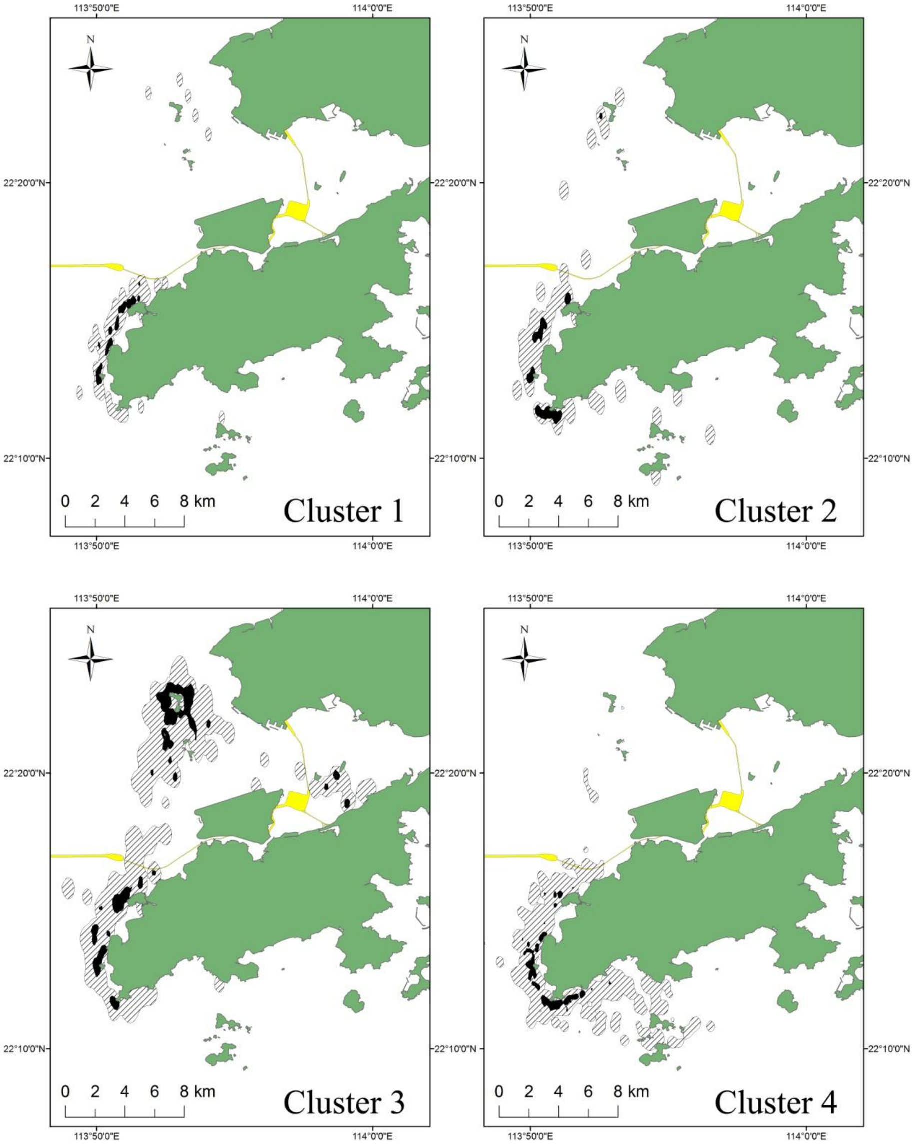


Figure 3.17 Kernel density estimates of 95% (hatched polygons) and 50% volumes (filled polygons) of area utilisation pattern of four clusters of Indo-Pacific humpback dolphins seen in Hong Kong waters > 14 times between May 2010 and December 2014, grouped into social clusters using the eigenvector method of Newman (2006).

3.4 Discussion

3.4.1 Groups and grouping pattern

Humpback dolphins in Hong Kong live in a fission-fusion society with fluid groups and generally weak inter-individual associations, a pattern seen previously in other populations and species of the genus *Sousa* (e.g. Karczmarski 1999; Chang 2011; Parra et al. 2011). The group sizes detailed in the current study are similar to those reported previously in Hong Kong (Jefferson 2000; 3.8 ± 3.63) and well within the range displayed by other humpback dolphin populations elsewhere (Jefferson and Karczmarski 2001). Similarly as seen for *S. sahulensis* off northeast Australia (Parra et al. 2011), groups size in Hong Kong varied with behaviour and socialising groups were generally larger than at any other behaviours. However, contrary to some other known cases (e.g. Parra et al. 2011; Keith et al. 2013), in Hong Kong waters the largest groups were observed during foraging. This most likely relates to prey availability, as dolphins are known to aggregate when prey are abundant or when shoaling fish are present (Würsig 1986; see also Chapter 2). Large and dense prey patches may attract more individuals to form foraging aggregations and at times facilitate cooperative foraging by limiting scramble competition (Gowans et al. 2008). Individuals in such large foraging group may not necessarily be associated in the social context but are together in close proximity because of their locally abundant common resource, the aggregation of prey. A substantial proportion (93%) of humpback dolphin prey in the PRE consists of the fish families such as Sciaenidae, Engraulidae, Trichiuridae and Clupeidae, most of which appear in large shoals (Barros et al. 2004). Such high proportion of shoaling fish in the humpback dolphins' diet may in part explain their gregariousness during foraging.

The individual association pattern displayed by humpback dolphins in Hong Kong was generally weak, as indicated by low values of both mean and maximum association indices. In fact, the values of HWI calculated for humpback dolphins in Hong Kong were comparatively lower than those reported elsewhere in the region (Chang 2011; Xu et al. 2012; Dungan et al. 2015). A direct comparison of HWI values may not be the most informative, however, because of the differences in the population numbers and, in some cases, differences in analytical treatment (e.g. inclusion of dependent calves by Dungan et al. 2015, which must have biased the mean HWI values upwards). Temporal analysis of group dynamics is far more telling, and far more representative in terms of a comparative approach. In Hong Kong, the grouping pattern was highly dynamic and the temporal models that best describe the observed data suggest that casual interactions are the norm for the dolphins in Hong Kong waters, as it also is in other species and population of humpback dolphins elsewhere (Karczmarski 1999; Chang 2011; Parra et al. 2011; Dungan et al. 2015).

3.4.2 Socio-spatial dynamics

High network strength and reach indicate that the dolphins in Hong Kong interact frequently with one another, but not to the level of a tightly homogeneous society, as the clustering coefficient was lower than in random networks. This is to be expected, given the openness of the population and the fluidity of the associations. Although the dolphins may associate with many other dolphins, their individual associates may not necessarily be connected with each other. Cluster analyses suggested five social groupings, referred hereafter as clusters, with a substantial number of dolphins falling into three of the clusters. Although associations within clusters were higher than among clusters, all clusters were tightly interconnected and hierarchical cluster analysis suggested that the grouping pattern may need to be viewed cautiously. Consequently, the overall social pattern seems to represent a closely interconnected, although not homogeneous society, with a fine-scale but diffused substructure, where some animals associate more often with each other (social clusters) than with other individuals, but not to a degree of social discreteness indicative of discernible communities (as defined by Wells et al. 1999).

Some of the clusters (Cluster 2 and 4) represented too small subset of the dataset to perform reliable socio-temporal analyses, while Cluster 3 generated an ambiguous pattern, possibly indicating that the amplitude of short-term variability may obscure a long-term pattern. This certain degree of ambiguity might be due to the tight interconnectivity of the five clusters and perhaps indicative of their temporarily ephemeral structure, with the fluid casual interactions between individuals representing the underlying long-term pattern.

The spatial pattern of the social clusters, partially overlapping but visibly different between most of the clusters, is indicative of a spatial gradient in the individual pattern of range use. The core areas for the three largest social clusters clearly differed, suggesting that fine scale spatial preferences play a substantial role in the maintenance of fine scale social structure of the larger dolphin society. At the same time, however, a substantial overlap in range use of each of the social clusters indicates a shared use of habitat in the broader context. Consequently, both spatial habitat preferences and individual association patterns are likely the driving forces that shape the social dynamics of humpback dolphins in Hong Kong waters.

3.4.3 Movement pattern

A large proportion of humpback dolphins in this study were seen only once and the probability of re-sighting of the same individual decreased sharply within a temporal scale of just few days in both northern and southern waters, suggesting that the majority have low site fidelity. Some dolphins, however, re-enter Hong Kong waters after spending some time outside Hong Kong territorial waters, as indicated by the pattern of LIRs. This is consistent with the recent findings by Chan and Karczmarski (2017), while the variable estimates of 'time in' and 'time out' suggest heterogeneity in individual-specific movement and residence pattern.

Contrasting modes of movement between Hong Kong’s northern and southern waters have been suggested in the past. Porter (1998) was the first to propose a limited exchange of dolphins between the north and south based on photographic identification and a genetic analysis on 10 stranded dolphins. Subsequent studies on individual home ranges, however, suggested that there were dolphins that utilised both areas (Hung and Jefferson 2004; Hung 2008) and genetic analyses did not reveal population division (Jefferson 2000). The present study supports the argument that dolphins frequently move between north and south, and a large proportion of individuals (47%) were seen in both north and south of the study area. At the same time, some individuals were only seen in either north or south, suggesting that some dolphins have comparatively restricted ranges. This is not merely an artefact of low sighting frequency, as such a restricted ranging pattern was also observed among some of the highly re-sighted individuals, and is likely either due to individual-specific preferences or perhaps due to competitive exclusion.

3.4.4 Comparison with previous studies in Hong Kong

Results from both the full dataset and the sub-sampled dataset restricted to 88 most frequently seen individuals (as in Dungan et al. 2012) indicated a considerably more dynamic and more complex pattern of socio-spatial structure than that suggested by Dungan et al. (2012). Instead of a two communities with different association patterns, this study revealed multiple closely interacting social clusters, not discernible communities, with fine-scale differences in their socio-spatial dynamics and differing pattern of range use, within a broader context of extensively shared habitats and largely similar association patterns. It is hard to be assured about the causes underlying such differences in the results. These differences appear to be unrelated to the analytical methods, as this current study performed the analysis using the same analytical tools as Dungan et al. (2012) and the larger dataset was specifically sub-sampled so that the same number of most frequently re-sighted individuals was used.

Potential causes could be the differences in the sampling years and/or differences in the number sightings of frequently re-sighted individuals. The former would suggest a stark change in dolphin socio-dynamics during 2000–2009 (Dungan et al. 2012) as compared to 2010–2014 (this study). One could attribute this change to environmental change, as the study period of the current research fell within the construction period of a large coastal infrastructure in the region; the construction of the Hong Kong–Zhuhai–Macau Bridge (HKZMB) commenced in December 2009 in mainland China and in March 2012 in Hong Kong. Cluster analyses of the data collected in Hong Kong waters before this construction started in Hong Kong did not, however, reveal any clear social division that could support the two-community hypothesis (see Chapter 4). Consequently, the recent construction activities are unlikely to be the main cause for the discrepancy between the two studies.

In this current study, a dataset consisting of 202 adult dolphins seen > 14 times and a sub-sampled dataset of 88 adults seen > 4 times were used; whereas Dungan et al. (2012) used a dataset of 88 individuals seen > 10 times. Although the results from dataset of dolphins seen > 14 times displayed 3–4 clusters, the majority of dolphins were grouped into two major clusters, thus appearing to match the finding of Dungan et al. (2012). This suggests therefore that restricting the analyses to only a subset of the most frequently re-sighted individuals could significantly bias the resulting pattern of social structure and superficially simplify the complexity of their social dynamics. Consequently, the study presented here should be seen as a revision of the previously suggested socio-spatial pattern of humpback dolphins in Hong Kong (Dungan et al. 2012) and a constructive critique of the limitations and implications that may follow when photo-ID data of highly dynamic fission-fusion dolphin societies are over-restricted.

3.4.5 Factors influencing the social dynamics of humpback dolphins in Hong Kong

The conceptual model proposed by Gowans et al. (2008) suggested that the major proximate factors driving the social pattern of inshore delphinids such as humpback dolphins include predation risk, predictability of inshore habitats, and prey distribution; and, as suggested by earlier studies of humpback dolphins in South Africa, behavioural differences of nursing females and mate-searching behaviour by males (Karczmarski 1999). The absence of large sharks or other top predators in the PRE rules out the risk of predation, while the other factors appear to be probable for dolphins in this area. Furthermore, habitat preferences, geographic proximity and the openness of the area may influence the social dynamics of Hong Kong’s dolphins.

Animals are known to aggregate at a location due to either sociality or external factors, such as prey distribution (Krause and Ruxton 2002; Gowans et al. 2008). As foraging grounds are most likely the areas with the highest abundance of prey, the strong resemblance of the area utilisation patterns of the social communities revealed in this chapter to the core and range of foraging grounds outlined in Chapter 2 supports the hypothesis that humpback dolphin social structure is strongly related to prey distribution (Gowan et al. 2008). In Hong Kong, humpback dolphins aggregate around these foraging areas and the geographic proximity between individuals with similar area preference may facilitate dolphin associations. In other words, individual differences in habitat use, due to individual preferences or perhaps competitive exclusion, may contribute to the establishment of a socio-spatial structure among the animals.

A previous study of humpback dolphins in Hong Kong suggested that there was considerable variability in individually-preferred areas (Hung and Jefferson 2004; Hung 2008). Direct evidence of individual spatial preference in the formation of social communities would require a study on the individual home range overlap within and among members of social communities. The construction of individual home ranges, however, requires a minimum of 30 identifications (Seaman et al. 1999). Only 13% (n = 26) of individuals in my dataset reached this requirement. Instead, this study used social clusters as the unit. The observed core areas of social clusters indicated a certain degree of segregation, in other words a spatial structure, and, given the fluid dynamic nature of humpback dolphin groups, suggests that spatial structure contributes to the formation of social clusters in Hong Kong. Furthermore, as there is no physical barrier between foraging grounds, this allows for a mosaic, yet overlapping spatial distribution among social units. Such an overlapping spatial pattern between communities has been observed in other cetaceans, such as bottlenose dolphins (*Tursiops* spp.). Social communities may exist in shared habitats (Lusseau et al. 2006; Louis et al. 2015; Titcomb et al. 2015) and community divisions could be driven by differences in fine scale area use and ranging patterns (Wiszniewski et al. 2009).

The observed spatial segregation could also be facilitated by fine scale habitat heterogeneity. In the PRE, differences in natural oceanographic features and anthropogenic activities may create different habitats for both prey and their predators. With more shipping channels and developed coastline, the level of anthropogenic disturbances is comparatively higher in the northern area. Individuals that are more adapted to disturbances or less selective in habitat choice are likely to reside in the northern area. The southern area is located further away from the river mouth and is subject to a greater influence of both seawater and the seasonal variability related to the out-flux of freshwater from the Pearl

River (Yin 2002). As a result, prey types and composition may differ across the PRE. Without fish distribution data, however, potential relationships between habitats and prey remain speculative. Furthermore, resource specialisation as the extreme of prey-type preference may result in difference in area use pattern. For instance, the nearshore form of bottlenose dolphin *Tursiops truncatus* in western North Atlantic feed on coastal fish while the offshore form feed mainly on deep-water squid (Hoelzel et al.1998). In a smaller spatial scale, bottlenose dolphin *T. truncatus* in the Normano-Breton gulf appears to be divided into three social clusters with spatial segregation and possibly difference in foraging behaviour and prey choice as indicated by difference in stable isotope signature among the clusters (Louis 2014). Similar correlation between space use, prey choice and social clustering may be present in humpback dolphins and to resolve the relations between prey and socio-spatial dynamics of humpback dolphins, fine scale analysis of spatial and temporal distribution of prey is needed. This would require an intensive survey of both dolphins and prey at the same temporal scale, which is logistically nearly impossible to achieve. As suggested in Chapter 2, acoustic surveys of sonically active fish that humpback dolphins prey on could serve as an effective alternative with which to resolve the prey-dolphin distribution relationship (Lin et al. 2015; L. Karczmarski, study currently proposed to the Research Grants Council, RGC). To investigate individual differences in prey choice, a stable isotopes study, to test whether or not dolphins have prey-type preferences (Newsome et al. 2010), could be conducted.

Habitat shape may also contribute to the social division between communities as it may affect resources and predator distribution, as well as confining dolphin movements and thereby the probability of encountering conspecifics (Titcomb et al. 2015). Associations are likely to be stronger in confined and narrow habitats (Titcomb et al. 2015). This may explain the weaker associations among dolphins in Hong Kong in comparison with other populations of humpback dolphins, such as those seen in Taiwan (Chang 2011; Dungan et al. 2015), because the habitats in Hong Kong are part of a wider estuarine system. Furthermore, the dolphins seen in Hong Kong waters represent part of a substantially larger population (Chan and Karczmarski, 2017) that extends further to the west of the PRE region, which likely affects the number of affiliates and the strength on individual associations.

At the same time, due to the lack of barriers, divisions between social clusters are weak in broad terms. On a fine-scale, habitats in Hong Kong are distributed along a relatively straight line; therefore, social clusters occupying the two opposite locations of the habitats in Hong Kong are comparatively less interconnected.

Other than individual differences in the pattern of range usage, the origin and maintenance of social structure may also be a result of age-specific behavioural differences (Lusseau and Newman 2004), sex (Stanton et al. 2011) and genetic relatedness (Connor et al. 2000; Frère et al. 2010; Wiszniewski et al. 2010). Similar to the male bottlenose dolphins in Shark Bay, Australia (Connor et al. 1992), male humpback dolphins are thought to form stronger bonds for cooperative mate-searching in Taiwan (Chang 2011) and Cleveland Bay (Parra 2005), and socio-sexual harassment by males, including infanticide was recently see in the PRE humpback dolphins (Zheng et al. 2016), but the specific factors driving such behaviours remain unexplored. Kinship is widely recognised as a major factor in the formation of strong affiliations (Hamilton 1964). It has been observed to be affecting group memberships in group-living mammals, such as African savannah elephants *Loxodonta africana* (Archie et al. 2006), African lions (Vander Waal et al. 2009) and various primates (reviewed in Silk 2002), but no study has been conducted to date on its role in the association pattern of humpback dolphins.

The contribution of kinship in alliance formation is known to vary greatly among cetaceans. Kinship may have a strong impact on the association patterns in some populations of bottlenose dolphins (*Tursiops* spp.) (e.g. Parsons et al. 2003), but may be far less so in other populations (e.g. Möller et al. 2001). While kinship has been suggested to be influencing alliance formation of male bottlenose dolphins (Parsons et al. 2003), females striped dolphins *Stenella coeruleoalba* are found to be more likely to be in association with female kin than males (Gaspari et al. 2007), suggesting kinship influence may differ between species. Although this current study focuses on adults only, with limited data on sex and no genetic data, the heterogeneity of association with different levels of casual acquaintances could be indicative of sex or kinship related differences in the association pattern (Connor et al. 2000; Frère et al. 2010). This highlights the need for further efforts to identify sex of the photo-catalogued dolphins and to conduct a socio-genetic study with the aim of investigating the relationship between sex, genetic relatedness, and the association pattern of individuals.

3.5 Conclusion

This chapter quantifies and models the pattern of socio-behavioural dynamics of humpback dolphins in Hong Kong waters and its relationship to area utilisation patterns, emphasising environmental and behavioural influences on the dolphin fission-fusion dynamics. The findings of this study advance the knowledge of socio-ecological dynamics of coastal delphinids in general and social structure of humpback dolphins in Hong Kong in particular. It revises the previously suggested two-community hypothesis and proposes an alternative model of the dolphins' socio-spatial dynamics, with multiple closely interacting social clusters that have well defined core areas but overlapping ranges in Hong Kong coastal waters. Individual pattern of range use and habitat utilisation is likely the driving force of social dynamics of humpback dolphins in Hong Kong and likely the primary determinant of their socio-spatial structure.

Chapter 4 Anthropogenic impacts on socio-behavioural dynamics of Indo-Pacific humpback dolphins in Hong Kong

4.1 Introduction

Anthropogenic activities are widespread throughout the marine environment and are particularly intense in coastal regions. Coastal activities such as land reclamation, dredging, piling, marine traffic, and fishery can cause abrupt and persistent changes in cetacean behaviours. Studies of anthropogenic impact on cetaceans commonly focus on changes in abundance (e.g., Bejder et al. 2006, Brandt et al. 2011), alterations in acoustic behaviours (e.g., Miller et al. 2000; Parks et al. 2007) and individual animals' immediate behavioural responses, such as changes in diving behaviours and behavioural states (e.g., Ng and Leung 2003; Constantine et al. 2004; Williams et al. 2009; Parsons 2012). Few studies have attempted to investigate broader-scale changes in the social dynamics of a population (e.g., Ansmann et al. 2012), and there is no empirical study that documents the socio-structural changes in relation to distributional changes.

In Hong Kong, anthropogenic activities overlap extensively with the habitat of Indo-Pacific humpback dolphins. Development pressure has escalated in western Hong Kong waters since the construction of the Hong Kong International Airport in 1992. There have been at least seven reclamation projects involving in total over 1,400 hectares (ERM 1994; Liu and Hills 1997; ERM 2000; ARUP 2009a; CEDD 2016; Marcotte et al. 2015), dredging over 300 hectares at contaminated mud-pits (ERM 2012) and two projects with percussive or bored piling during construction (Würsig et al. 2000; ARUP 2009b). Another major type of activity in the region is marine traffic. There is a cargo shipping channel at northern Lantau Island and three high-speed ferry routes at both northern and southern Lantau. Moreover, fisheries are in operation throughout the year. Before the trawl ban in Hong Kong in 2013, fishing boats included trawlers, gillnetters, and purse seiners (Hung 2008). Other types of vessels are mostly for recreational activities, such as dolphin watching, which is centred off western Lantau Island, where local villagers offer short trips from Tai O throughout the day.

Among these various types of activities, this chapter focuses on coastal constructions and fishery, as major construction projects and changes in fishery activities took place during the study period (2010-2014).

During the study period (2010-2014), construction of the Hong Kong–Zhuhai–Macau Bridge (HKZMB) commenced in mainland China in December 2009 and proceeded to Hong Kong in November 2011. The construction in Hong Kong comprises four major sections, which include Hong Kong Link Road (HKLR), Hong Kong Boundary Crossing Facilities (HKBCF), Tuen Mun-Chek Lap Kok Link (TM-CLKL), and Tuen Mun Western Bypass (TMWB). The former three are situated in the marine habitat. The construction work began with the HKBCF on 12 March 2012 (AECOM 2012). It involved reclamation of about 130 hectares of land northeast of Hong Kong International Airport and building facilities on this artificial island. The next portion was the 12 km HKLR. In the form of a dual three-lane carriageway, HKLR connects the HZMB Main Bridge at the territorial boundary of the Hong Kong Special Administrative Region (HKSAR) to the HKBCF. Construction started on 17 October 2012 at the section between HKBCF and the Hong Kong International Airport (BMT Asia Pacific 2013). The work extended from the airport to the HKSAR territorial boundary in February 2013 (Cinotech 2013). The last project involving marine construction is the 9 km TM-CLKL. It connects Tuen Mun and northern Lantau Island by a dual two-lane carriageway with a 5 km underwater tunnel subsection. It required reclamation of about 16.5 hectares. It commenced on 31 October 2013 (ERM 2014). Overall, the entire construction project could contribute to the loss and degradation of humpback dolphins’ habitat and disturbances to dolphins in Hong Kong through reclamation, bored piling, dredging, water pollution, and increased marine traffic (ARUP 2009a, 2009b).

An apparent shift in the distribution of humpback dolphins in Hong Kong was first reported in mid-2000s (Jefferson 2007), while an abandonment of the eastern side of Lantau Island was first noted in 2002 (Jefferson 2007). Following was a gradual reduction of dolphin occurrence around the Brothers Islands and northern Lantau and an increase in abundance in waters off western Lantau (Hung 2008). Marcotte et al. (2015) suggested that cumulative impacts of anthropogenic activities disrupted the dolphin distribution in northern Lantau and the implementation of two new high-speed ferry routes in the region in 2004 contributed to the reduction of dolphin density around the Brothers Islands. Dolphin encounter rates in waters off northern Lantau further declined in 2012-2015, with the abundance estimates dropping to a historic low (Hung 2016). At the same time, occurrence continued to increase in the western and south-western Lantau region. Hung (2016) suggested that the consistently low occurrence of dolphins around northern Lantau Island since 2012 was unlikely a natural fluctuation but related to the construction of the HKZMB in Hong Kong because the timing coincided with the commencement of HKZMB construction. Hung (2016) also noted changes in the range use of selected individuals during the construction of the HKZMB. A large proportion of the dolphins that used to frequent the northern region have now shifted their range to the waters off west and south-west Lantau (Hung 2016), while the individuals that were seen primarily in the southern region either increased their use of the western Lantau waters or have shifted from west Lantau to waters off south-west Lantau (Hung 2016).

While the construction of the HKZMB appears to have caused a distributional change at the individual and population levels, its influence on the social dynamics of humpback dolphins in Hong Kong remains unexplored. There is also no empirical study to date on the change in cetacean social structure in relation to habitat loss and degradation. This chapter investigates changes in social dynamics of humpback dolphins, their distribution, range use pattern and movement in Hong Kong waters during the construction of the HKZMB.

Another focus of this chapter is to investigate the fishery influence on social dynamics. Fisheries can have profound impacts on the social structuring of group-living marine animals. Dolphins are attracted to feed around fishing nets such as gillnets, trammel nets, and trawling nets because of the aggregation of prey (Fertl and Leatherwood 1997), and such behaviour has been seen across species and locations (Fertl and Leatherwood 1997; Rayment and Webster 2009; Ansmann et al. 2012). It has been proposed that dolphins have learnt the benefits of foraging in association with fishing boats (Leatherwood 1975), and calves may learn this behaviour from their mothers through observation and participation (Shane et al. 1986).

As the behaviour propagates, it may trigger a modification of the social structure (Ansmann et al. 2012) and, in some cases, even promote a development of cooperative foraging with fishermen (Daura-Jorge et al. 2012). Trawler-associating and non-trawler-associating Indo-Pacific bottlenose dolphins *Tursiops aduncus* were seen to form distinct social communities in Moreton Bay, Australia (Chilvers and Corkeron 2001). Upon a reduction in trawling activities, restructuring of social networks was documented (Ansmann et al. 2012).

In the Pearl River Estuary, humpback dolphins are known to forage in association with fishing vessels including trawlers, purse seine vessels, and gillnet vessels (Jefferson 2000; Piwetz et al. 2015). Jefferson (2000) and Hung (2008) both reported that dolphins forage for hours around trawlers. Large foraging groups following trawlers, particularly pair-trawlers, were reported (Jefferson 2000) and it was speculated that preference for such foraging behaviour may vary between individuals (Jefferson 2000; Hung 2008), albeit no empirical evidence have ever been produced. In response to the mounting evidence of overfishing, first detected in Hong Kong in 1998 (ERM 1998), a ban on trawling came into operation on 31 December 2012 as a conservation measure to protect and restore fishery resources (HKSAR Government 2010; AFCD 2012). This created a unique opportunity to examine the impacts of a trawl ban on the social dynamics of humpback dolphins in Hong Kong. This chapter examines the group dynamics of trawler-associating and non-trawler-associating dolphins and the movement of trawler-associating dolphins before and after the trawl ban.

More broadly, this chapter investigates the impacts of habitat loss and degradation due to large-scale coastal construction projects and impacts of fisheries on socio-spatial ecology of coastal dolphins which in turn provides insights into the processes that affect their social structure.

4.2 Methods

4.2.1 Study area

See the description in Chapter 2.

4.2.2 Field data collection

All field data were collected in the same way as described in Chapter 2. The protocol of collecting photographic data and the relevant geographically referenced data was the same as described in Chapter 3.

4.2.3 Impacts of the construction of the HKZMB in Hong Kong

As the construction of the HKZMB was divided into different sections with commencement dates of construction spanning from March 2012 to February 2013, the commencement dates of the various section of the construction project had to be considered to structure the dataset appropriately for further analyses. The date of 1 November 2012 was adopted to demarcate the period "prior" and "during" construction; by this date a major construction around Brothers Islands had already commenced, the construction of the HKBCF had been on-going for ~7 months, and the HKLR (the section between HKBCF and Scenic Hill) was under construction for half a month. Consequently, data collected between May 2010 and October 2012 were used to illustrate the situation prior to the construction and data from November 2012 to December 2014 were used to investigate the impacts of construction.

To achieve a fair representation of social structure (i.e. r>0.4; see Chapter 3 for the explanation of r), only individuals seen more than three times were used for social analysis. No sighting restriction was set for movement analysis.

To detect whether there was a structural change, the community structure before and during construction was determined by the eigenvector-based method using a divisive algorithm developed by Newman (2006) and modularity calculated under the control on gregariousness (Newman 2004) (see Methods in Chapter 3). A network diagram was drawn using NETDRAW 2.097 (Borgatti 2002). The number of individuals that comprised each of the clusters in both periods, before and during the construction was calculated and compared.

To investigate impacts of the construction project on the dolphins' range use pattern, area utilisation before and during construction at both the population and social cluster level were modelled and compared. All dolphin encounters before and during the construction, with geographic coordinates (GPS location data) recorded at 10-minute interval throughout the encounter were used to produce the area utilisation distribution models representing the two corresponding periods (see Methods in Chapter 2). To illustrate the distributional change among individuals that were seen both before and during construction, sighting locations of all the individuals in common for the two periods that were used in social analyses were pooled together to construct the area utilisation distributions. For the pattern at the level of social clusters, sighting locations of all individuals in each cluster were pooled to construct the area utilisation distributions (see Methods in Chapter 3). Area utilisation distributions were constructed using kernel density estimation (see Methods in Chapter 3) and the local convex hull method (see Methods in Chapter 2). At the level of social clusters, utilisation distributions were drawn using only kernel density estimation, as the local convex hull method produces highly restricted distributions from small datasets.

To investigate if the dolphins' site fidelity to the northern and southern waters differed before and during construction, movement pattern within and between the north and south, as defined in Chapter 3, were determined by calculating the lagged identification rates at the two areas before and during construction. The geographic partitioning of the study area into "north" and "south" and relevant calculation method were the same as described in Chapter 3. Same as Chapter 3, the analysis was repeated with the inclusion of lower quality photos (i.e. photos with quality ≥60 were included), as movement analysis may be less sensitive to heterogeneity in photo quality.

4.2.4 Impact of trawling

To evaluate the impact of the trawl ban on association patterns, the dataset was divided into data taken before the trawl ban (2010-2012) and after the trawl ban (2013-2014). Trawler-associating dolphins and non-trawler-associating dolphins were defined based on field observation of the presence and absence of association with trawlers in Hong Kong in 2010-2012. To achieve a fair representation of the social structure (i.e. $r>0.4$, in which r the same as described in Chapter 3), only individuals sighted more than four times were used for social analysis. No sighting restriction was set for site fidelity analysis.

The social structure was displayed as a social network diagram drawn in NETDRAW 2.097 (Borgatti 2002). Mantel tests were performed on data taken before and after the trawl ban to test whether the associations within and between trawler-associating and non-trawler-associating dolphins were similar in each period. To investigate whether there was any change in the site fidelity of trawler-associating dolphins before and after the trawl ban, lagged identification rates (LIRs) of trawler-associating dolphins at the two periods were calculated and repeated with the inclusion of lower quality photos (see Methods in Chapter 3). All analyses were performed in MATLAB R2013b using the SOCPROG 2.6 (Whitehead 2015).

4.3 Results

4.3.1 Impacts of the construction of the HKZMB in Hong Kong

4.3.1.1 Dataset before and during the HKZMB construction

From May 2010 to October 2012, 149 days were spent in the study area; while from November 2012 to December 2014, the study area was surveyed for 146 days. In total, 114 dolphins were photo-identified before the construction and 185 dolphins during the construction, with ID-images meeting all requirements for photo quality, group coverage, and sighting frequency for social analyses. For movement analysis, all adults with photo quality $Q\geq70$ were used, which amounted to 259 individuals before the construction and 280 individuals during the construction. Movement analysis was repeated with lower photo quality restriction (i.e. $Q\geq60$) and this included 268 individuals before the construction and 287 individuals during the construction.

The correlation between true and estimated association indices was fair for both datasets (before construction: $r=0.384\pm0.026$; during construction: $r=0.436\pm0.02$). Social differentiation was high throughout the study period (before construction: $S=0.807 \pm0.035$; during construction: $S=0.864\pm0.031$).

4.3.1.2 Community structure

Cluster analysis based on Newman’s (2006) eigenvector method assigned individuals into six clusters both before and during construction (Table 4.1, Fig. 4.1, 4.2). The modularity was higher than 0.3 (before construction: Q=0.382; during construction: Q=0.338), supporting the grouping into clusters as meaningful (Newman 2004).

There were 91 individuals in common for both datasets. During the construction period, Clusters 1, 3, 4, and 6 joined with new individuals and formed Cluster A. Cluster 2 and 5 divided into five clusters, forming Clusters B to F. Members of Cluster 2 divided relatively evenly into the five clusters, while most individuals in Cluster 5 that were present during construction remained in the same cluster (Table 4.1).

Table 4.1 Number of individuals in each cluster and number of individuals in common for clusters before and during construction of the HKZMB in Hong Kong, for Indo-Pacific humpback dolphins seen in Hong Kong waters more than three times. Study period was May 2010 to October 2012 before construction and November 2012 to December 2014 during construction. Eigenvector method (Newman 2006) was applied for cluster identification.

Clusters during construction	Clusters before construction						Individuals not recorded before construction	Total
	1	2	3	4	5	6		
A	4		24	11		5	22	66
B		5			1	1	14	21
C		1			1		11	13
D	1	3		1	1		6	12
E		2			18		11	31
F		5			7		30	42
Individuals not recorded during construction	1	3	6	1	8	4		
Total	6	19	30	13	36	10		

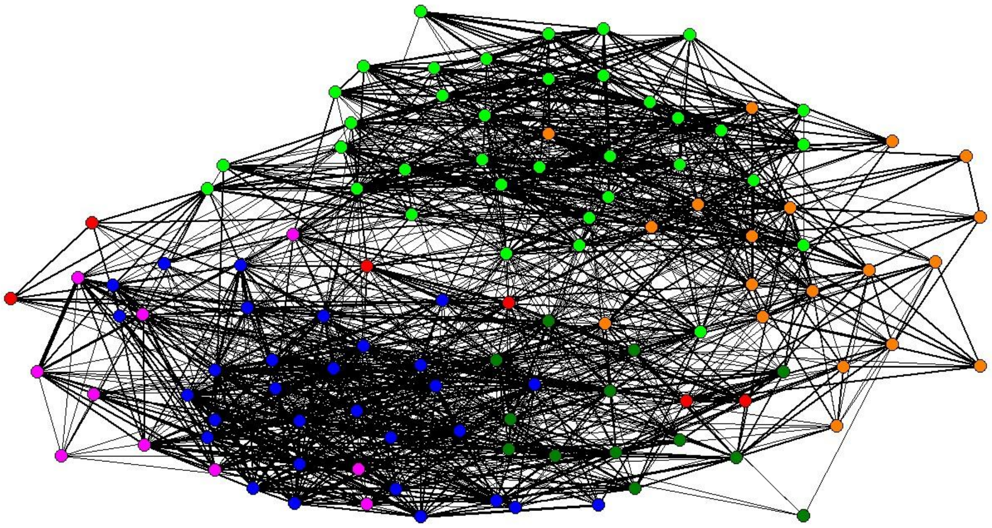


Figure 4.1 Network diagram of Indo-Pacific humpback dolphins seen in Hong Kong waters > 3 times before the construction of the HKZMB (May 2010 to October 2012). Individuals are shown as nodes. Line thickness represents association strength. Individuals of Cluster 1 (*n*=6) are denoted as red nodes, Cluster 2 (*n*=19) as orange, Cluster 3 (*n*=30) as blue, Cluster 4 (*n*=13) as dark green, Cluster 5 (*n*=36) as green, and Cluster 6 (*n*=10) as purple.

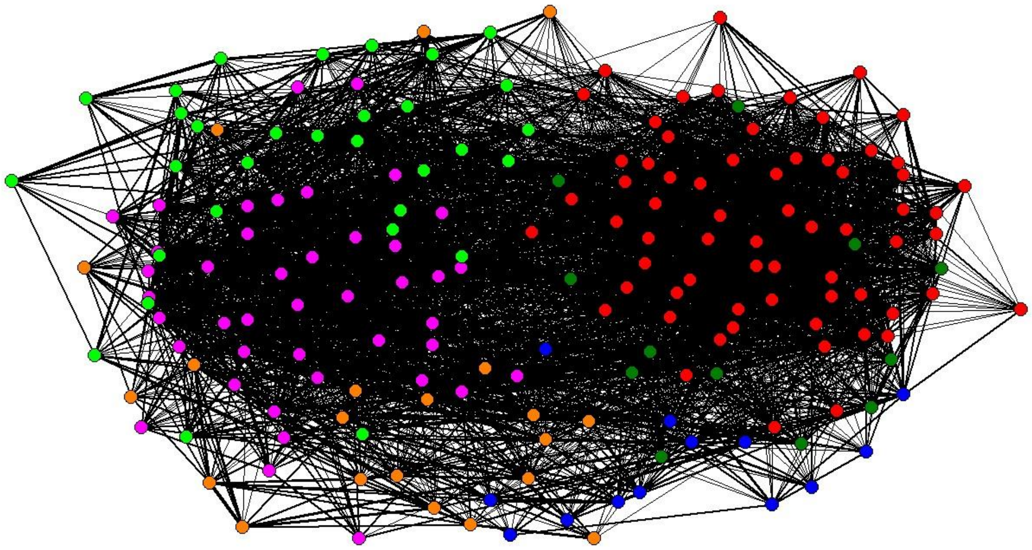


Figure 4.2 Network diagram of Indo-Pacific humpback dolphins seen in Hong Kong waters > 3 times during the construction of the HKZMB (November 2012 to December 2014). Individuals are shown as nodes. Line thickness represents association strength. Individuals of Cluster A (*n*=66) are denoted as red nodes, Cluster B (*n*=21) as orange, Cluster C (*n*=13) as blue, Cluster D (*n*=12) as dark green, Cluster E (*n*=31) as green, and Cluster F (*n*=42) as purple.

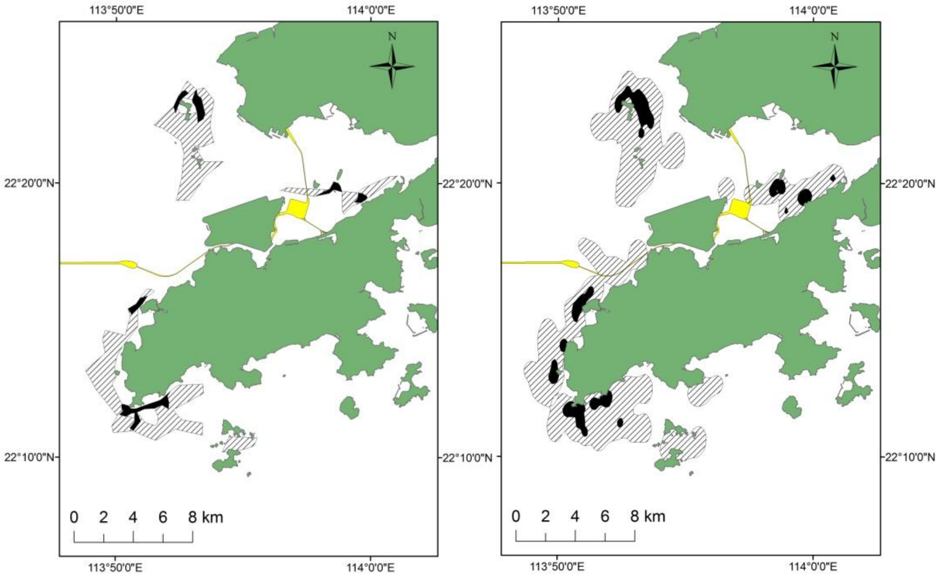
4.3.1.3 Spatial distribution

Both the KDE and LoCoH methods indicated a difference in overall range use (95% utilisation distribution) and core area distribution (50% utilisation distribution) before and during construction (Fig. 4.3). Both the range and core areas that covered the Brothers Islands before construction were not seen there anymore during the construction. Range use in the northern area was reduced to mainly Sha Chau and Lung Kwu Chau during construction. The core areas around Lung Kwu Chau shifted from the east to the west of the island. In the south, the core areas were scattered off west and south Lantau Island before construction, and expanded to form a continuum along western Lantau Island during construction.

A similar change in the utilisation distribution pattern was apparent among individuals that were seen in both periods, before and during construction (Fig. 4.4). A reduction of area utilisation in the northern waters was particularly evident, with core areas delineated with the KDE method diminished to a small area at the southern tip of Lung Kwu Chau and no core areas detected with the LoCoH method in the north during the construction project.

At the level of social clusters, only Clusters 2 and 5 before construction and Clusters E and F during construction used the northern waters as part of their core areas (Figs. 4.5, 4.6). All other clusters restricted their core areas to the south. The Brothers Islands were used only by Cluster 5 as a core area before the construction (Fig. 4.5) but were not part of the core areas for any cluster during construction (Fig. 4.6). The shift in core areas from the east to the west side of Lung Kwu Chau was evident in all clusters that used that area (i.e. Clusters E and F) and core areas of Cluster F at Lung Kwu Chau decreased in size (Fig. 4.6). Among clusters that had their core areas in the north (i.e. Clusters 2 and 5 in Fig. 4.5, Clusters E and F in Fig. 4.6), their ranges and core areas expanded farther south along the coast of Lantau Island during construction and the core areas of Cluster F formed a continuum along western Lantau Island. Clusters that had their core areas in the south (i.e. Clusters 1, 3, 4, and 6 in Fig. 4.5 and Clusters A to D in Fig. 4.6), retained their range use pattern broadly similar before and during the construction, but core areas off south Lantau appeared to have expanded during construction.

(A) Before construction of the HKZMB



(B) During construction of HKZMB

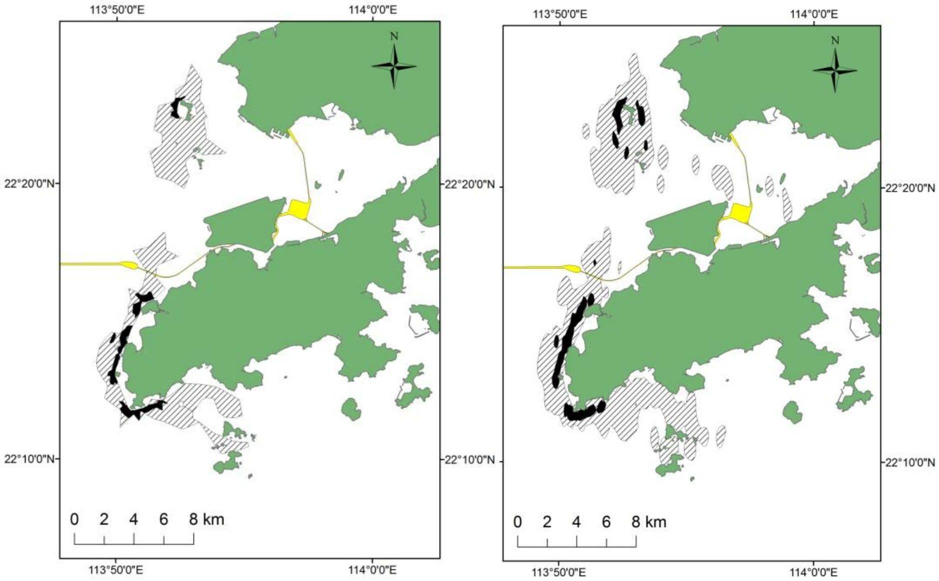
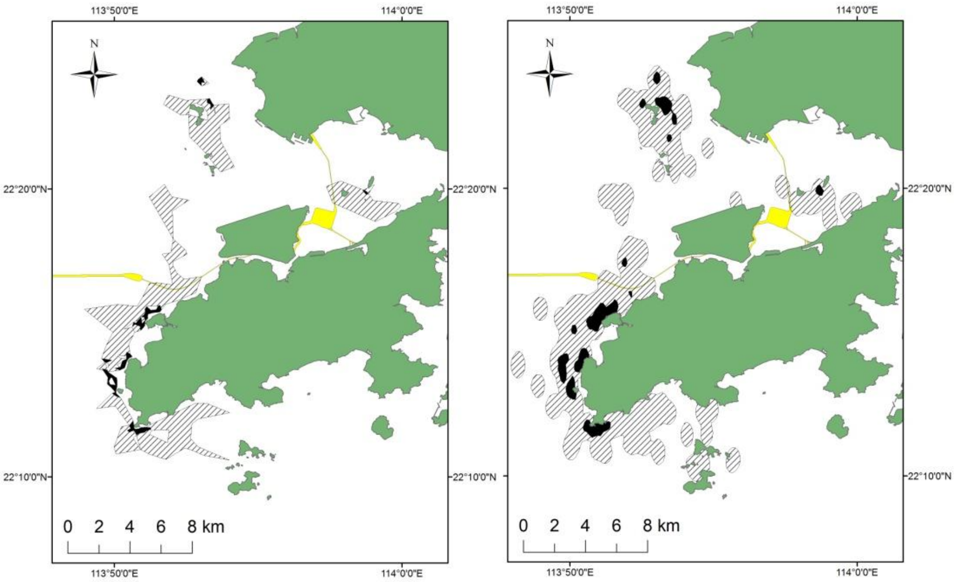


Figure 4.3 Local Convex Hull (LoCoH; left) and kernel density estimation (KDE; right) with 95% (hatched polygons) and 50% isopleths (filled polygons) utilisation distributions for Indo-Pacific humpback dolphins in Hong Kong waters before and during the construction of the Hong Kong–Zhuhai–Macau Bridge (HKZMB).

(A) Before construction of the HKZMB



(B) During construction of the HKZMB

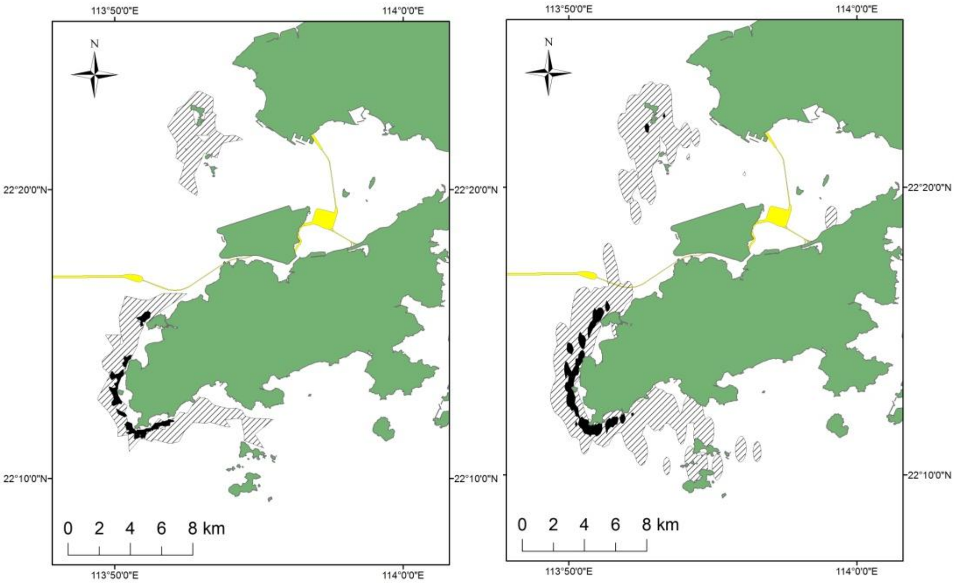


Figure 4.4 Local Convex Hull (LoCoH; left) and kernel density estimation (KDE; right) with 95% (hatched polygons) and 50% isopleths (filled polygons) utilisation distributions for Indo-Pacific humpback dolphins in Hong Kong that were seen in both periods, before and during the construction of the HKZMB. Only individuals used in social analyses were included here.

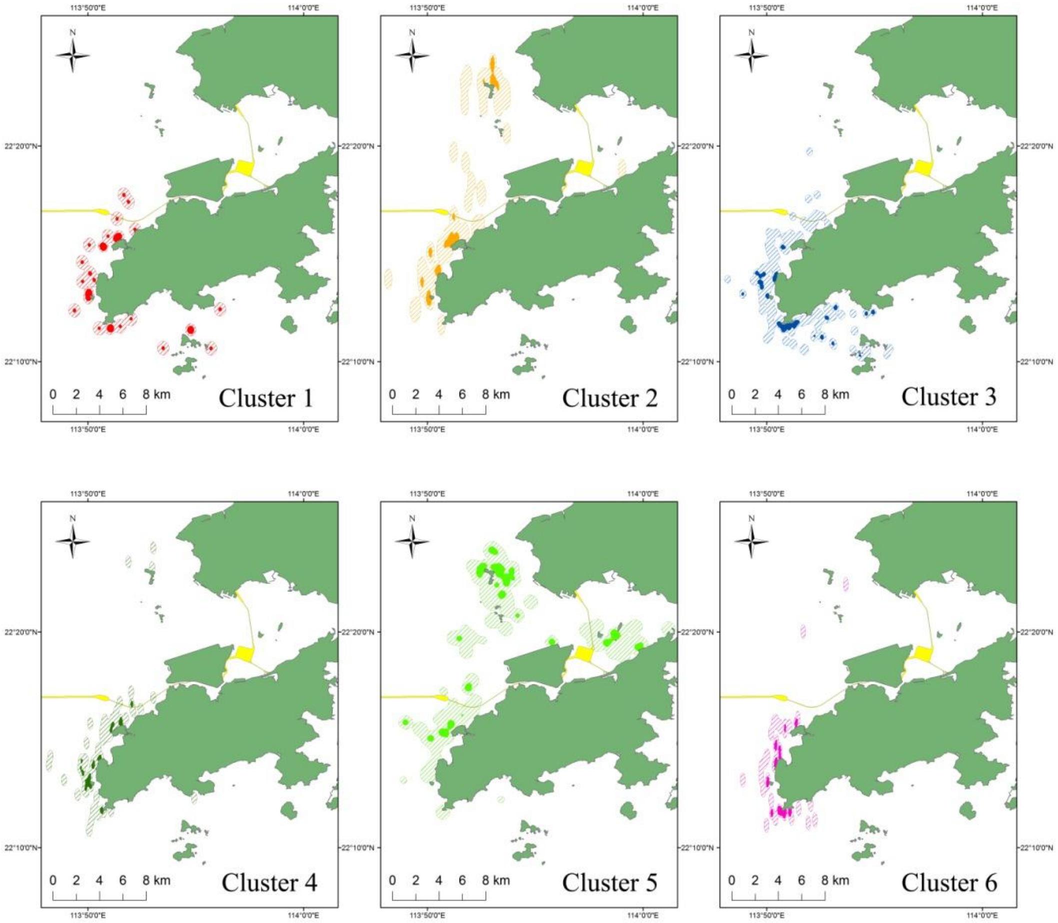


Figure 4.5 Kernel density estimation (KDE) with 95% (hatched polygons) and 50% isopleths (filled polygons) utilisation distributions for social clusters of Indo-Pacific humpback dolphins seen > 3 times in Hong Kong before the construction of the HKZMB (May 2010 to October 2012). Clusters were identified using Newman's (2006) eigenvector method.

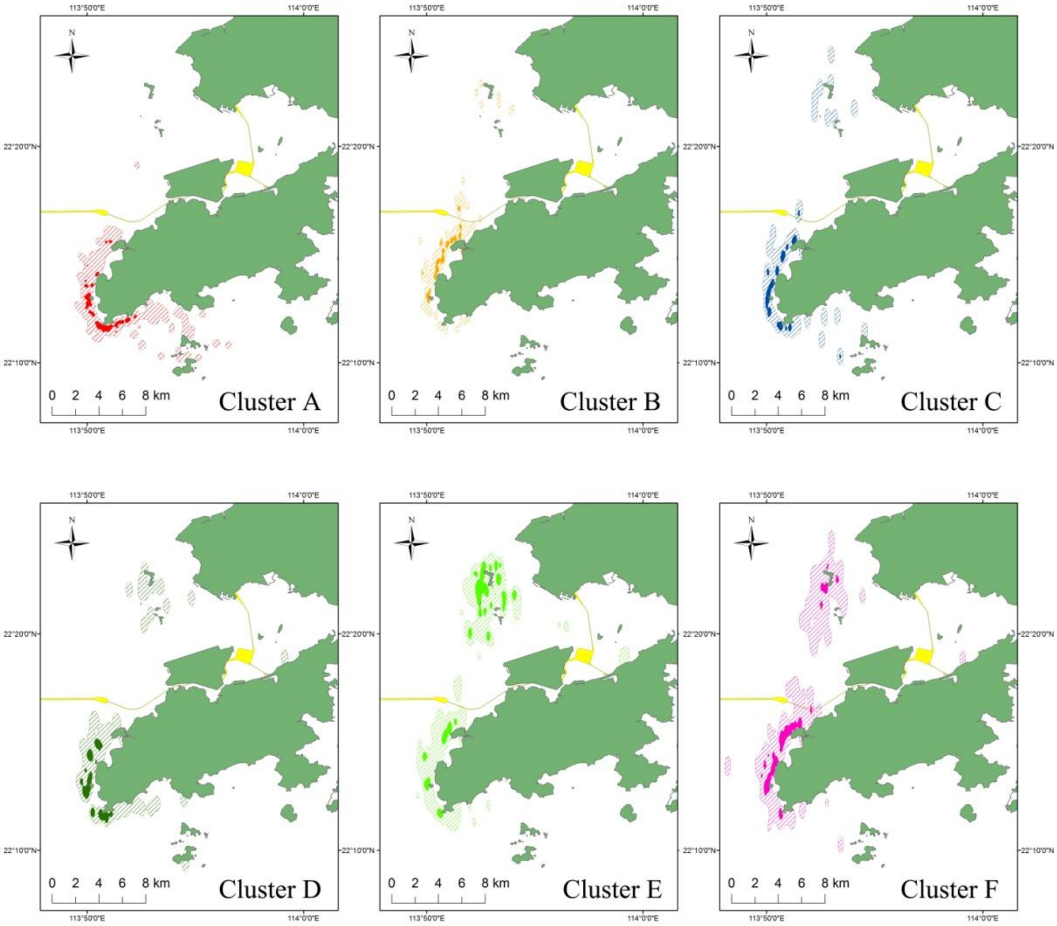


Figure 4.6 Kernel density estimation (KDE) with 95% (hatched polygons) and 50% isopleths (filled polygons) utilisation distributions for social clusters of Indo-Pacific humpback dolphins seen in Hong Kong > 3 times during the construction of the HKZMB (November 2012 to December 2014). Clusters were identified using Newman's (2006) eigenvector method.

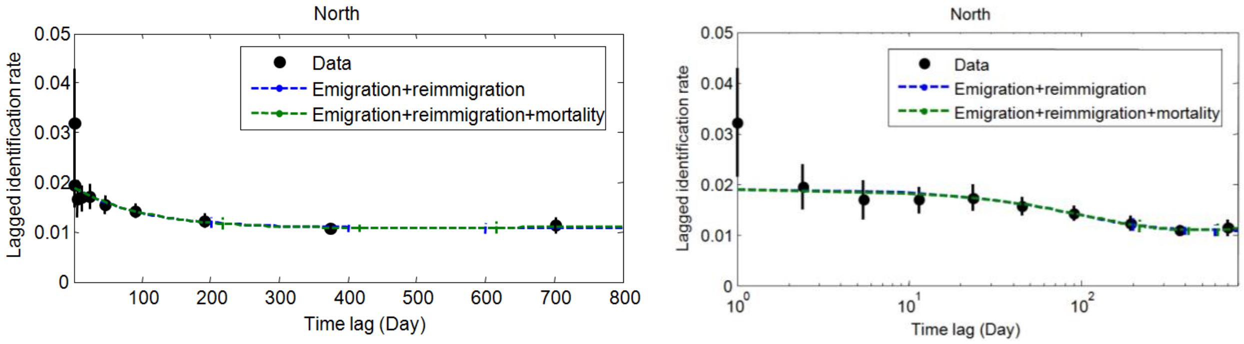
4.3.1.4 Movement pattern

In the north, dolphin movement before construction was best described by "emigration + reimmigration" and "emigration + reimmigration + mortality" models. During construction, the best-fitted models included not only "emigration + reimmigration" but also the "emigration" model (Fig. 4.7; Table 4.2), and the slope of decline of lagged identification rates (LIR) was steeper and error bars were larger (Fig. 4.7).

In the south, the pattern of LIR before and during construction was best described by similar models, with "emigration + reimmigration" and "emigration + reimmigration + mortality" representing the best fit model before the construction and "emigration + reimmigration" the best fit model during construction (Fig. 4.8; Table 4.3), although "emigration + reimmigration + mortality" was also acceptable. The error bars of LIRs were large throughout the period of construction (Fig. 4.8).

Dolphins moved between the north and south in both periods before and during the construction, and similar models could be fitted for both periods (Tables 4.4 and 4.5). The error bars of LIRs for dolphins moving from north to south were larger before construction (Fig. 4.9); while during the construction the opposite occurred, error bars were large for LIRs of dolphins moving from the south to north (Fig. 4.10).

(A) Before construction of the HKZMB



(B) During construction of the HKZMB

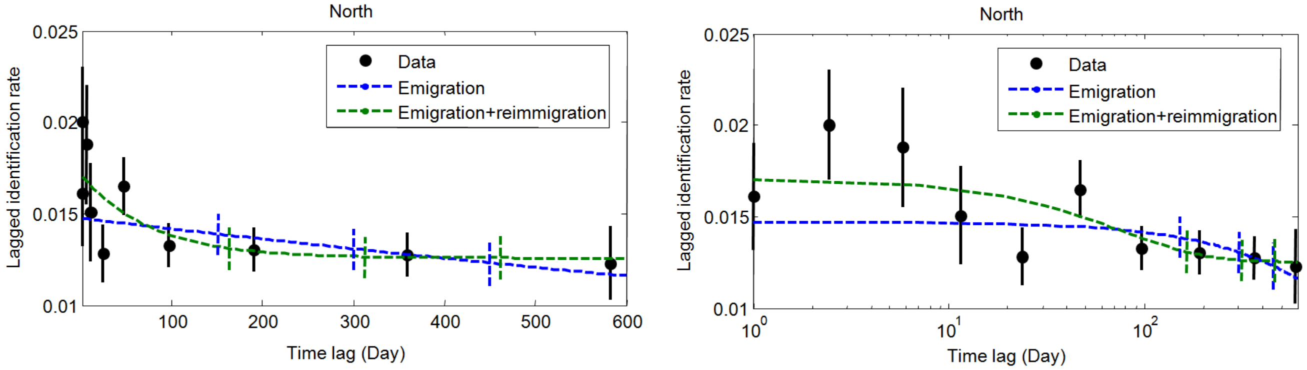
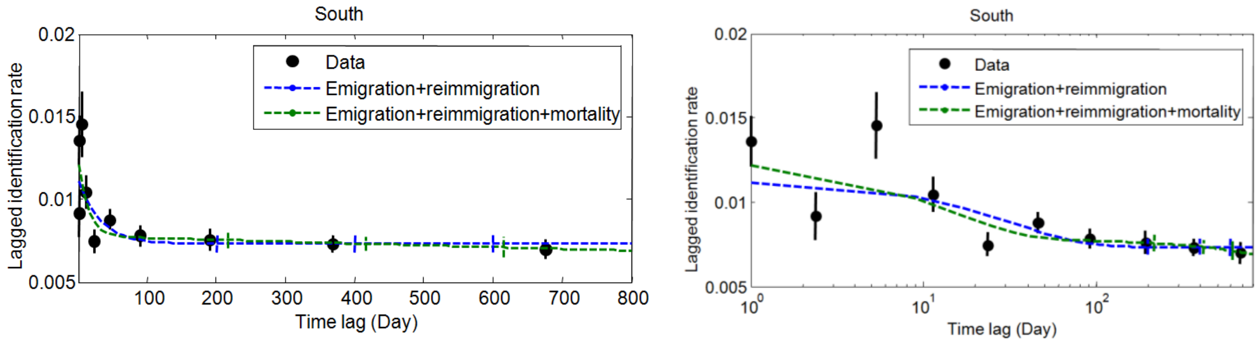


Figure 4.7 Lagged identification rates in linear time lag (left) and log time lag (right) of Indo-Pacific humpback dolphins in the north of the study area (western Hong Kong waters). Observed data are denoted as black dots. Dotted lines represent best-fitted models with ΔQAIC ranging within 2 units. Vertical lines indicate bootstrap estimates of SE.

Table 4.2 Movement models fit to lagged identification rates of Indo-Pacific humpback dolphins in the north of the study area (north-western Hong Kong waters) before (May 2010 to October 2012) and during (November 2012 to December 2014) the construction of the HKZMB. ∆QAIC of 0-2 are in bold.

Model	Before construction		During construction	
	QAIC	∆QAIC	QAIC	∆QAIC
Closed	10665.4	30.7	15029.0	6.4
Emigration	10644.8	10.1	**15024.6**	**2.1**
Emigration + reimmigration	**10634.7**	**0**	**15022.5**	**0**
Emigration + reimmigration + mortality	**10636.6**	**1.9**	15025.5	3.0

(A) Before construction of the HKZMB



(B) During construction of the HKZMB

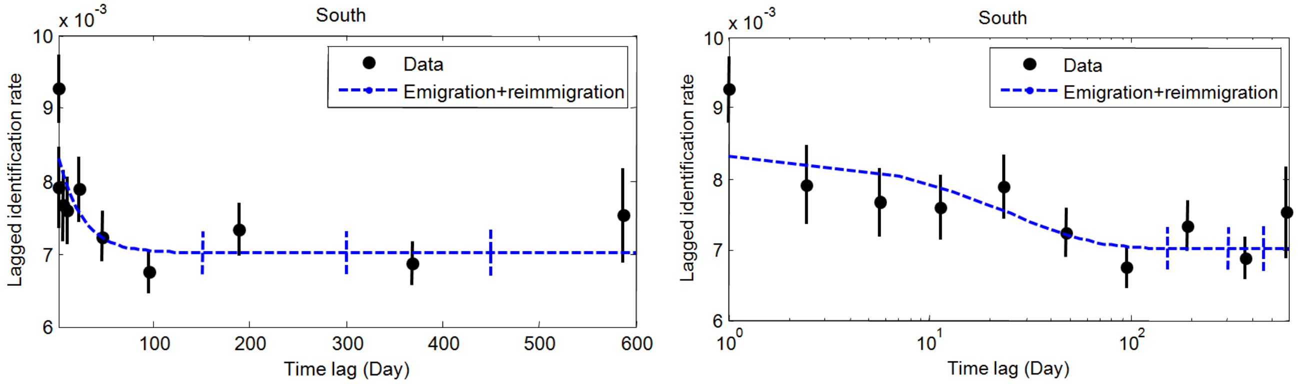
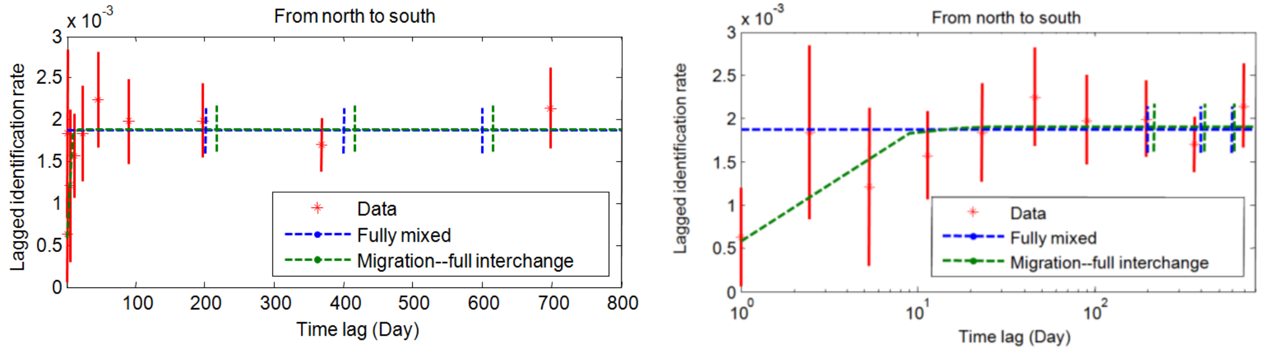


Figure 4.8 Lagged identification rates in linear time lag (left) and log time lag (right) of Indo-Pacific humpback dolphins in the south of the study area (western Hong Kong waters). Observed data are denoted as black dots. Dotted lines represent best-fitted models with ΔQAIC ranging within 2 units. Vertical lines indicate bootstrap estimates of SE.

Table 4.3 Movement models fit to lagged identification rates of Indo-Pacific humpback dolphins in the south of the study area (south-western Hong Kong waters) before (May 2010 to October 2012) and during (November 2012 to December 2014) the construction of the HKZMB. ΔQAIC of 0-2 are in bold.

Model	Before construction		During construction	
	QAIC	ΔQAIC	QAIC	ΔQAIC
Closed	27518.1	23.3	151179.9	17.0
Emigration	27507.5	12.8	151172.7	9.8
Emigration + reimmigration	**27494.8**	**0**	**151162.9**	**0**
Emigration + reimmigration + mortality	**27496.1**	**1.4**	151166.5	3.6

(A) Before construction of the HKZMB



(B) During construction of the HKZMB

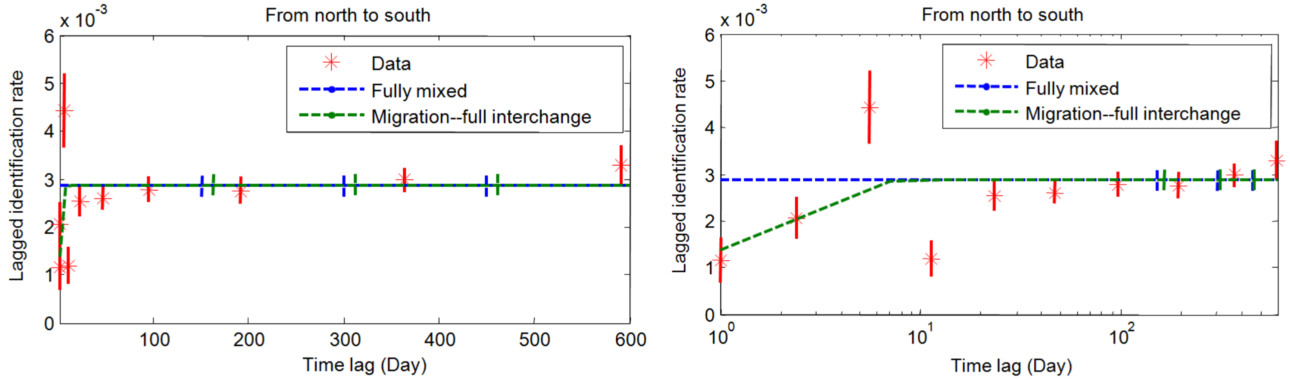
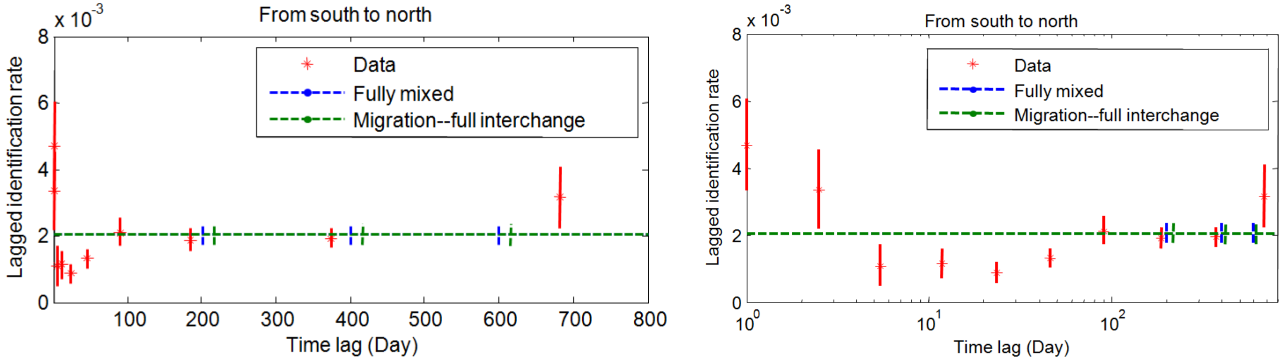


Figure 4.9 Lagged identification rates in linear time lag (left) and log time lag (right) of Indo-Pacific humpback dolphins moving from north to south within western Hong Kong waters. Observed data are denoted as black dots. Dotted lines represent best-fitted models with ΔQAIC ranging within 2 units. Vertical lines indicate bootstrap estimates of SE.

Table 4.4 Models fit to lagged identification rates of Indo-Pacific humpback dolphins moving from north to south within western Hong Kong waters before (May 2010 to October 2012) and during (November 2012 to December 2014) the construction of the HKZMB. ∆QAIC of 0-2 are in bold.

Model	Before construction		During construction	
	QAIC	∆QAIC	QAIC	∆QAIC
Fully mixed	**3299.3**	**0**	**15890.8**	**1.1**
Migration-full interchange	**3299.6**	**0.3**	**15889.6**	**0**

(A) Before construction of the HKZMB



(B) During construction of the HKZMB

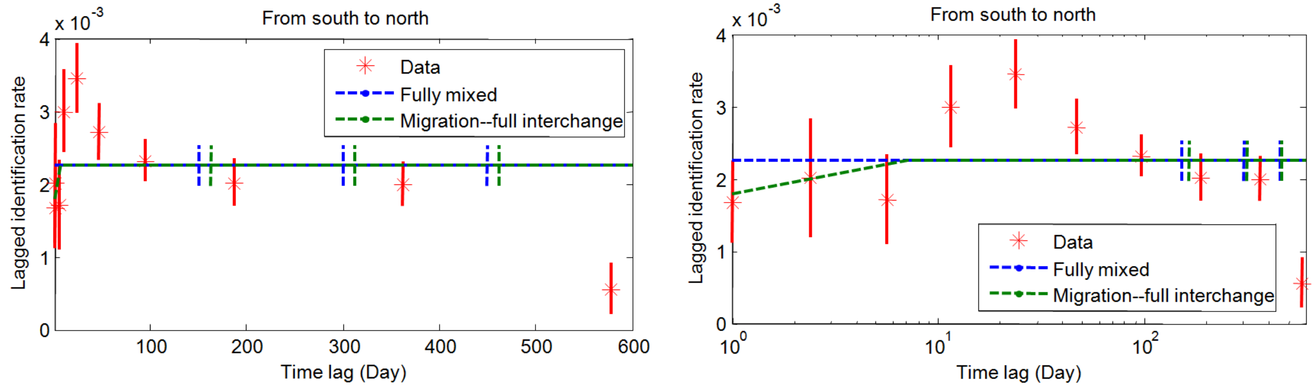


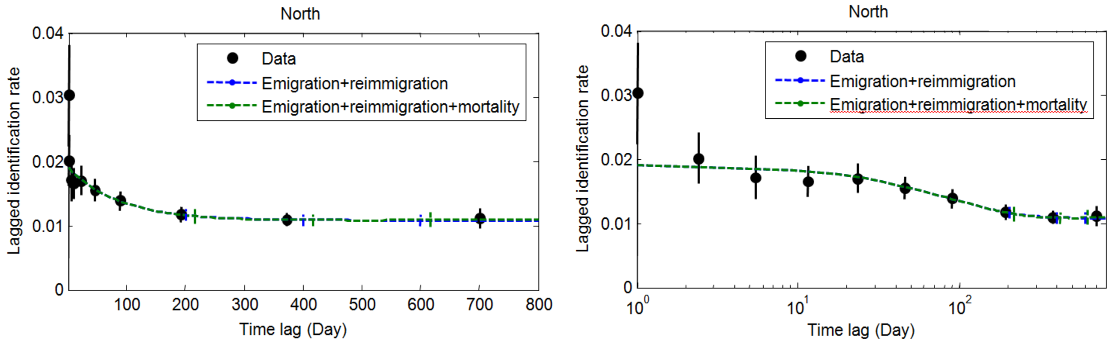
Figure 4.10 Lagged identification rates in linear time lag (left) and log time lag (right) of Indo-Pacific humpback dolphins moving from south to north of western Hong Kong waters. Observed data are denoted as black dots. Dotted lines represent best-fitted models with ΔQAIC ranging within 2 units. Vertical lines indicate bootstrap estimates of SE.

Table 4.5 Models fit to lagged identification rates of Indo-Pacific humpback dolphins moving from south to north within western Hong Kong waters before (May 2010 to October 2012) and during (November 2012 to December 2014) the construction of the HKZMB. ΔQAIC of 0-2 are in bold.

Model	Before construction		During construction	
	QAIC	ΔQAIC	QAIC	ΔQAIC
Fully mixed	**3054.2**	**0**	**6451.7**	**0**
Migration-full interchange	**3056.2**	**2.0**	**6453.4**	**1.7**

Results generated from the dataset with inclusion of lower quality photos (ie. image quality ≥ 60) consistently presented similar changes in movement patterns within and between north and south of the study area (Figs 4.11- 4.14; Tables 4.6-4.9). Compared with the results generated with higher quality photos, same sets of models represented the best movement models describing the LIRs in all cases, except for dolphins moving from south to north before construction. Instead of two equally supported models (“fully mixed” and “migration-full interchange” models), the LIR of dolphins moving from south to north before construction was best-described by the “fully mixed” model (Fig. 4.14; Table 4.9). However, the QAIC of the best fit model differed still relatively little (ΔQAIC =3) from that of the next best model (Table 4.9).

(A) Before construction of the HKZMB



(B) During construction of the HKZMB

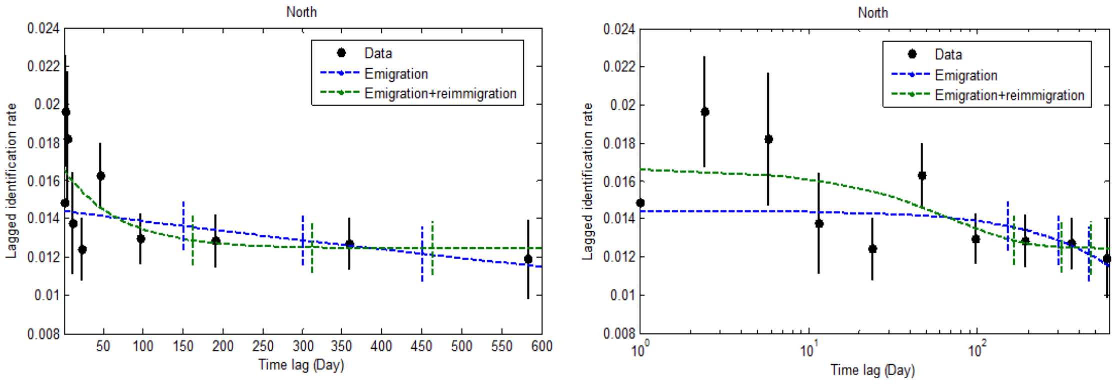
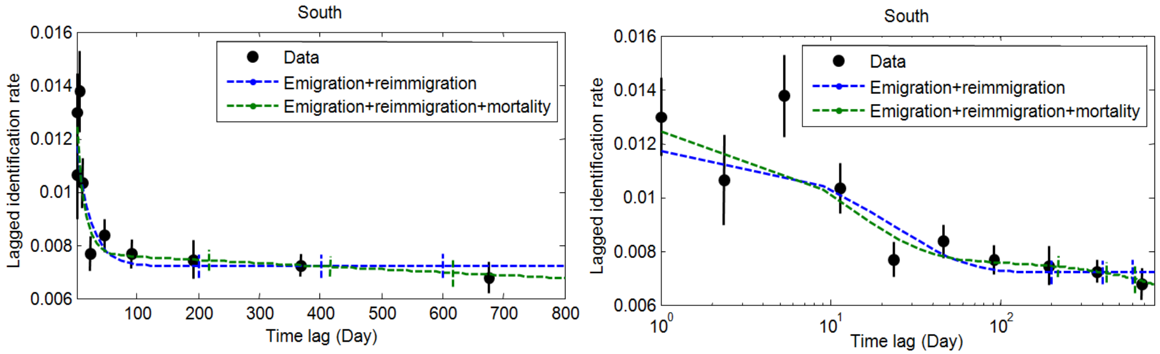


Figure 4.11 Lagged identification rates in linear time lag (left) and log time lag (right) of Indo-Pacific humpback dolphins in the north of the study area (western Hong Kong waters) with image quality ≥60. Observed data are denoted as black dots. Dotted lines represent best-fitted models with ΔQAIC ranging within 2 units. Vertical lines indicate bootstrap estimates of SE.

Table 4.6 Movement models fit to lagged identification rates of Indo-Pacific humpback dolphins in the north of the study area (north-western Hong Kong waters) with image quality ≥60 before (May 2010 to October 2012) and during (November 2012 to December 2014) the construction of the HKZMB. ΔQAIC of 0-2 are in bold.

Model	Before construction		During construction	
	QAIC	ΔQAIC	QAIC	ΔQAIC
Closed	9975.6	28.7	17116.4	5.8
Emigration	9957.1	10.2	17111.9	**1.3**
Emigration + reimmigration	9946.9	**0**	17110.6	**0**
Emigration + reimmigration + mortality	9948.9	**2.0**	17113.1	2.5

(A) Before construction of the HKZMB



(B) During construction of the HKZMB

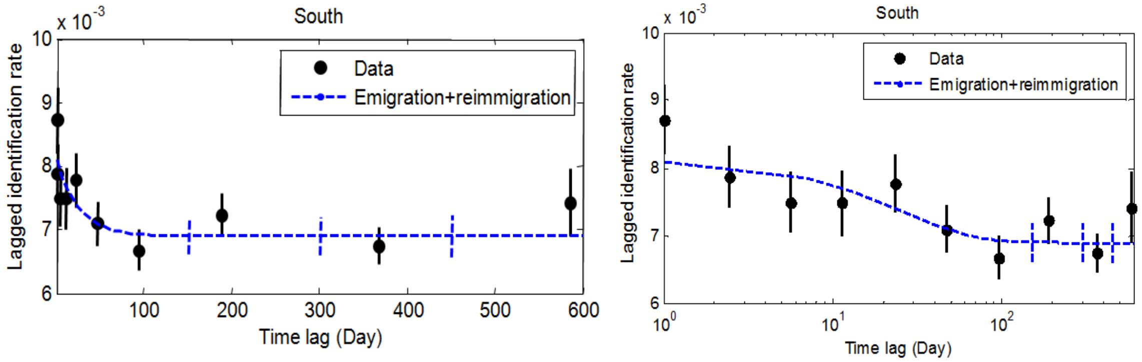
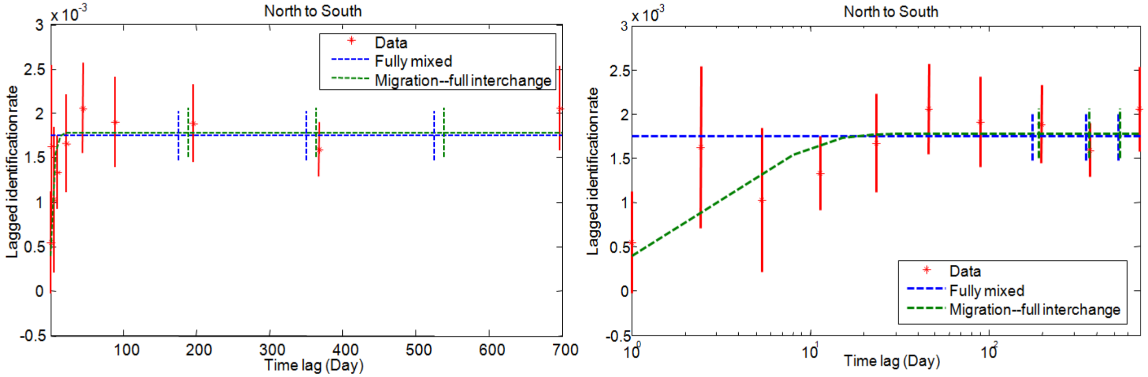


Figure 4.12 Lagged identification rates in linear time lag (left) and log time lag (right) of Indo-Pacific humpback dolphins in the south of the study area (western Hong Kong waters) with image quality ≥60. Observed data are denoted as black dots. Dotted lines represent best-fitted models with ΔQAIC ranging within 2 units. Vertical lines indicate bootstrap estimates of SE.

Table 4.7 Movement models fit to lagged identification rates of Indo-Pacific humpback dolphins in the south of the study area (south-western Hong Kong waters) with image quality ≥60 before (May 2010 to October 2012) and during (November 2012 to December 2014) the construction of the HKZMB. ΔQAIC of 0-2 are in bold.

Model	Before construction		During construction	
	QAIC	ΔQAIC	QAIC	ΔQAIC
Closed	30442.6	30.7	172134.6	16.7
Emigration	30428.8	16.9	172125.2	7.3
Emigration + reimmigration	30411.9	**0**	172117.9	**0**
Emigration + reimmigration + mortality	30412.5	**0.6**	172121.8	3.9

(A) Before construction of the HKZMB



(B) During construction of the HKZMB

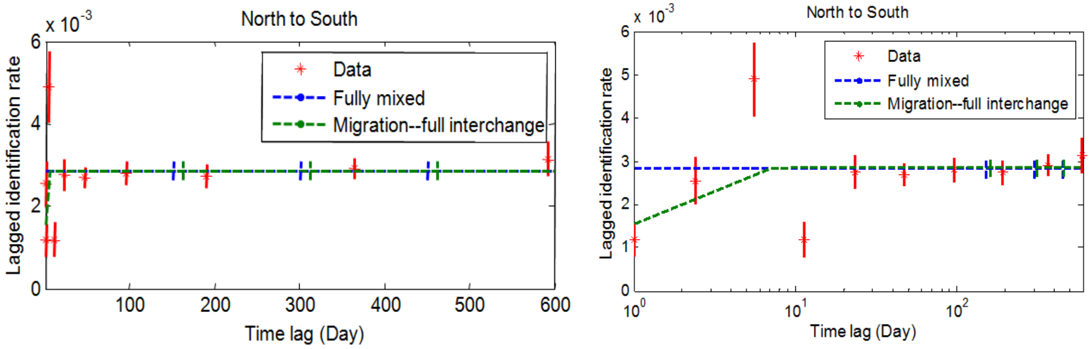
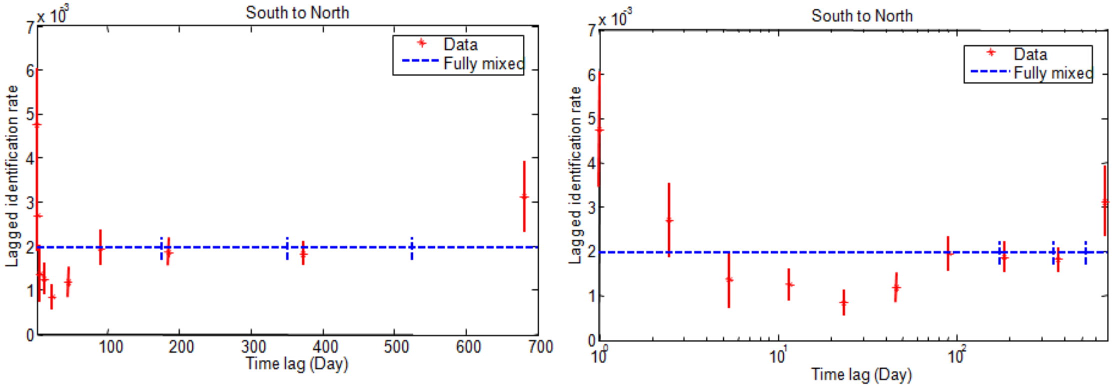


Figure 4.13 Lagged identification rates in linear time lag (left) and log time lag (right) of Indo-Pacific humpback dolphins moving from north to south within western Hong Kong waters with image quality ≥60. Observed data are denoted as black dots. Dotted lines represent best-fitted models with ΔQAIC ranging within 2 units. Vertical lines indicate bootstrap estimates of SE.

Table 4.8 Models fit to lagged identification rates of Indo-Pacific humpback dolphins moving from north to south within western Hong Kong waters with image quality ≥60 before (May 2010 to October 2012) and during (November 2012 to December 2014) the construction of the HKZMB . ΔQAIC of 0-2 are in bold.

Model	Before construction		During construction	
	QAIC	ΔQAIC	QAIC	ΔQAIC
Fully mixed	2906.2	**0**	18799.5	**1.1**
Migration-full interchange	2906.4	**0.4**	18798.4	**0**

(A) Before construction of the HKZMB



(B) During construction of the HKZMB

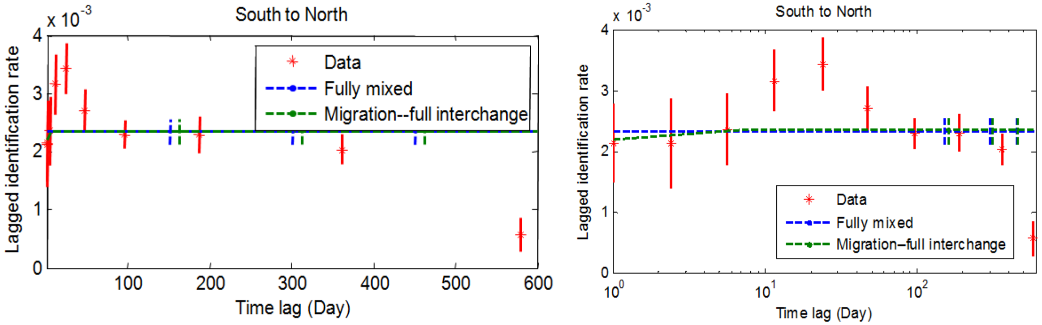


Figure 4.14 Lagged identification rates in linear time lag (left) and log time lag (right) of Indo-Pacific humpback dolphins moving from south to north of western Hong Kong waters with image quality ≥60. Observed data are denoted as black dots. Dotted lines represent best-fitted models with ΔQAIC ranging within 2 units. Vertical lines indicate bootstrap estimates of SE.

Table 4.9 Models fit to lagged identification rates of Indo-Pacific humpback dolphins moving from south to north within western Hong Kong waters with image quality ≥60 before (May 2010 to October 2012) and during (November 2012 to December 2014) the construction of the HKZMB. ΔQAIC of 0-2 are in bold.

Model	Before construction		During construction	
	QAIC	ΔQAIC	QAIC	ΔQAIC
Fully mixed	2947.6	**0**	7912.7	**0**
Migration-full interchange	2950.6	3.0	7914.7	**2.0**

4.3.2 Impact of trawling

4.3.2.1 Datasets before and after the trawl ban in Hong Kong

From 2010 to 2012, a total of 146 survey-days were spent out at sea in the study area, and from 2013 to 2014 the study area was surveyed for 149 survey-days. To achieve a fair representation of the social structure for both sampling periods, only the sighting histories of dolphins seen > 4 times were used for social analysis, which resulted with a dataset of 126 individuals during 2010-2012 and 160 during 2013-2014 (Table 4.10). For analysis of movement of trawler-associating dolphins, ID-images of adults that met the photo quality criteria Q ≥ 70 were used; this amounted to 84 individuals before the trawl ban and 69 individuals after the trawl ban. Movement analysis was repeated on dolphins with photo quality ≥ 60 and this was represented by 88 individuals before the trawl ban and 73 individuals after the trawl ban.

The social structure of dolphins in both periods were highly differentiated (Table 4.10). Ninety-eight individuals were seen in both periods, before and after the trawl ban, of which 52 did not associate with trawlers and 46 were trawler-associating dolphins. The majority of trawler-associating dolphins (73%) were still seen in Hong Kong waters after the trawl ban.

Table 4.10 Details of datasets collected before and after the trawl ban (2010-2012 and 2013-2014, respectively). Only individuals seen in Hong Kong waters > 4 times were included.

	Before trawl ban	After trawl ban
Non-trawler-associating dolphins	63	90
Trawler-associating dolphins	63	55
New individuals after trawl ban	-	15
Total individuals	126	160
Social differentiation (*S*)	0.805±0.033	0.874±0.029
Correlation between true and estimated association indices (*r*)	0.378±0.022	0.490±0.021

4.3.2.2 Associations

The network diagrams did not display strong differentiation between trawler-associating and non-trawler-associating dolphins (Fig. 4.15). Associations among trawler-associating and between the two types of dolphins both increased after the trawl ban, while associations among non-trawler-associating dolphins remained the same (Table 4.11). Before the trawl ban, associations within the same dolphin types were higher than those between types (Mantel test: t = 4.0452, p = 1). After the trawl ban, associations within and between the two dolphin types were not significantly different (Mantel test: t = -0.236, p = 0.40656).

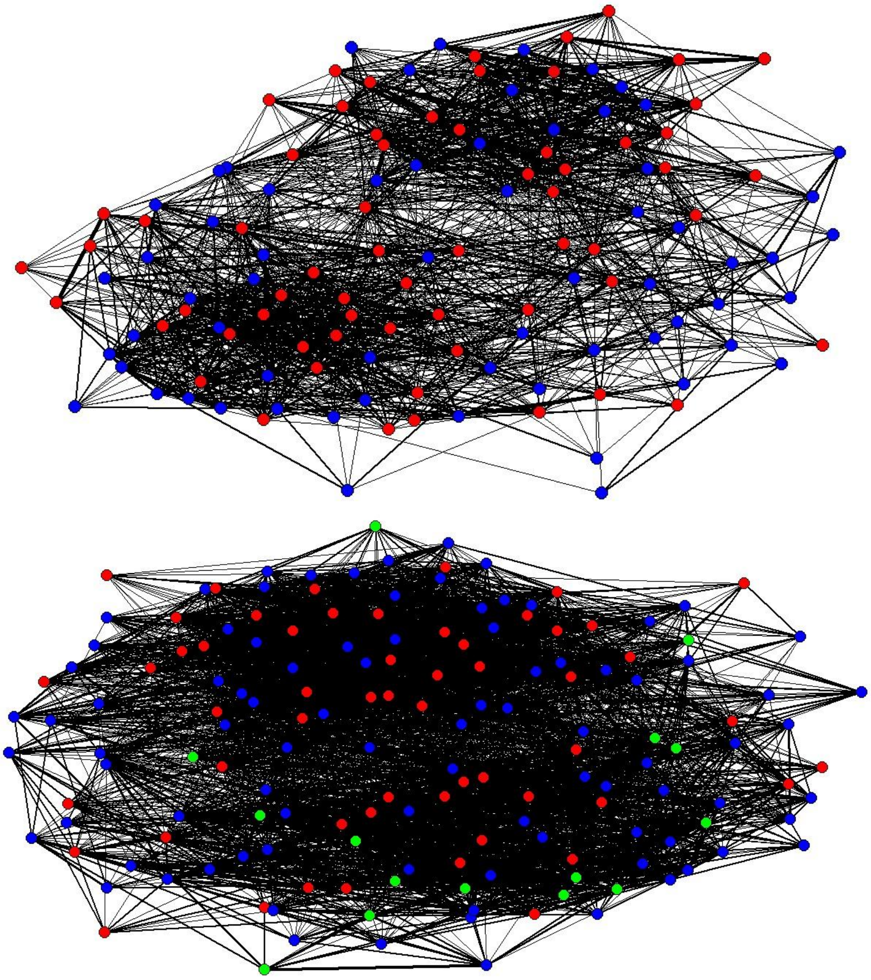


Figure 4.15 Network diagram of Indo-Pacific humpback dolphins seen in Hong Kong more than four times before (upper graph) and after trawl ban (lower graph). Individuals are denoted as nodes. Trawler-associating dolphins are in red, non-trawler-associating dolphins are in blue, and new individuals sighted after trawl ban are in green.

Table 4.11 Mean±SD HWI of Indo-Pacific humpback dolphins seen in Hong Kong waters more than four times before (2010-2012) and after the trawl ban (2013-2014).

Mean individual HWI	Before trawl ban	After trawl ban
All individuals	0.03±0.01	0.04±0.02
Trawler-associating dolphins	0.04±0.02	0.05±0.02
Non-trawler-associating dolphins	0.03±0.01	0.03±0.01
Between trawler-associating and non-trawler-associating dolphins	0.03±0.01	0.04±0.02

4.3.2.3 Site fidelity of trawler-associating dolphins

Among trawler-associating dolphins, the lagged identification rates before the trawl ban dropped within a shorter time period than after the trawl ban (Fig. 4.16). Before the trawl ban, all models had similar QAIC, which indicated considerable heterogeneity; however, “emigration + reimmigration” was the model with the lowest QAIC, the same as after the trawl ban (Table 4.12).

LIRs generated with the datasets that included lower quality photos (i.e. image quality ≥ 60) showed the same pattern (Fig 4.17). Before the trawl ban, all models had ΔQAIC values less than 5, which still suggested heterogeneity in the dataset. After the trawl ban, same set of models as those fitted for the dataset with only higher quality photos represented the best fit (Table 4.13).

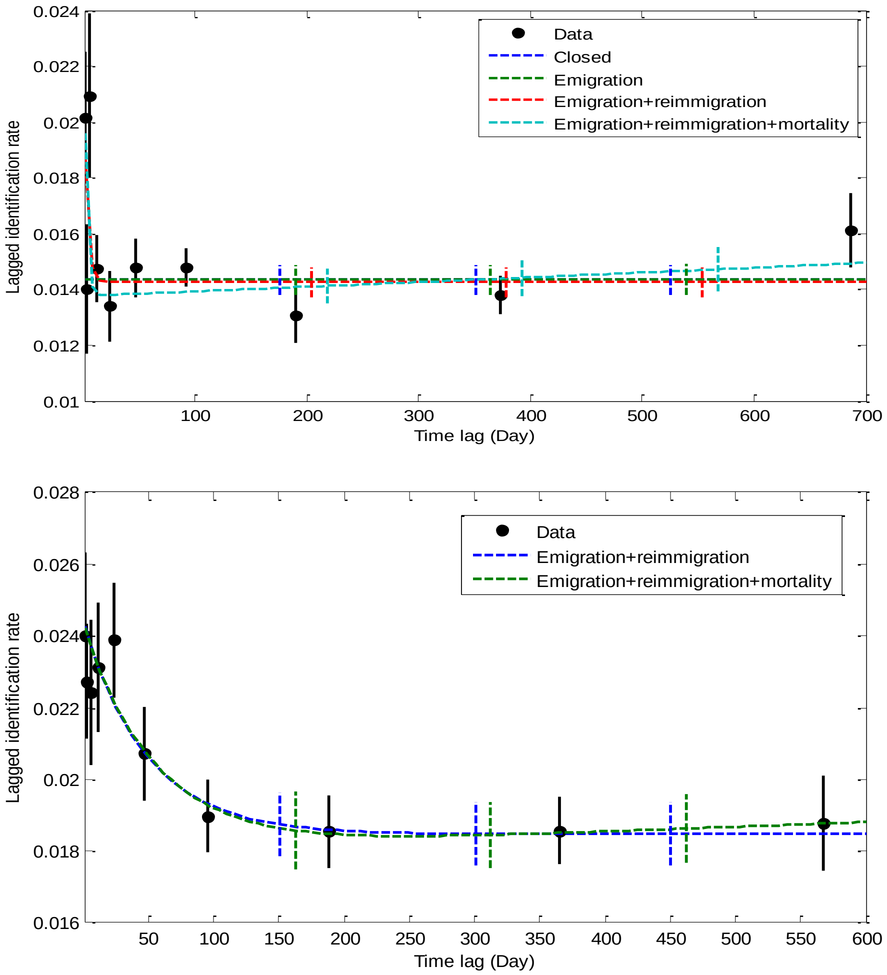


Figure 4.16 Lagged identification rates of trawler-associating Indo-Pacific humpback dolphins before (upper graph) and after the trawl ban (lower graph) in Hong Kong. Vertical lines indicate jack-knifed error bars. Broken lines represent best-fitted models with ΔQAIC within 2 units. Vertical broken lines indicate bootstrap estimates of SE.

Table 4.12 Movement models fit to lagged identification rates of trawler-associating dolphins before (2010-2012) and after the trawl ban (2013-2014) in Hong Kong. ΔQAIC of 0-2 are in bold.

Model	Before trawl ban		After trawl ban	
	QAIC	ΔQAIC	QAIC	ΔQAIC
Closed	**32042.8**	**0.1**	84978.5	41.5
Emigration	**32044.8**	**2.1**	84961.6	24.6
Emigration + reimmigration	**32042.7**	**0**	**84937.0**	**0**
Emigration + reimmigration + mortality	**32042.9**	**0.2**	**84938.7**	**1.7**

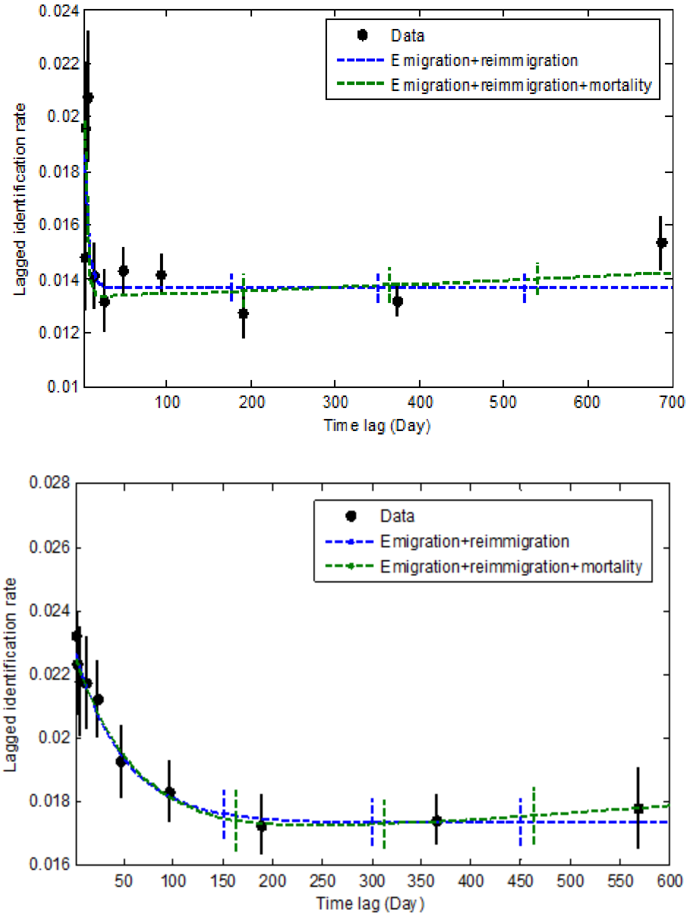


Figure 4.17 Lagged identification rates of trawler-associating Indo-Pacific humpback dolphins with image quality ≥60 before (upper graph) and after the trawl ban (lower graph) in Hong Kong. Vertical lines indicate jack-knifed error bars. Broken lines represent best-fitted models with ΔQAIC within 2 units. Vertical broken lines indicate bootstrap estimates of SE.

Table 4.13 Movement models fit to lagged identification rates of trawler-associating dolphins with image quality ≥60 before (2010-2012) and after the trawl ban (2013-2014) in Hong Kong. ΔQAIC of 0-2 are in bold.

Model	Before trawl ban		After trawl ban	
	QAIC	ΔQAIC	QAIC	ΔQAIC
Closed	34372.7	2.4	121974.1	59.0
Emigration	34374.7	4.4	121950.2	35.1
Emigration + reimmigration	34370.3	**0**	121915.1	**0**
Emigration + reimmigration + mortality	34371.4	**1.1**	121916.2	**1.1**

4.4 Discussion

4.4.1 Impacts of the Hong Kong–Zhuhai–Macau Bridge construction

This study documented remarkable changes in both the social and spatial patterns of humpback dolphins in Hong Kong during the construction of the HKZMB. Dolphins abandoned their core area around the Brothers Islands and reduced their usage around Lung Kwu Chau, especially the north-eastern side of the island. There was a notable shift of utilisation towards the south, with all social clusters consolidating their core areas in the south, while those that used to use northern Hong Kong waters as part of their core areas extended their ranges further south off Lantau Island. This is unlikely to be an artefact of any potential difference in survey effort distribution between the two survey periods as the overall shift in core areas was also detected in the dataset after subsampling that equalised the number of survey days across the whole study area (Fig. 4.3). Different clusters responded differently to the construction activities. The two clusters that used the north as part of their core habitats have divided, with one splitting more substantially and reducing usage of the north more significantly than the other. On the other hand, clusters that used to use primarily the south have coalesced to form one large cluster that intensified its use of the south as its core area. This shift in the range use pattern was further reflected in the changes of dolphin movement. As dolphins reduced their usage of the northern area, “emigration” became one of the best-fit models describing the movement in the north. Large error bars of LIRs in both north and south during construction indicated increased heterogeneity in residency as individuals gradually changed their area use pattern. Furthermore, as indicated by the error bars of LIRs, there was less heterogeneity in movement from the north to the south during construction, as individuals were moving south more decisively.

This shift in area utilisation is in agreement with the abundance estimates and sighting distribution reported by Hung (2016), which showed a steep decline in abundance in northern Lantau Island but increased sightings in southwest Lantau waters since 2012. The restructuring of social clusters and changes in site fidelity between the north and south described in this chapter represent the social perspective and broad-scale movement of the differential change in individual ranges suggested by Hung (2016). As the study period was short (two years) within the minimum of six years of constructions in Hong Kong waters (ARUP 2009a), this study provides only an early stage response of the on-going process. Dolphins were likely in the process of exploring and adapting to the disturbances during the study period as indicated by the heterogeneity in site fidelity to the northern and southern areas.

Changes in area use patterns of cetaceans have been seen previously, but the causes could be manifold and difficult to determine (e.g., Hartel et al. 2015). Similarly, given that the dolphins in Hong Kong waters are subjected to multiple stressors (Karczmarski et al. 2016a) and the environmental factors are interweaved, it could be argued that the disruption of socio-spatial patterns may not be solely due to the construction of the HKZMB but due to other factors, such as cumulative impacts from previous construction and marine traffic off northern Lantau Island (e.g. Marcotte et al. 2015) as well as prey distributional change that may or may not be due to habitat degradation. It is impossible to reject such a possibility. However, as the shift appeared to have intensified with the expansion of the construction (Hung 2016) and because the project itself was the only large-scale construction work that overlapped with dolphins' core habitat during the study period, the construction of the HKZMB has to be regarded as a contributing factor, likely the primary factor causing the observed change of socio-spatial dynamics of humpback dolphins in Hong Kong.

The process in which animals gradually change their pattern of range use involves learning and exploration, and the underlying mechanisms are not yet fully understood. Individuals may explore and adapt to new environments alone, or may learn by observing others and communicating with their associates. Dolphins are capable of social learning (Kuczaj et al. 2012) and communication (Janik 2014). It has been hypothesised that frequent group changes may facilitate transfer of information on resources availability (Lusseau et al. 2006).

The difference in response at the individual level and the level of social clusters highlights the individual differences in spatial and social preferences. Cluster E continued to utilise the northern area as part of its core habitat, suggesting that some individuals appeared to be less susceptible to the disturbance. Preference for specific areas may be caused by natal philopatry (Tsai and Mann 2013), prey type preference, and related foraging strategy (Weiss 2006; Torres et al. 2009). An individual's conditions could also limit its ability to respond to environmental conditions, such that animals in poor condition may forage in risky habitats (Beale and Monaghan, 2004; reviewed in Tuomainen and Candolin 2011). As indicated above, most members of Cluster 5 remained in the same cluster and contributed 58% of members of Cluster E during construction. This suggests that individuals stayed in the north potentially because of association preference. However, this must be interpreted with caution, as the apparent association preference could be due to the similarity of spatial preferences (area use patterns) between individuals rather than association preference.

Evaluating the importance of social and spatial preference on shaping social dynamics is not easy, as the two factors closely interact and may limit one another (Sih et al. 2009). Spatial patterns determine movement patterns and, in turn, control the encounter probability and interaction rate between individuals (Edenbrow et al. 2011). Social preference may limit range use and dispersal because the decision of where to be may be affected by the preferred associates (Farine and Sheldon 2015). In Hong Kong, social clusters may have overlapping ranges, indicating that social preference may contribute to social structure (Chapter 2). However, social preference is incapable of explaining the high fluidity of groupings, as indicated by the disintegration of Cluster 2 and the fusion of Clusters 1, 3, 4, and 6 during construction activities. This suggests that social preference may not be the predominant factor that shapes the community structure in Hong Kong (see also Chapter 3). It appears that prey and foraging ground distribution is the main driving force behind the spatial patterns of range use and, in turn, the community divisions and fluid groupings. As animals gather off the south coast of Lantau Island, an area with the largest foraging ground in Hong Kong waters (Chapter 2), they associate more and develop stronger affiliations. Those that frequent primarily the northern area form their own social groupings and associate less with individuals that prefer the south. The importance of animal distribution in forming association has been suggested in studies of other species that exhibit high fission-fusion dynamics. For instance, it has been shown that association strength relates more with space use pattern than kinship among female Eastern grey kangaroos *Macropus giganteus* (Best et al. 2014). Modelling by Ramos-Fernandez et al. (2006) has shown that resource distribution, along with only basic foraging dispersal rules but no social interactions, could generate fluid but non-random associations similar to that of fission-fusion societies of spider monkeys *Ateles* spp. While their finding does not imply that social preferences or age and sex differences are not important in group formation, it supports that individuals' space use patterns under the influence of food distribution could play a pivotal role in the formation of complex societies (Ramos-Fernandez et al. 2006).

4.4.2 Impacts of trawling

In general, trawler-associating dolphins appeared to be moving in and out of Hong Kong throughout the study period. However, before the trawl ban, the pattern was much more unpredictable, as indicated by highly fluctuating LIRs and the insignificant difference of ΔQAIC (less than 2 units) of all movement models fitted to the observed data. Such unpredictability in sighting trawler-associating dolphins before the trawl ban is very likely because their occurrence in Hong Kong was depended on the occurrence of trawlers in the area, which was unpredictable. Furthermore, this supports the notion by Jefferson's (2000) and Hung's (2008) that dolphins foraging behind trawlers prefer to be in association with trawlers. In other words, some dolphins have a greater preference to forage behind trawlers than others.

However, unlike bottlenose dolphins in Moreton Bay (Chilvers and Corkeron 2001), such a preference for trawlers was not strong enough to generate a strong social segregation between trawler-associating and non-trawler-associating dolphins. The two types of dolphins in Hong Kong still associated with each other when trawlers were not around, even before the trawl ban.

Since the trawl ban was implemented only in Hong Kong and trawling is still largely in operation throughout the Estuary, dolphins that were known to forage in association with trawlers had the choice to forage outside Hong Kong after the local trawl ban. However, the results indicated that a high proportion of dolphins that previously foraged with trawlers were still present in Hong Kong after the trawl ban was in place. Contrary to expectations, a slower decline of LIRs indicates that they were more likely to stay in Hong Kong longer after the trawl ban, and this is not an artefact of the increase in survey effort, as the calculation of lagged identification rates incorporated sightings as a measure of survey effort. It appears that, because of the overall reduction in the number of trawlers in the PRE, the cost of finding trawlers exceeded the advantage of feeding behind trawlers, so the dolphins changed their feeding habits from seeking trawlers across the PREto staying and feeding in a particular area. Such a change in behaviour highlights the plasticity of foraging behaviours and dolphins' resilience to anthropogenic change. As trawler-associating dolphins were spending more time in Hong Kong, they had a higher chance to associate with non-trawler-associating dolphins and, as reported in this study, associations between these two types of dolphins increased in Hong Kong after the trawl ban.

Other factors could have contributed to an increase in the fidelity to Hong Kong among trawler-associating dolphins after the trawl ban. One could be a change in prey density or distribution, which may or may not be due to the trawl ban. However, this cannot be tested as there is no sufficient data on prey distribution. Alternatively, the dolphins shifted their range use pattern to Hong Kong because of the construction of the HKZMB. The shift in space use caused by the HKZMB is suggested in Section 4.4.1 of this chapter and Hung (2016) because utilisation of the southern area of Hong Kong increased after the construction of the HKZMB commenced. Despite these potential factors, the results remain indicative that trawler-associating dolphins may not necessarily stay with trawlers and that they may adjust their feeding habits in accordance with environmental conditions.

Network parameters before and after the trawl ban were not compared, as they would be expected to be higher after the trawl ban because of increased resightings and individuals. While this analysis was not applied in the current study, significantly higher network mean strength, reach, clustering coefficient, and affinity have been observed in bottlenose dolphins after a reduction in trawling in Moreton Bay (Ansmann et al. 2012). In fact, Ansmann et al. (2012) reported that higher network parameters were not an artefact of increased sightings and individuals, as both of these confounding parameters had smaller values after the reduction in trawling. Higher strength and reach in social network imply not only the formation of a more compact society but also an increase in the potential of information and disease transmission (Farine and Whitehead 2015). In the absence of a localised and easy food source provided by trawlers, the increase in information transfer between dolphins that foraged in association with trawlers and those that did not follow trawlers may have facilitated the adaptation of trawler-associating dolphins to an environment without trawlers. Ansmann et al. (2012) proposed that, lacking an easy and opportunistic food source from trawlers, dolphins need to forage on natural food sources that are comparatively variable in space and time and the demand for cooperation and learning between dolphins increases, resulting in a well-connected social network after a trawl ban. A similar process may have operated in Hong Kong.

Foraging strategies are known to function as contributing factor in shaping delphinid social strategies (Gowans et al. 2008). An intrapopulation structure may arise in the presence of interaction with fisheries, such as trawlers (Chilvers and Corkeron 2001; Ansmann et al. 2012) and artisanal fishermen (Daura-Jorge et al. 2012), and from differences in foraging tactics, such as sponging (Mann et al. 2012). Similarly, the change in associations between trawler-associating and non-trawler-associating dolphins after the trawl ban in Hong Kong could be an evidence of behavioural influence on social structuring.

4.5 Conclusion

This chapter has documented the social and spatial responses of humpback dolphins to two types of anthropogenic activities: large-scale coastal construction and trawling. Humpback dolphins restructured their social dynamics and shifted their core areas and range use pattern during the construction of the HKZMB in Hong Kong. Some dolphins had a stronger preference for foraging around trawlers, which contributed to weaker associations between trawler-associating and non-trawler-associating dolphins before the trawl ban in Hong Kong. After the trawl ban, trawler-associating dolphins stayed in Hong Kong longer and associations between the two types of dolphins increased. The weakened association between individuals with different foraging behaviours prior to the trawl ban and changes in site fidelity and associations after the trawl ban suggest that trawler association as a foraging strategy could be a factor that influences social dynamics. The rapid change in association patterns in both cases indicates that humpback dolphins have considerably high behavioural and social plasticity; perhaps a feature more pronounced in the dolphins inhabiting the PRE region in response to large-scale, diverse, and long-present anthropogenic impacts.

Chapter 5 Area utilisation of Indo-Pacific humpback dolphins in eastern Pearl River Estuary

5.1 Introduction

Understanding the area utilisation pattern of a species is necessary to establish effective conservation measures (Simmonds et al. 1996; Agardy et al. 2011). As illustrated in Chapter 2, the range use pattern of a species reflects its choice of habitat and incorporation of behavioural data into utilisation distribution models enhances the analyses and our understanding of the functions of specific areas and habitats. Furthermore, identification of behaviourally important areas and factors affecting key behaviours are fundamental to the delineation of priority sites for protection. In Chapter 2, the area of interest was confined to Hong Kong only, which is located at the eastern section of the Pearl River Estuary (PRE) and represents the eastern boundary of the PRE humpback dolphin population. As Hong Kong waters are only a small section of the PRE and integrally connected with the ecological ecosystem of the estuary, broadening our knowledge of the area utilisation pattern onto a larger spatial scale is instrumental to a holistic approach to understanding of humpback dolphins population ecology.

Studies on the population range have been conducted in the PRE since the mid-1990s (Jefferson 2000; Chen et al. 2010). These studies revealed that humpback dolphins are present throughout the PRE and the population boundary extends from the mouth of Humen to the west of the estuary beyond Xiachuan Island. No clear spatial division has been detected so far. In general, they avoid extremely shallow waters (less than three metres) and deep offshore waters (over 20 metres in depth). Seasonal shift in dolphin distribution in Hong Kong and Lingding Bay has been suggested (Parsons 1998; Jefferson 2000; Hung 2008; Chen et al. 2010) and more recently quantified by Chan and Karczmarski (2017). During the dry season, dolphins appear to be more evenly distributed throughout eastern PRE (EPRE), and during the wet season, dolphins shift towards the eastern and southern part of the EPRE. Apparently, this pattern corresponds to the seasonal prey distribution (Chen et al. 2010). However, the area utilisation pattern remains unknown. Given the political border between Hong Kong and mainland waters, previous studies were conducted either in mainland China only (Chen et al. 2010) or, in most cases, in Hong Kong (Jefferson 2000; Hung 2008; Chan and Karczmarski 2017). Due to limited survey efforts covering the entire area, the relative importance of different areas could not be inferred from those studies. This also obscures the interpretation of the importance of Hong Kong waters to humpback dolphins in the PRE and of the marine protected area network across the broader PRE region.

There are two marine protected areas (MPAs) in EPRE, and both are dedicated to the conservation of humpback dolphins: Sha Chau and Lung Kwu Chau Marine Park in Hong Kong (see Chapter 2 for details) and the Guangdong Pearl River Estuary Chinese White Dolphin National Nature Reserve in mainland China. The MPA in mainland China was first established as a Nature Reserve in October 1999 and was later upgraded to a National Nature Reserve in June 2003. It is currently the largest MPA in the PRE, covering about 460 km^2, and is divided into three zones based on the protection levels stated in the Measures on the Management of Marine Nature Reserves and the Regulations on Nature Reserves. According to the Regulations, in the core area (140 km^2), entry is prohibited and scientific research is strictly controlled. In the buffer area (192 km^2), only scientific studies can be carried out. In the experimental area (128 km^2), educational activities and tourism are allowed with approval (Dang 2014).

Despite detailed zonings and regulatory requirements, anthropogenic activities continue within the protected area. For instance, the Hong Kong-Zhuhai-Macau Bridge (HKZMB) traverses all three zones with a 6.7 km underwater tunnel placed in the core area of the MPA. The lack of enforcement is of great concern. However, the more fundamental question that should be asked is whether and how humpback dolphins are utilising the MPA. Its design and zoning are not based on any scientific knowledge of the range use pattern of humpback dolphins in the area and there is no scientific support that the MPA design is in fact appropriate for humpback dolphins.

This chapter extends the study undertaken in Hong Kong waters to the entire EPRE. It aims to identify the area utilisation pattern by humpback dolphins in the region, investigate the factors that influence their occurrence and critical behaviours, and evaluate the usefulness of the current MPAs in protecting critical habitats. Specifically, this chapter focuses on identifying the core areas of biologically important behaviours of humpback dolphins in the EPRE, assessing the relative importance of variables affecting foraging behaviour and estimating the overlap between core areas and the existing MPAs in the region.

5.2 Methods

5.2.1 Study area

This study focused on the EPRE (Fig. 5.1). Since dolphins are known to reside throughout the entire PRE without any clear subdivision, the western boundary for this study was defined arbitrarily at the south of Macau. The shorelines in the EPRE outside Hong Kong are mostly rocky, anthropogenically-altered, or entirely constructed by land reclamation and are occasionally muddy or sandy. There are seven cargo-shipping lanes and numerous high-speed ferry lanes connecting HKSAR with seven ports in mainland China and Macau. During the study period, the 40 km long HKZMB was being constructed and the project involved constructing underwater tunnels, artificial islands, a main bridge, and link roads across Lingding Bay. Construction commenced in December 2009 in mainland China and was initiated in November 2011 in Hong Kong. It is expected to be completed in December 2017.

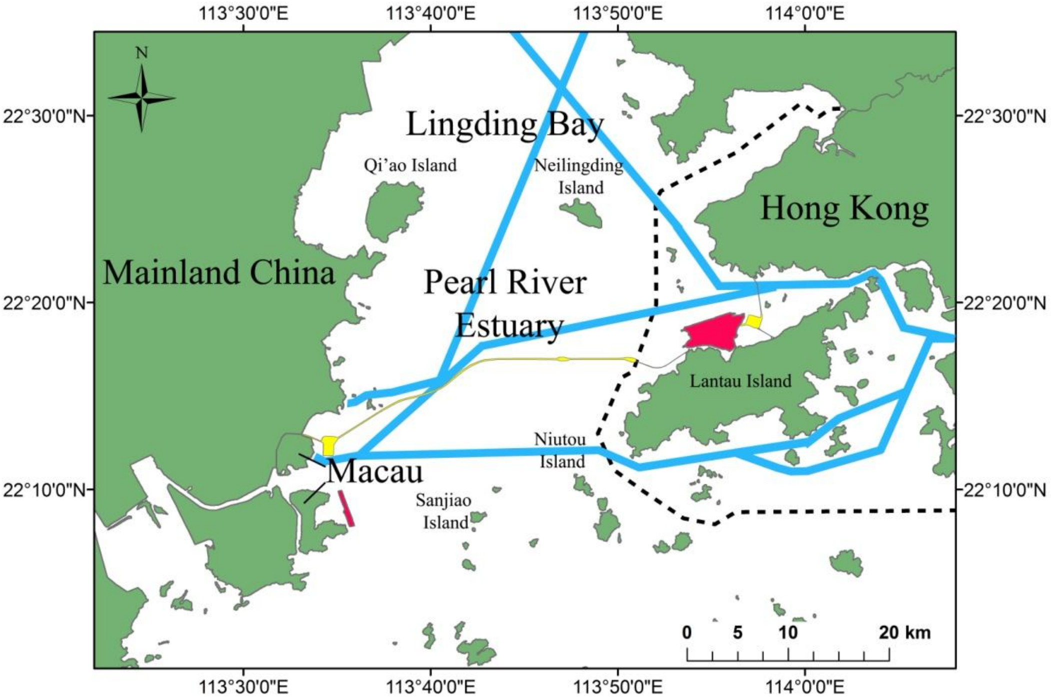


Figure 5.1 The study area, Eastern Pearl River Estuary (EPRE) comprises of the Hong Kong Special Administrative Region (HKSAR), mainland China, and the Macau Special Administrative Region. The administrative boundary of HKSAR is denoted by a black broken line. Airports, which include the Hong Kong International Airport and Macau International Airport, are indicated in red. The Hong Kong-Zhuhai-Macau Bridge (HKZMB) and its associated facilities (under construction during the study period) are indicated as yellow and include the main bridge of the HKZMB, the Hong Kong Link Road, associated border-passing facilities, and the Tuen Mun-Chek Lap Kok Link. High-speed ferry channels are denoted in blue lines.

5.2.2 Field data collection

The field data collection protocol in Hong Kong was the same as described in Chapter 2, and the study period was from October 2011 to December 2015.

Field surveys outside Hong Kong waters were conducted from April 2011 to December 2015 using small boats ranging from 7.8-8.2 m and equipped with SUZUKI 90-120 4-stroke out-broad engines. Survey protocol, including the field sampling method and the definitions of the dolphin behaviours, were the same as that applied in Hong Kong (described in Chapter 2), with data collected during photo-identification boat surveys conducted without predesigned routes. However, as the study area in mainland waters was larger than in Hong Kong, only part of the area could be covered at any given survey.

For surveys conducted outside Hong Kong, equipment used to measure water depth included a hand-held Hawkeye H22PX depth finder or a Hondex PS-7 portable depth sounder, which delivered measurements with a precision of 1/10 unit (0.1m). Geographic locations were recorded using the Garmin Geographic Positioning System receiver GPSMAP 76.

5.2.3 Utilisation distribution analyses

Utilisation distributions were estimated using kernel density estimation (KDE) and local convex hull (LoCoH). The projected coordinate system adopted was WGS84-UTM 50N.

The procedure for LoCoH analyses was the same as described in Chapter 2. KDE was applied for additional reference. LoCoH is considered more conservative in estimating utilisation distributions (Signer et al. 2015) and, given that the dataset used in this study was smaller and the study area was much larger than that described in Chapter 2, could underestimate the distributions.

Like LoCoH, KDE outputs a probabilistic model of utilisation distribution (Worton 1989, 1995; Seaman and Powell 1996). Probability contours (i.e. kernels) are placed around data points according to the intensity of utilisation. The 50% and 95% kernels are commonly considered as the core area and range used by the animals (Fieberg and Börger 2012), and they were adopted by this study. Adaptive kernel density estimates with least-squares cross-validation (LSCV) for bandwidth selection were applied. The adaptive kernel method was used as it has been suggested to perform better in estimating the shape of the utilisation distribution than the fixed kernel method (Silverman 1986). KDE is very sensitive to bandwidth selection, which determines the size of the kernels (Worton 1995). Simulations have indicated that the LSCV for bandwidth selection produces the most accurate estimate of home range (Seaman and Powell 1996). However, if the LSCV algorithm failed to converge in minimising the mean integrated square error (MISE), biased cross-validation (BCV) would be applied for bandwidth selection. BCV performs similarly to LSCV except it aims to find a suitable bandwidth that minimises the estimate of asymptotic mean integrated square error (AMISE) (Sain et al. 1994). Despite simulations suggesting that BCV performs as reliably as LSCV (Sain et al. 1994), it is not widely used in cetacean studies. KDE was calculated using the Home Range Estimate extension tool (Rodgers et al. 2007) in ArcGIS 9.3.1 (ESRI 2008).

Two datasets were analysed: EPRE without Hong Kong and EPRE with Hong Kong. For the dataset without Hong Kong, all records collected in 10-minute intervals for each encounter were included. For the dataset of EPRE including Hong Kong, only the first records of each encounter were used for analyses as the average time spent on each encounter was longer in Hong Kong.

5.2.4 MPAs coverage of core areas and ranges

To evaluate the adequacy of the existing MPAs in protecting the core areas and range of humpback dolphins in the EPRE, the percentage coverage of the Sha Chau and Lung Kwu Chau Marine Park and the Guangdong Pearl River Estuary Chinese White Dolphin National Nature Reserve on the 50% and 95% utilisation distributions were calculated for both datasets (i.e. with and without Hong Kong data).

5.2.5 Factors influencing foraging probability

Foraging probability was modelled with a generalised linear mixed model with dolphin groups as the random variables. Fixed variables included year and season as temporal factors, water depth, distance to shore, tidal state and geographic positions as these hydrographic and physical variables are known to affect humpback dolphin distribution and behaviour whenever it was investigated (Karczmarski et al. 2000a; Parra et al. 2006; Keith et al. 2013; Lin et al. 2013; see also Chapter 2). Season was defined as wet season (April to September) and dry season (October to March) based on volume discharge of the Pearl River (Zhao 1990; Dong et al. 2006). Latitude was a proxy for distance to the river outlets, of which higher latitudes are closer to the outlets. Interactions between latitude, longitude and distance to shore were included. Depth was recorded in the field in association with behavioural data. Distance from shore was estimated using ArcMap 9.3.1 (ESRI 2008). Tidal states were derived from the tide table produced by the China Shipping Service. Four tidal states were considered. ‘High’ and ‘Low’ referred to the time periods between an hour before and after the high and low tides. ‘Flood’ and ‘Ebb’ were the tidal states between the defined ‘High’ and ‘Low’.

Analytical tools and procedures were the same as described in Chapter 2.

5.3 Results

5.3.1 Database

From 2011 to 2015, 307 surveys were completed in the EPRE outside Hong Kong, with 1123.6 hours spent at sea. A total of 870 dolphin encounters were recorded and 338.4 hours were used in collecting environmental data and recording dolphin behaviour. Data was sub-sampled to minimise the difference in survey effort, measured by a number of surveys across the whole area. The distribution of surveys after sub-sampling is shown in Figure 5.2. Highly surveyed areas were surveyed 100 times. After sub-sampling, a total of 241 surveys were used for further analyses.

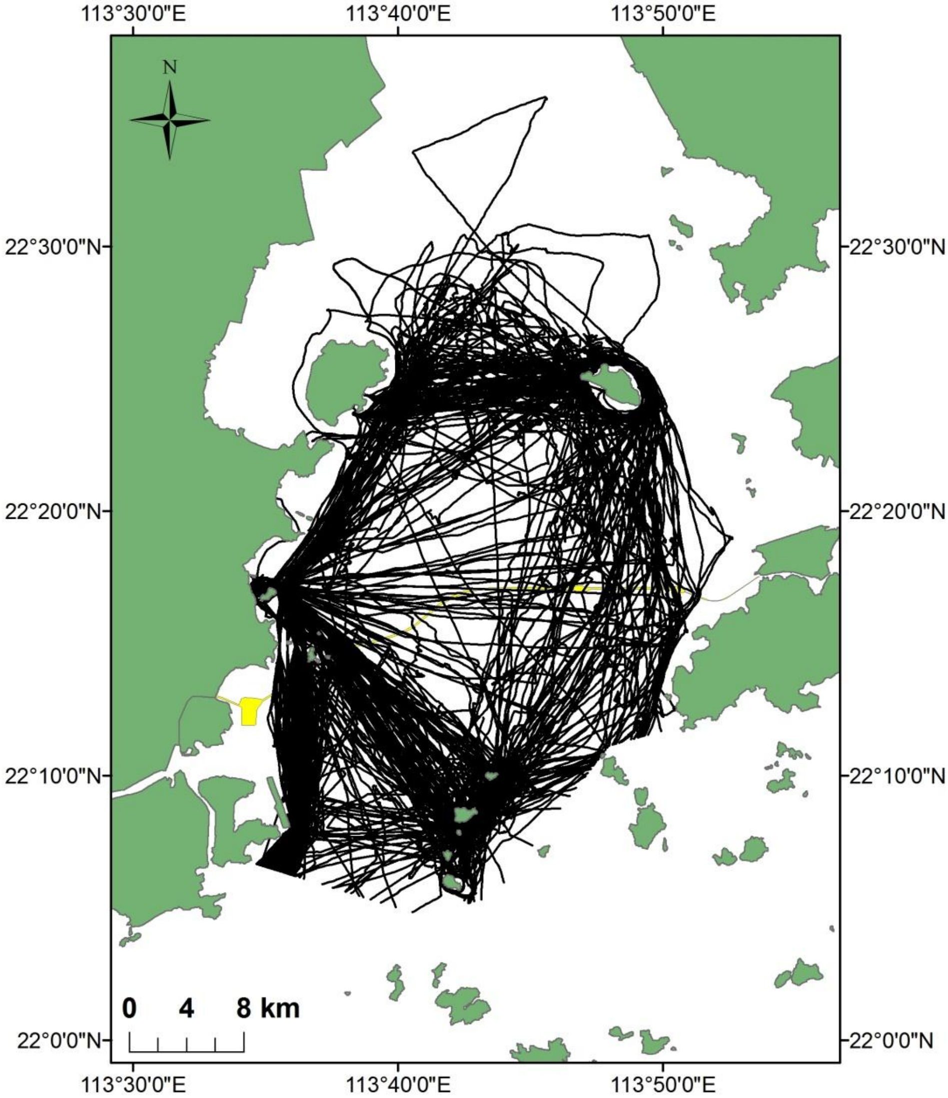


Figure 5.2 Distribution of surveys conducted outside Hong Kong during 2011–2015 after sub-sampling.

From 2011 to 2015, 302 surveys were conducted in Hong Kong, with 1360.2 hours at sea. In total 1518 dolphin encounters were recorded and 548.4 hours were spent collecting behavioural data and the associated environmental data. A total of 139 surveys in Hong Kong were used, and the entire study area in Hong Kong was surveyed 100 times (Table 5.1; Fig 5.3).

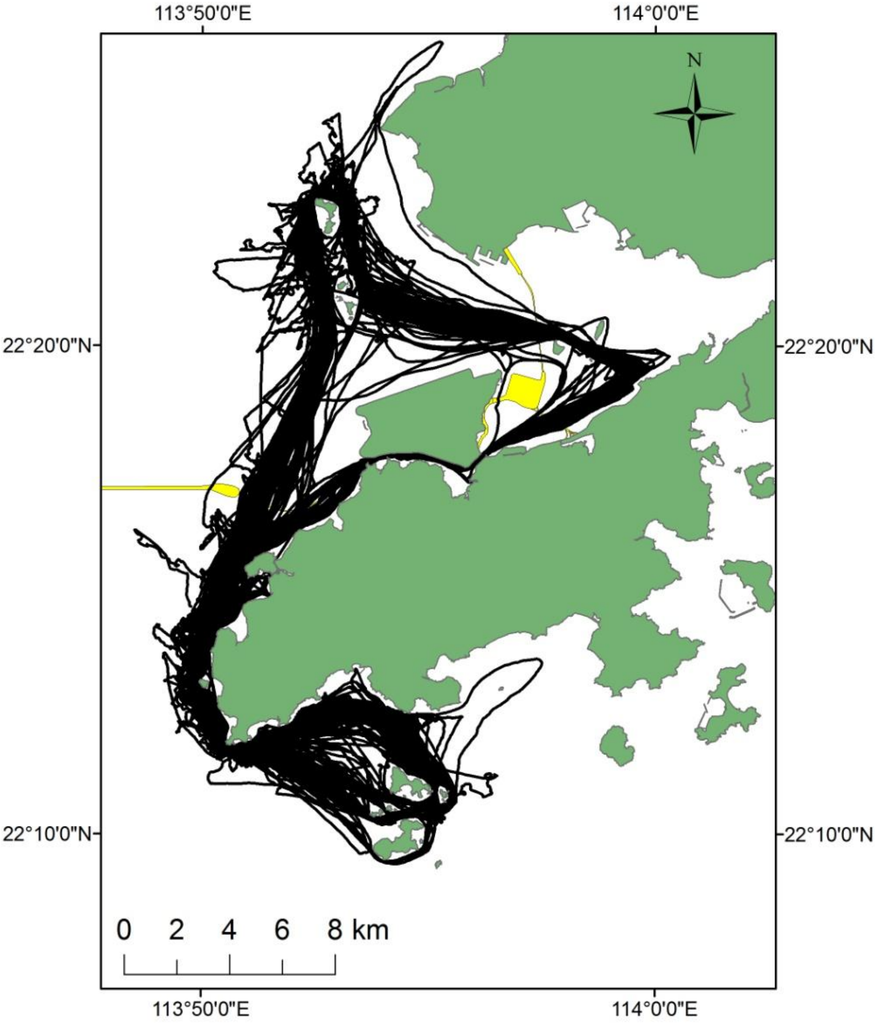


Figure 5.3 Distribution of surveys conducted in Hong Kong during September 2012– December 2015 after sub-sampling. Prior to September 2012, survey tracks were not available and the effort was quantified based on the surveyed areas marked on datasheets.

Table 5.1 Survey effort in Hong Kong during 2011–2015 after sub-sampling that equalised the number of surveys conducted in Hong Kong.

	Number of survey days					
	2011	2012	2013	2014	2015	Total
Full area coverage	0	4	19	19	19	61
North only	2	11	11	8	7	39
South only	2	11	11	8	7	39
Total	4	26	41	35	33	139

5.3.2 Area utilisation pattern

5.3.2.1 Eastern Pearl River Estuary excluding Hong Kong

During bandwidth selection for KDE, the algorithm for LSCV failed to converge when analysing the dataset of EPRE excluding Hong Kong. BCV was applied for bandwidth selection in this case.

The overall area utilisation pattern derived from the sub-sampled dataset identified two comparatively large core areas (50% isopleth) off western Neilingding Island, Sanjiao Island, and the surrounding islands. There were also two smaller core areas (50% isopleth) east off Qi’ao Island and south off Macau. The range (95% isopleth) extended beyond and connected the core areas (Fig. 5.4).

In the EPRE excluding Hong Kong, the most frequently recorded behaviour was foraging (51.9%), followed by travelling (21%). Milling was not often seen (7%), and socialising and resting were scarce (cumulatively less than 5%). Behaviour classified as ‘undetermined’ and cases of ‘mixed’ behaviour, where two behaviours are equally dominant, were not used in further spatial and temporal analyses (Table 5.2 for details).

Significant autocorrelations were detected (Swihart & Slade Index > 0.6; Schoener Index < 1.6 or > 2.4) (see Table 5.3). In general, the LoCoH method produced more confined areas than the KDE method (Table 5.3).

The ranges and core areas of observed behaviours overlapped extensively with each other, but spatial estimates differed (Table 5.3; Fig.5.5 to Fig.5.8). The 50% utilisation distribution (UD) for foraging and travelling were both clustered around coastal areas (Figs 5.5 and 5.6) and resembled the UD of all behaviours combined (Fig. 5.4). The UD of travelling extended further and broader than foraging and had high coverage over the whole study area. The sample size for milling was small and its UD was considerably scattered and small (Table 5.3). Socialising and resting were too sparse for UD calculation. For socialising records, 89% (*n* = 42) were within the foraging range, and 19% (*n* = 9) were within foraging cores.

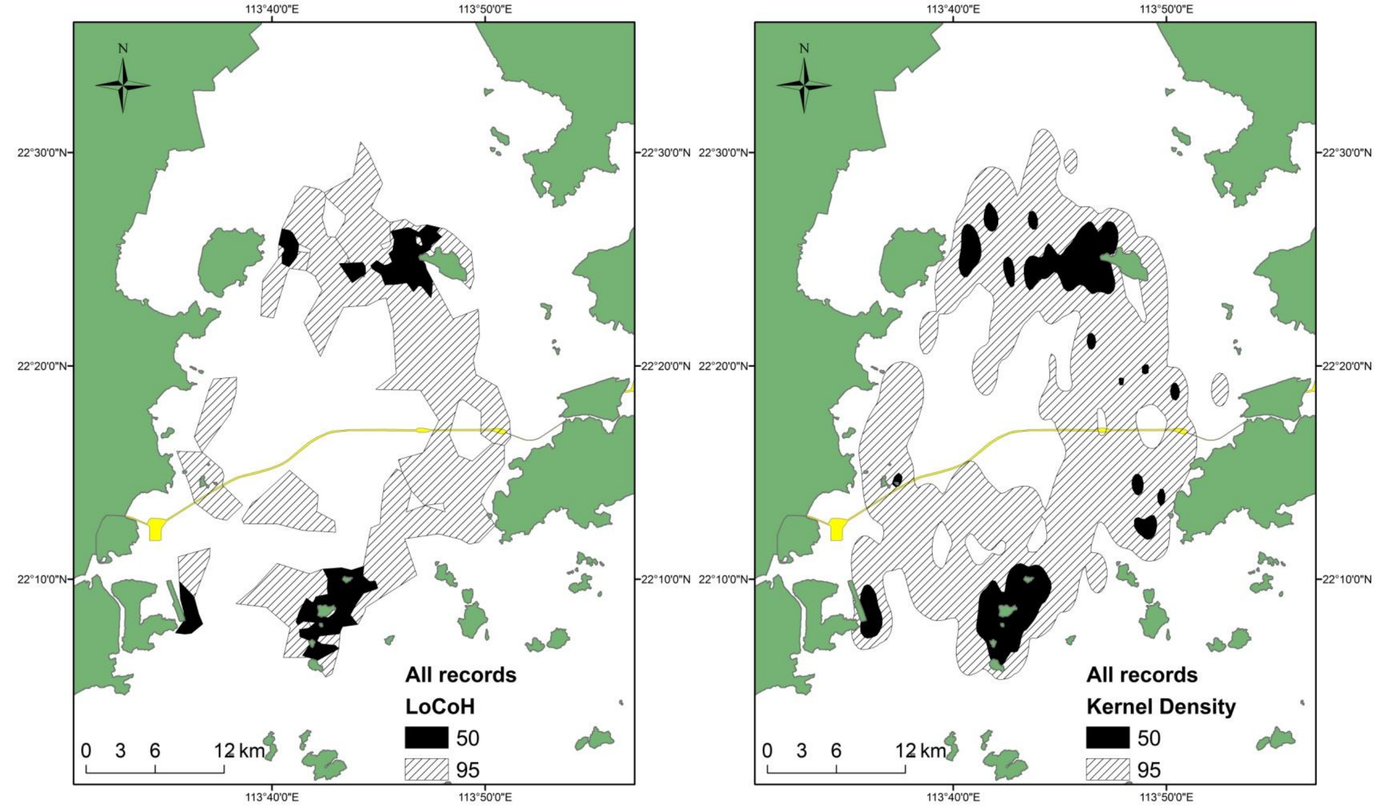


Figure 5.4 Area utilisation pattern of Indo-Pacific humpback dolphins estimated with 50% and 95% isopleths of Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) for all sightings recorded during 2011–2015 in the eastern Pearl River Estuary (EPRE) excluding Hong Kong.

Table 5.2 Number of GPS points of humpback dolphin behaviour recorded in the eastern Pearl River Estuary (EPRE) excluding Hong Kong during 2011–2015.

	Total	Percentage
Foraging	627	51.9
Travelling	254	21.0
Milling	84	7.0
Socialising	47	3.9
Resting	12	1.0
Foraging-Travelling	101	8.4
Foraging-Milling	37	3.1
Foraging-Socialising	11	0.9
Milling-Socialising	3	0.2
Travelling-Milling	1	0.1
Travelling-Resting	1	0.1
Undetermined	29	2.4
Total	1207	100

Table 5.3 Calculated areas (in km^2) for Local Convex Hull (LoCoH) estimates and Kernel Density estimation (KDE) at 95% and 50% utilisation distributions for sightings recorded during 2011–2015 in eastern Pearl River Estuary (EPRE) excluding Hong Kong. The values of the Swihart & Slade Index > 0.6 (Swihart and Slade 1985) or Schoener Index < 1.6 or > 2.4 (Schoener 1981) indicate significant autocorrelation in the data. H_{ref} refers to the reference bandwidth of KDE and h is the bandwidth used for KDE. Sample sizes of socialising, resting and mixed behaviours were too small to generate utilisation distribution estimates.

	LoCoH 50%	LoCoH 95%	KDE 50%	KDE 95%	Swihart & Slade Index	Schoener Index	h	h_{ref}	n
All records	52.36	388.94	84.83	641.32	2.20	0.40	0.06	0.31	1207
Foraging	35.01	275.57	50.92	403.98	2.01	0.57	0.04	0.34	627
Travelling	36.82	287.25	96.24	613.34	1.33	1.04	0.08	0.40	254
Milling	3.15	46.63	35.30	181.51	1.59	0.60	0.05	0.48	84

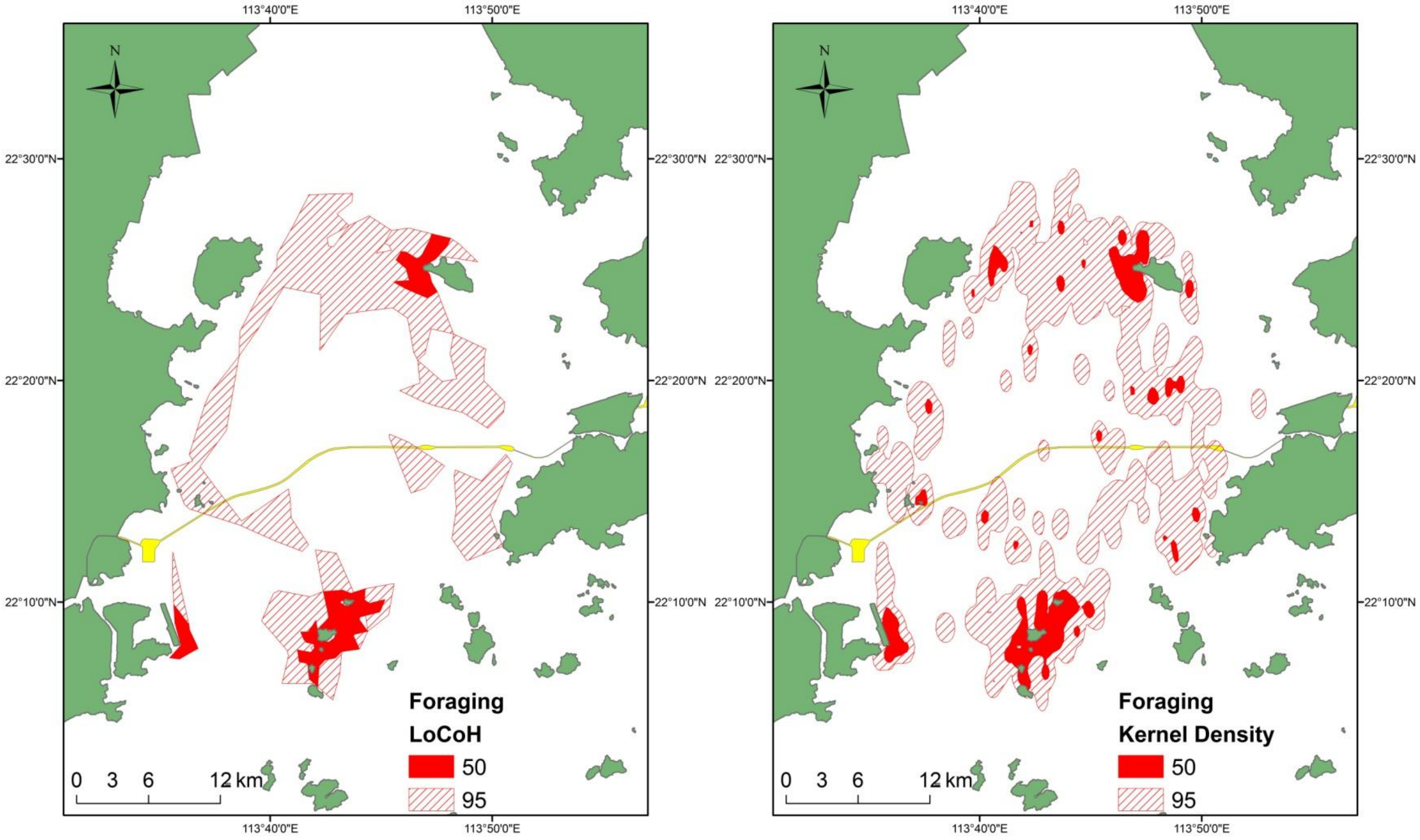


Figure 5.5 Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) with 95% and 50% isopleths utilisation distributions for foraging of Indo-Pacific humpback dolphins in the eastern Pearl River Estuary (EPRE) excluding Hong Kong, during 2011–2015.

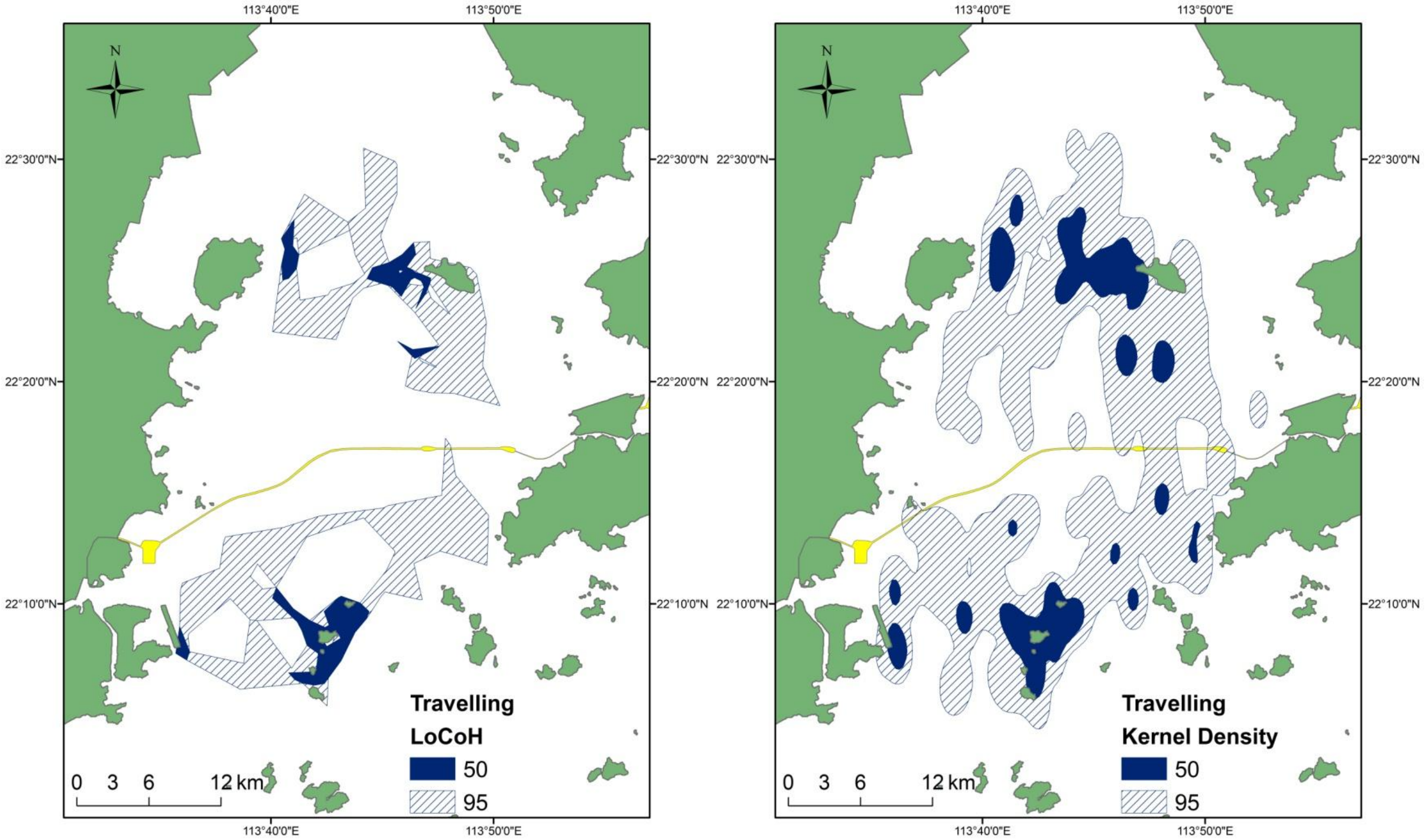


Figure 5.6 Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) with 95% and 50% isopleths utilisation distributions for travelling of Indo-Pacific humpback dolphins in the eastern Pearl River Estuary (EPRE) excluding Hong Kong, during 2011–2015.

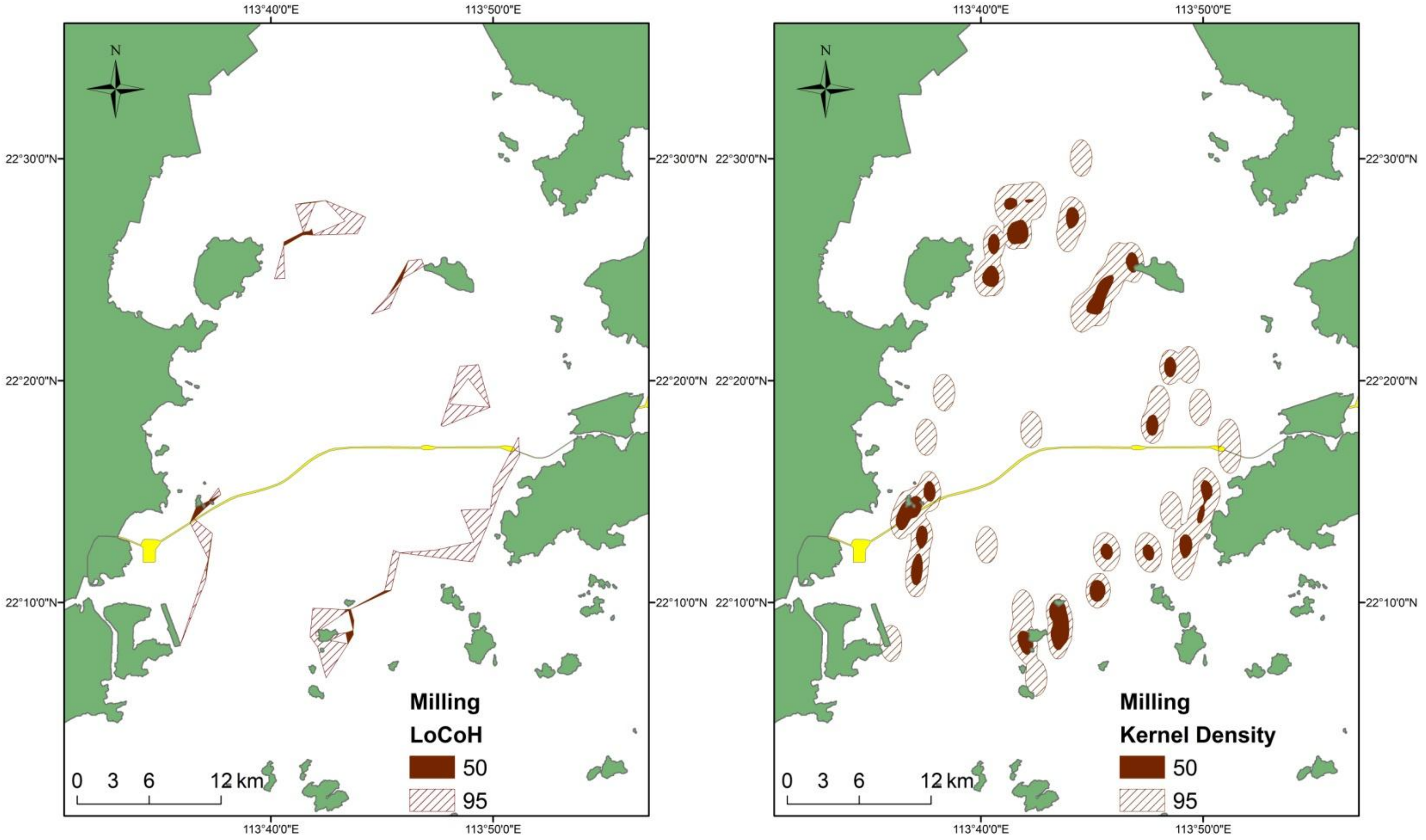


Figure 5.7 Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) with 95% and 50% isopleths utilisation distributions for milling of Indo-Pacific humpback dolphins in the eastern Pearl River Estuary (EPRE) excluding Hong Kong, during 2011–2015.

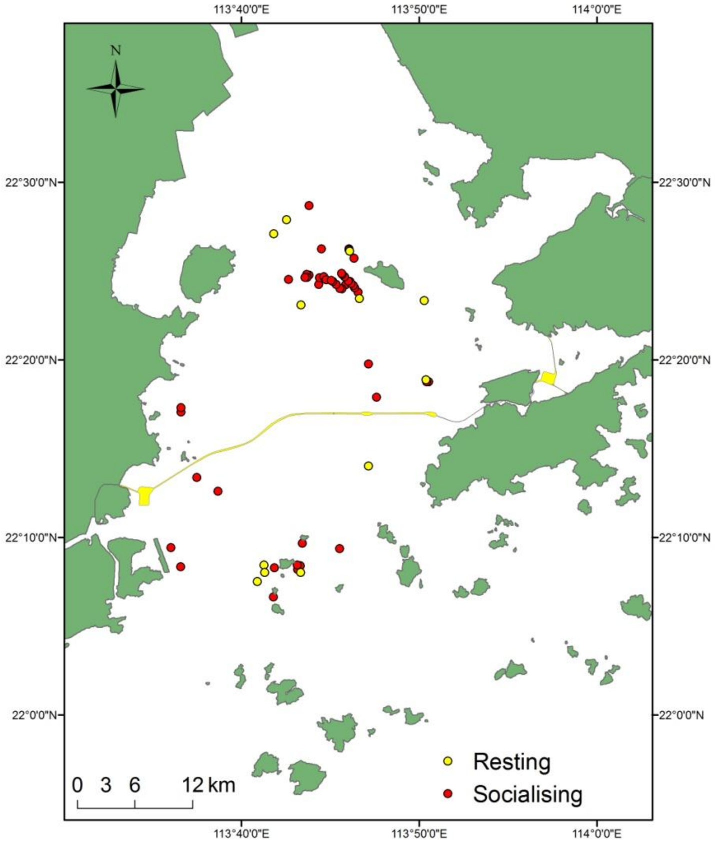


Figure 5.8 Sightings of resting and socialising Indo-Pacific humpback dolphins in the eastern Pearl River Estuary (EPRE) excluding Hong Kong, during 2011–2015.

5.3.2.2 Eastern Pearl River Estuary

In the whole of EPRE, including Hong Kong, four core areas (50% isopleth) were identified. Two relatively large core areas were located in Hong Kong, around Lung Kwu Chau and off west/southwest coast of Lantau Island. The two core areas in mainland China waters were comparatively small and located at western Neilingding Island and around Sanjiao Island. All core areas were connected by the ranges (95% isopleth), which covered Hong Kong and the mid-EPRE more extensively than the remaining area (Fig. 5.9).

Percentages of the observed behaviour were similar to those before inclusion of the Hong Kong data (Table 5.4 for details), with foraging seen most frequently, followed by travelling and milling. Socialising and resting were rarely seen.

The UD derived from behavioural data resembled the overall utilisation pattern in the EPRE, of which the 50% UD in Hong Kong was larger and more notable than those in mainland China (Table 5.5; Figs. 5.10 to 5.13). Travelling was more widespread than all other behaviours (Fig. 5.11). Milling was concentrated in Hong Kong and was rarely recorded outside Hong Kong (Fig. 5.12). Socialising and resting records were too few for UD calculation (Fig. 5.13). Socialising appeared to be concentrated within core areas with 45% (n = 10) inside foraging core areas defined by the LoCoH method, 55% (n = 12) inside foraging core areas defined by the KDE method and 86% (n = 19) in foraging ranges defined by the KDE/LoCoH methods. Resting was seen too infrequently to generate any spatial models.

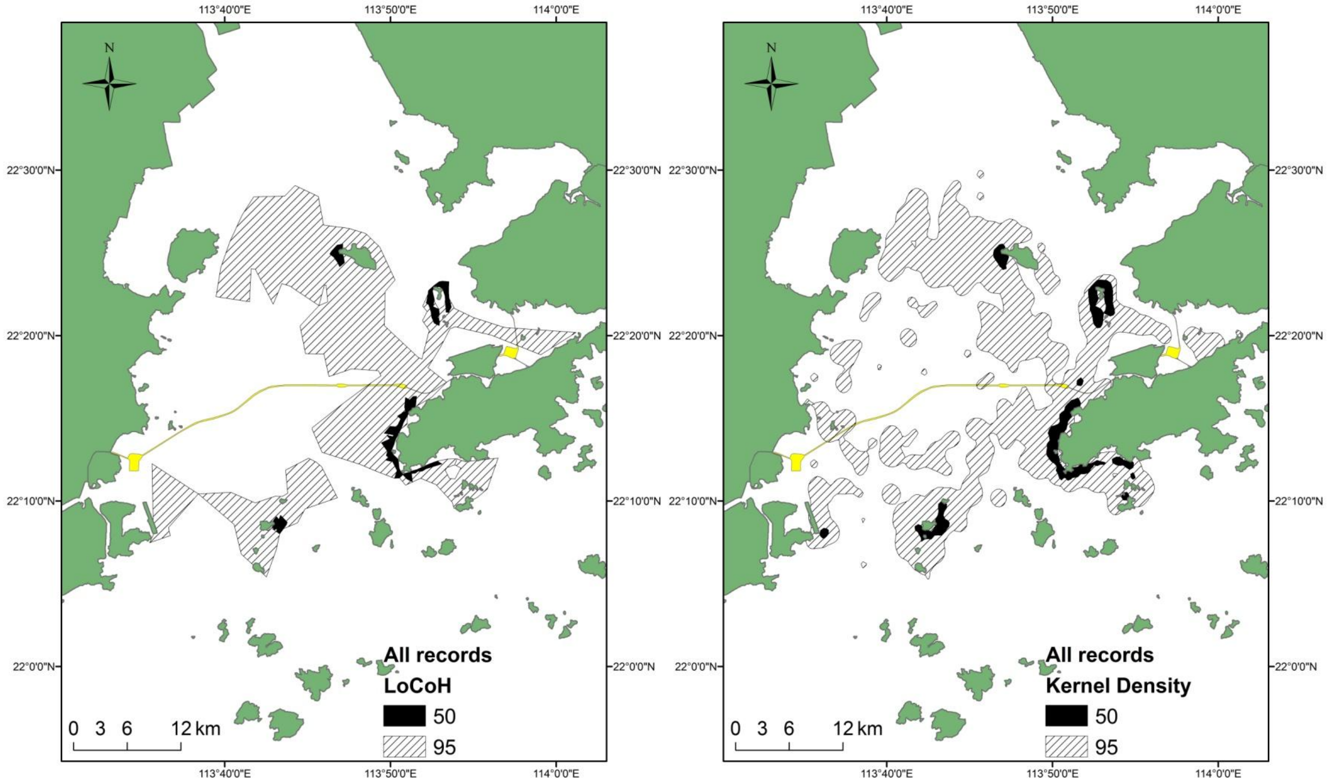


Figure 5.9 Area utilisation pattern of Indo-Pacific humpback dolphins estimated with 50% and 95% isopleths of Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) for all sightings recorded in the eastern Pearl River Estuary (EPRE) during 2011–2015.

Table 5.4 Number of GPS points of humpback dolphin behaviour recorded in the eastern Pearl River Estuary (EPRE) during 2011–2015. Only the first GPS point of each encounter was used for analysis.

	Total	Percentage
Foraging	542	51.9
Travelling	245	23.5
Milling	105	10.1
Socialising	22	2.1
Resting	8	0.8
Foraging-Travelling	35	3.4
Foraging-Milling	27	2.6
Foraging-Socialising	3	0.3
Milling-Socialising	3	0.3
Milling-Resting	2	0.2
Travelling-Milling	8	0.8
Travelling-Resting	1	0.1
Undetermined	43	4.1
Total	1044	100

Table 5.5 Calculated areas (in km^2) for Local Convex Hull (LoCoH) estimates and Kernel Density estimation (KDE) at 95% and 50% utilisation distributions for sightings recorded during 2011–2015 in the eastern Pearl River Estuary (EPRE). The values of the Swihart & Slade Index > 0.6 (Swihart and Slade 1985) or Schoener Index <1.6 or >2.4 (Schoener 1981) indicate significant autocorrelations in the data. h_{ref} refers to the reference bandwidth of KDE, and h is the bandwidth used for KDE. Sample sizes of socialising, resting and mixed behaviours were too small to generate utilisation distribution estimates.

	LoCoH 50%	LoCoH 95%	KDE 50%	KDE 95%	Swihart & Slade Index	Schoener Index	h	h_{ref}	n
All records	17.97	463.96	34.64	520.99	1.38	0.66	0.03	0.31	1044
Foraging	10.90	301.93	31.40	470.73	1.29	0.84	0.04	0.35	542
Travelling	21.74	296.07	46.09	388.71	1.12	0.96	0.04	0.40	245
Milling	3.35	115.30	24.37	207.82	1.14	0.98	0.05	0.46	105

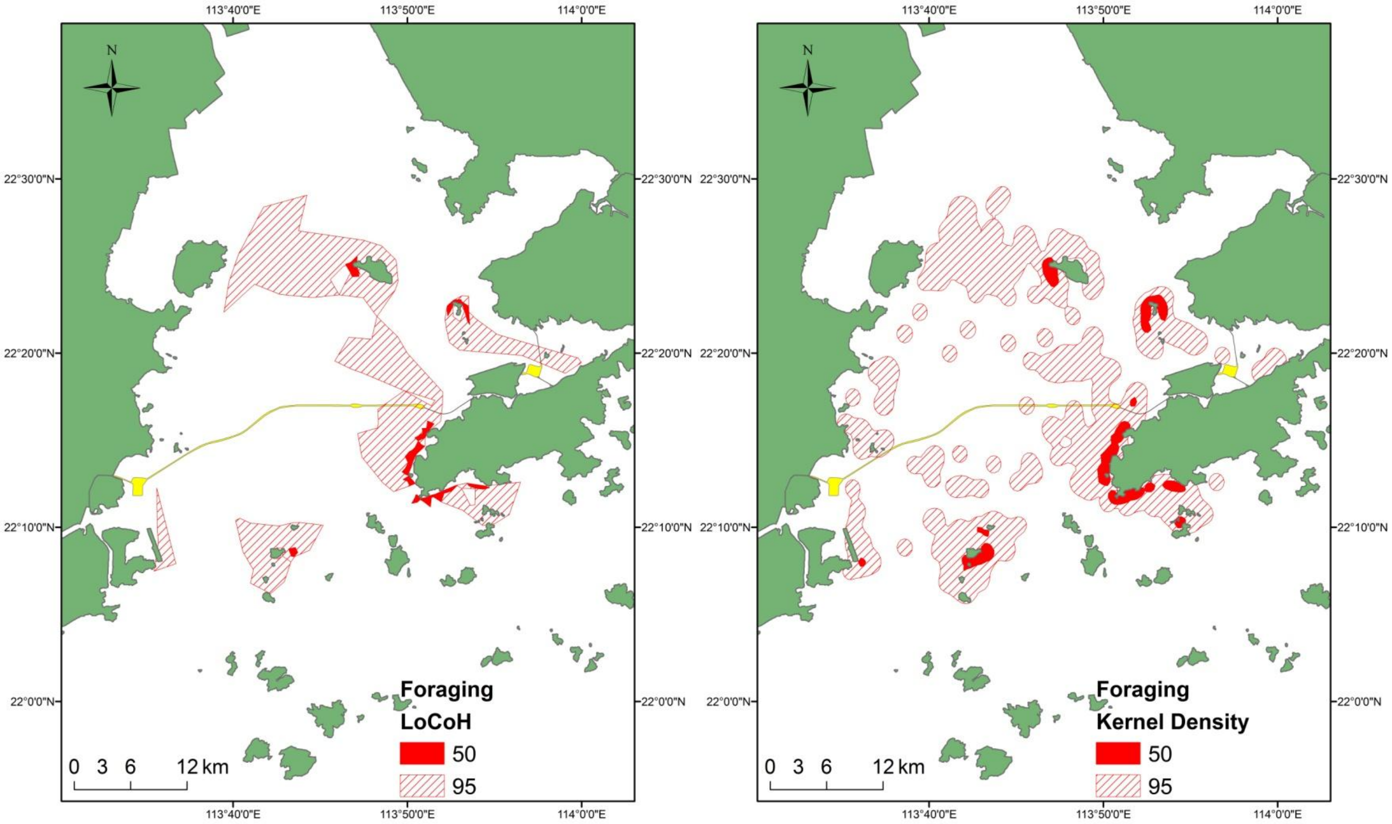


Figure 5.10 Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) with 95% and 50% isopleths utilisation distributions for foraging of Indo-Pacific humpback dolphins in the eastern Pearl River Estuary (EPRE) during 2011–2015.

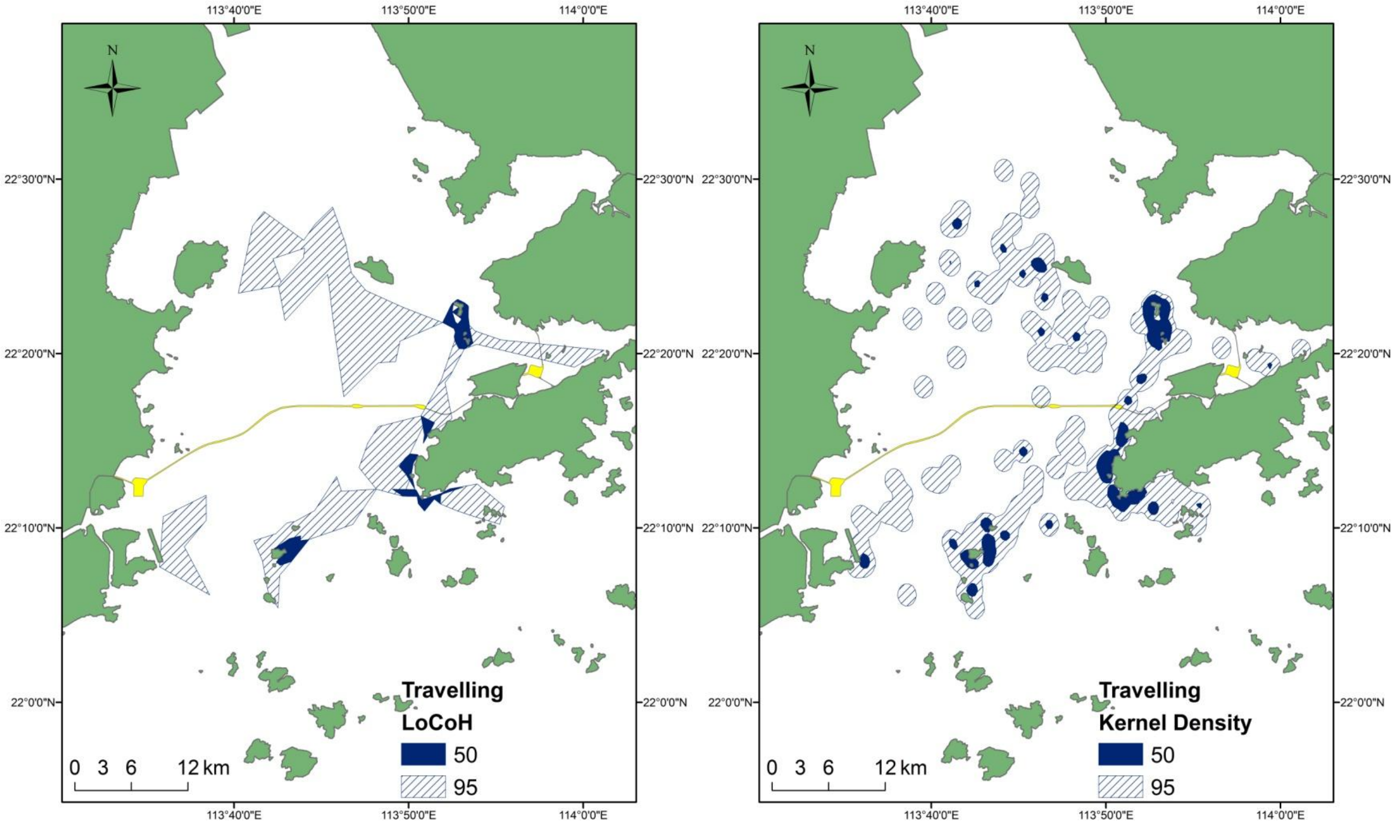


Figure 5.11 Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) with 95% and 50% isopleths utilisation distributions for travelling of Indo-Pacific humpback dolphins in the eastern Pearl River Estuary (EPRE) during 2011–2015.

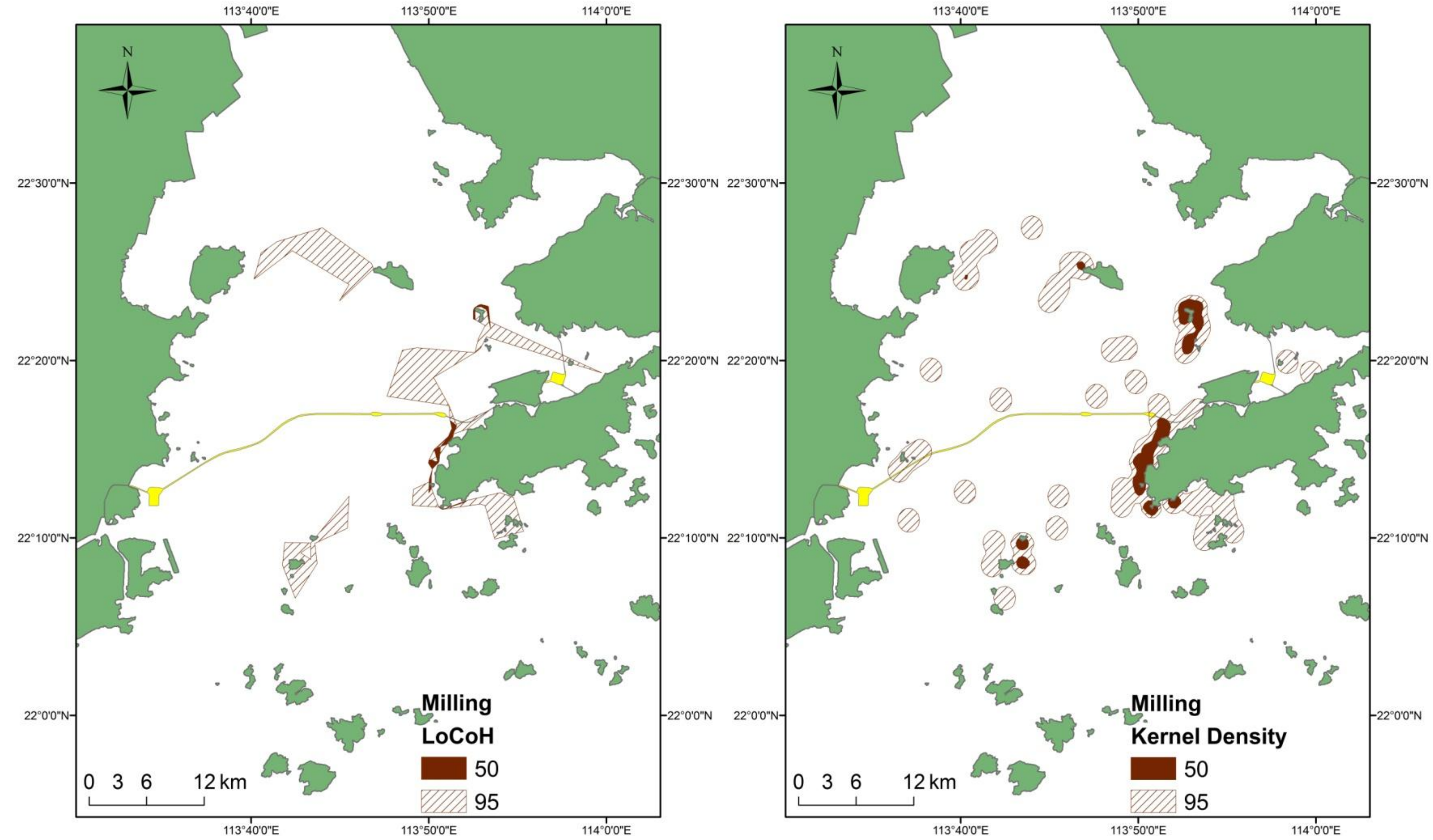


Figure 5.12 Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) with 95% and 50% isopleths utilisation distributions for milling of Indo-Pacific humpback dolphins in the eastern Pearl River Estuary (EPRE) during 2011–2015.

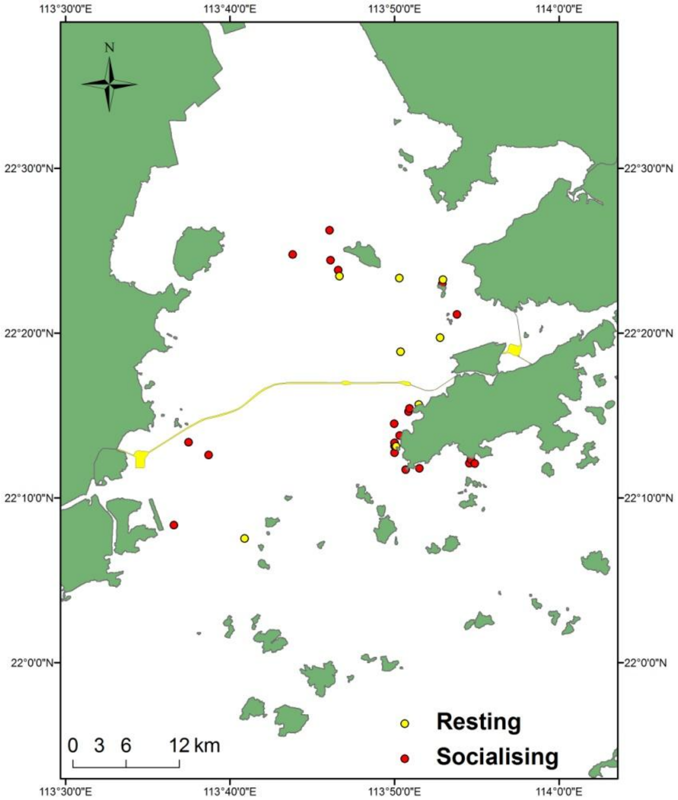


Figure 5.13 Sightings of resting and socialising Indo-Pacific humpback dolphins in the eastern Pearl River Estuary (EPRE) during 2011–2015. Only the first record of each encounter was included.

5.3.2.3 Dolphin core areas and ranges vs. MPAs

The majority of core areas and ranges (50% and 95% UD) of all sighting records and individual behaviours were outside MPAs (Table 5.6 and 5.7; see also figures in Appendices 4–13). The percentage of foraging areas, both 50% core and 95% range UD under legal protection was remarkably small. The inclusion of Hong Kong increased the coverage of 50% and 95% UD of all records and of individual behaviours under the protection of MPAs, but it remained small (Table 5.7; figures in Appendices 9–13).

Table 5.6 Percentages of area covered by an existing Marine Protected Area (MPA) in the eastern Pearl River Estuary (EPRE) excluding Hong Kong, during 2011–2015.

	LoCoH 50%	LoCoH 95%	KDE 50%	KDE 95%
All records	4.67	44.70	11.78	42.87
Foraging	1.61	32.91	11.81	38.58
Travelling	4.31	43.05	17.16	42.12
Milling	0.28	34.83	19.58	32.20

Table 5.7 Percentages of area covered by existing Marine Protected Areas (MPAs) in the eastern Pearl River Estuary (EPRE), including Hong Kong, during 2011–2015.

	LoCoH 50%	LoCoH 95%	KDE 50%	KDE 95%
All records	23.12	42.61	21.16	35.57
Foraging	13.74	33.88	15.44	31.15
Travelling	35.87	39.80	27.27	36.12
Milling	20.38	29.81	28.62	25.75

5.3.2.4 Factors influencing foraging probability

Fixed variables recorded during the years 2011–2015 in the EPRE outside of Hong Kong and used for a generalised linear mixed effect model are listed in Table 5.8. No collinearity among variables was found (VIF < 3, Table 5.8) and all variables were used. Interaction between latitude and longitude was included in model averaging as this inclusion reduced the AIC of the global model. There was a considerable model uncertainty; 54 models had Δ AIC < 10. Akaike weight of the most parsimonious model was small (0.24). More than 70% of models with Δ AIC < 10 contained one of the six variables: year, distance to shore, season, longitude, latitude and the interaction term. High Akaike weights of these variables indicated that their impacts on foraging probability were higher than other fixed variables, which include group size, depth, and tidal state (Table 5.9). Year, distance to shore, season and the interaction term were also found to be significant factors in the averaged model ($p < 0.05$, Table 5.9).

The high relative importance of the year suggested that foraging probability fluctuated between years (Table 5.9). Distance to shore had a negative coefficient, indicating higher foraging probability when closer to shore (Table 5.9; see also Fig. 5.4). The presence of an interaction term of latitude and longitude among important variables indicated foraging occurred at specific locations (see also Fig. 5.4). Latitude and longitude were not significant variables and their high relative importance was due to the high importance of their interaction term. When the interaction term of the variables is included, the variables on their own have to be included in the modelling process. Foraging probability decreased during wet season. Low relative importance and standard errors larger than coefficient estimates were found among group size, depth, and tidal state, indicating their relationships with foraging probability were weak (Table 5.9). Areas under the ROC curves of all testing data based on 5-fold cross validation were 0.61 to 0.77, suggesting that the averaged model has fair predictive power.

Table 5.8 Summary and variance inflation factors (VIF) of fixed variables of humpback dolphin sightings seen in the eastern PRE (EPRE) outside Hong Kong during 2011–2015. Categorical data such as Year and Tidal state do not produce mean and range. Year 2011, dry season and ebb tide were used as reference levels of the three categorical variables in the calculation of variance inflation factors.

	Mean (±SD)	Range	VIF	*n*
Longitude	113.7263 (0.06)	22.09018–22.50832	1.70	462
Latitude	22.28342 (0.12)	113.586–113.8732	1.66	462
Group size	4.53 (3.57)	1–25	1.12	462
Depth (m)	8.61 (4.60)	3.1–33	1.62	462
Distance to shore (m)	2840.98 (2584.53)	33–12568	1.44	462
Year 2011	-	-	-	110
Year 2012	-	-	1.83	102
Year 2013	-	-	1.90	84
Year 2014	-	-	1.60	64
Year 2015	-	-	2.34	102
Wet season	-	-	1.63	232
Dry season	-	-	-	230
Tidal state Ebb	-	-	-	157
Tidal state Flood	-	-	1.68	170
Tidal state High	-	-	1.34	84
Tidal state Low	-	-	1.29	51
Longitude: Latitude	-	-	1.52	-

Table 5.9 Model averaged coefficients and the relative importance of variables ($\sum w_i$) for mixed effect models with AIC difference (Δ AIC) < 10 for foraging probabilities of humpback dolphins in the eastern PRE (EPRE) outside Hong Kong. Study period was from 2011–2015. Year, season and tidal state were treated as categorical variables, with 2011, dry season and ebb tide as reference levels. The interaction term is indicated with a colon. Pr(>|z|) < 0.05 are in bold.

	Estimate	Std. Error	*z* value	Pr(>|z|)	$\sum w_i$
(Intercept)	-0.662	0.537	1.232	0.218	
Year					1
2012	1.170	0.552	2.114	**0.034**	
2013	1.619	0.607	2.661	**0.008**	
2014	1.101	0.683	1.608	0.108	
2015	2.669	0.776	3.433	**0.001**	
Distance to shore	-0.527	0.228	2.303	**0.021**	0.92
Season					0.91
Wet season	-0.986	0.436	2.255	**0.024**	
Latitude	-0.119	0.204	0.580	0.562	0.84
Longitude	-0.001	0.235	0.005	0.996	0.82
Longitude: Latitude	0.761	0.287	2.646	**0.008**	0.76
Group size	0.187	0.194	0.965	0.335	0.36
Depth	-0.025	0.233	0.106	0.915	0.27
Tidal state					0.15
Flood	-0.768	0.492	1.556	0.120	
High	-0.273	0.527	0.516	0.606	
Low	-0.628	0.629	0.996	0.319	

5.4 Discussion

5.4.1 Autocorrelation and potential bias

Significant autocorrelations were detected in all datasets. Autocorrelation may potentially increase Type I error and lead to negatively biased estimates in utilisation distribution (Swihart and Slade 1985). However, it has been argued that serial independence is not a prerequisite for utilisation distribution estimators, such as kernel estimates (De Solla 1999) and data sub-sampling prior to analyses may cause information loss and reduce biological relevance of the estimates (Reynolds and Laundre 1990; De Solla 1999; Bundell et al. 2001). In order to examine whether the locations of biologically important areas and the relative sizes of these areas remain unaffected by autocorrelation, utilisation distribution analyses were repeated using a dataset with only the first locations of each encounter. Although autocorrelation was only reduced rather than being eliminated in the overall and foraging sightings, the resultant utilisation distribution pattern remained the same as that generated from the complete dataset which indicated two large core areas off western Neilingding Island, Sanjiao Island, and the surrounding islands and also two small core areas around the east off Qi’ao Island and south off Macau (see Appendices 14-19). This gave an additional support to the general pattern of spatial use of the PRE waters estimated from the complete dataset.

The current dataset does not allow further sub-sampling to eliminate autocorrelation and therefore, it is recommended to continue data collection and repeat the analyses with uncorrelated data at a later stage. Nonetheless, this current study provides the first valuable insights into the utilisation distribution of humpback dolphins in the EPRE.

Furthermore, the similarity between the results from the complete dataset and the dataset with only the first records of each encounter confirms that potential human disturbance due to data collection did not have apparent impacts on the results. Patterns from the complete dataset are therefore reliable representation of the dolphin's utilisation distribution.

5.4.2 Spatio-behavioural dynamics in EPRE

Humpback dolphins in the EPRE outside Hong Kong display similar pattern of habitat choice as that seen in Hong Kong waters (see Chapter 2). Foraging was the most frequently seen behaviour and its extensive spatial overlap with the overall area utilisation pattern suggests that foraging governs the overall pattern of range use. The foraging core areas identified in this study are likely the areas with high abundance of the dolphins' prey, and the areas are spatially separated, suggesting that the prey distribution is patchy. However, with no data on prey distribution at present, it is not possible to confirm this hypothesis.

A mixed effect model, which was applied to model foraging probability against other behaviours, indicated that foraging probability is lower as the distance from shore increases, indicating that offshore areas are unlikely to be their preferred foraging grounds. This is not an artefact of a lack of data taken offshore as offshore areas were also surveyed (Fig. 5.2) and sightings were recorded within a considerable range from 33 m to 12568 m from shore. This implies that the central section of the EPRE, which lacks any island, is not a favoured area for the dolphins but generally a transit area used for travelling between foraging grounds. As the survey coverage was relatively scattered in the centre of the study area, the coverage of the dolphin range in this area is likely underestimated, but, as indicated above, it is unlikely to generate bias.

All four spatially separated core areas identified in the EPRE outside Hong Kong are close to shore. While the western Neilingding Island, eastern Qi'ao Island, and Sanjiao Island and its surrounding islands are relatively natural and undisturbed, the core area at Macau is situated along the runway of Macau International Airport, which is built on reclaimed land and has been in operation since November 1995 (Macau International Airport Co. Ltd. 2012). This indicates that dolphins may at times use anthropogenically altered areas, such as those reclaimed from the sea, which has not been observed in Hong Kong (Chapter 2). However, this should not be generalised. It has been a long time since the Macau airport reclamation and conditions such as the proximity to estuary mouth may have facilitated prey re-colonisation, as the river discharge brings nutrients to the area. The marine exclusion zone of the airport may have also proved helpful, reducing human disturbance of the area.

Considering the whole EPRE, including Hong Kong, two phenomena could be observed: (1) core areas in Hong Kong remain and are comparatively larger than those in mainland water; and (2) sizes of core areas in the mainland are reduced and only two core areas remain important. These suggest that the EPRE waters outside Hong Kong, particularly the reclaimed land around Macau and eastern Qi’ao Island, could be of secondary importance to humpback dolphins in the EPRE. Comparatively, Hong Kong waters may already be a more favourable option throughout the EPRE. While this may indicate the habitat quality is more satisfactory in Hong Kong, given the high level of disturbance and habitat degradation throughout the EPRE, the utilisation pattern observed is also likely a result of a lack of better habitat options.

Disturbance studies based on predation risk theory predict that intense disturbance acts similarly to predation risk and causes shifts in animals’ choice of habitats at the expense of accessing resources or no change in habitat choice if other options are too far or of too poor quality (Frid and Dill 2002; Gill et al. 2001). For example, bottlenose dolphins (*Tursiops truncatus*) were seen moving away from foraging grounds when marine traffic was high (e.g. Allen & Read 2000; Lusseau 2004). In a terrestrial environment, the pygmy marmoset (*Cebuella pygmaea*) changed its habitat preference from lower stratum to upper level in response to tourists and boat presence (de la Torre et al. 2000). Such shift in habitat use may have occurred in the EPRE, and dolphins may remain in the area because of limited habitat choice in the region. Moreover, dolphins could be utilising the area because of social relations with other individuals utilising the same area and/or lack of knowledge on habitat quality across the Estuary (Bejder et al. 2009).

Factors influencing foraging probability in the EPRE outside Hong Kong include distance to shore, year, season and locations. Similar to that of Hong Kong (Chapter 2), foraging occurs at specific coastal areas (i.e. around Sanjiao Island and Neilingding Island) and fluctuates between years without a clear trend. This is similar to Hong Kong (Chapter 2), presumably because dolphins’ choice of habitats is similar and both areas are subjected to stochastic changes between years. Humpback dolphins in the EPRE outside Hong Kong prefer rocky shores. The same preference has been described in Hong Kong (Chapter 2; Hung 2008) and for Indian Ocean humpback dolphins (*Sousa plumbea*) in South Africa (Saayman and Tayler 1973; Karczmarski et al. 2000) and Oman (Balwin et al. 2004) and for Australian humpback dolphins (*Sousa sahulensis*) in Queensland (Parra and Cagnazzi 2016). Foraging decreases during wet season outside Hong Kong and such seasonal change in foraging probability was only detected outside Hong Kong. This appears to be consistent with the seasonal shift in distribution in the EPRE. During wet season, distribution shift towards Hong Kong (Chen et al. 2010) and demographic analyses suggested that large number of dolphins enter Hong Kong in this period (Chan and Karczmaski 2017). This corresponds to a shift in resources distribution as the Pearl River discharge increases during wet season and, as such, foraging outside Hong Kong decreases. Depth is not a key determinant of foraging outside Hong Kong, which is the same as in Hong Kong (Chapter 2), implying that foraging probability is unaffected as long as the area is within the 30 m depth preference limit of humpback dolphins (Jefferson and Smith 2016). Tidal influence on foraging probability is not prominent, which is also the same as in Hong Kong (Chapter 2). As mentioned in Chapter 2, this could suggest that tidal effects may have been diluted because of the distance from the river mouth (Lin et al. 2013) or different methods or spatial scale shall be used (e.g. Parsons 1998; Fury and Harrison 2011; Lin et al. 2013). Follow-up analyses may consider investigating the tidal impacts on dolphins' behaviours at specific foraging grounds.

Unlike in Hong Kong (Chapter 2), foraging probability does not increase with group size and appears to be unaffected by group size. This suggests that large foraging groups may not be forming as readily as in Hong Kong. This may relate to the sizes of the habitats, as larger habitats may have higher prey abundance and attract more dolphins. The area utilisation distribution in the EPRE appears to support this notion. The sizes of core foraging areas in mainland China are found to be smaller than those in Hong Kong.

Based on the results that coastal rocky areas are favourable foraging grounds of humpback dolphins in Hong Kong and the EPRE, northern Niutou Island, which is situated at the south-eastern corner of the study area but not included in the analyses, is potentially an important area. The area had been occasionally surveyed and sightings had been recorded, but the area was excluded from analysis due to very low survey effort. At the same time, it is noted that the island has been developed to a certain extent. It has been developed to serve for quarrying and a large precast concrete yard has been built (Wai Kee Holding Ltd. 2015). Ships are expected to frequent around the area to transport concrete products. The limited undisturbed shorelines and close proximity to heavy marine traffic (e.g. Rongshutou channel) could be unfavourable to humpback dolphins. More surveys are, therefore, recommended to verify if the area should be considered as a core area or not.

5.4.3 Conservation implication

Overlaying the area use pattern of dolphins, current MPA locations and locations for development projects in the EPRE bring out two immediate conservation concerns in this region, which may have serious implications for the survival of the population if not addressed appropriately. One is the complete lack of coverage of the existing MPAs on these biologically critical habitats. This is not surprising as the design of the PRE Chinese White Dolphin National Nature Reserve in mainland waters was without consideration on the habitat choice of the target species, the dolphins. It is apparent that ignorance about animal behaviour could greatly reduce the effectiveness of the protected area in achieving its conservation goals (Beissinger 1997; Shumway 1999; Caro 2007). This case could serve as an example of a lack of incorporation of animals’ habitat preference into MPA design, and the consequence is a failure of the protected area to provide the most needed protection for its target species. As a result, tightening enforcement of the MPA would have limited effect, as the fundamental cause of failure is poor MPA design. A revision on the MPA boundary is critically needed if the MPA is to be used to truly protect the humpback dolphins.

Another concern is the spatial overlap of one of the critical areas with the current development projects in the southern EPRE. The Zhuhai Guishan Offshore Wind

Farm has been approved to be built around Sanjiao Island in 2016 and plans to be in operation in 2017. This project fully coincides with the core area around Sanjiao Island. It was proposed initially in 2013 to build 66 3MW wind turbines (SIDRI 2013) and has been reduced to 37 turbines in 2015 with 3 6MW wind turbines and 34 3MW wind turbines (SIDRI 2015). Studies on the impacts of offshore wind farms on cetaceans found that the noise produced by piling and associated activities during the construction phase has severe impact directly (Madsen et al. 2006), including potential hearing impairment at close range (Madsen et al. 2006) and displacement of animals (Carstensen et al. 2006; Brandt et al. 2011; Dahne et al. 2013). As for long-term impacts on cetaceans, opinions are divided. Slow recovery of porpoises has been detected throughout the nine years after construction (Teilmann & Carstensen 2012). On the other hand, an increase in porpoise occurrences at wind farm area compared to pre-construction period has been recorded (Scheidat et al. 2011), which could be due to an increase of fish in wind farms and/or exclusion of most marine traffic (Scheidat et al. 2011). Such contrast in observation at different locations indicates that the long-term impacts could be site-specific. Moreover, it has been speculated that wind turbines act similarly to artificial reefs (Inger et al. 2009) and local increase in fish abundance around artificial reefs could be due to attraction to the site rather than an actual net increase in abundance (Bohnsack 1989). This questions the ecological benefits of offshore wind farms to marine species, and it remains unresolved due to limited research.

At Sanjiao Island, serious negative impacts during the construction phase are expected as wind turbines are being built at one of the two large core foraging grounds in the EPRE, causing a loss of a biologically important site and displacement of dolphins to neighbouring core areas. As for long-term impacts, there is no indication of whether a net increase in fish would occur or not. Any reduction in boats is unlikely to bring significant benefits, as the area prior to construction is relatively undisturbed and mainly visited by artisanal fishing boats. On the other hand, the potential negative long-term impacts could be severe as they include degradation or loss of a foraging ground and reduction of ecological value of EPRE. Given the severity of negative impacts during its construction phase and potentially in the longer term, the construction of a wind farm at

Sanjiao Island should not have taken place. This also demonstrates that if animal behaviour, in this case the spatio-behaviour pattern, is not incorporated in MPA design, critical habitats may become vulnerable to development.

5.5 Conclusion

This study is the first in the region that investigates the population-wide area utilisation pattern of humpback dolphins in the whole EPRE. It directly indicates the locations of the core habitats in the EPRE and suggests that Hong Kong waters are of considerable importance to the dolphins in the context of their PRE-wide range. A complete mismatch between dolphins' utilisation distribution and MPA design in mainland waters was identified and may serve as an example of a failure to incorporate scientific knowledge into conservation management. The serious lack of protection of biologically important areas in EPRE is of immediate concern, particularly as one of the identified core areas in mainland overlaps with the current wind farm construction.

Chapter 6 General discussion and conclusions

In the face of multiple threats, the Indo-Pacific humpback dolphin (*Sousa chinensis*) in the PRE faces many conservation challenges. This study aimed to advance the understanding on the area utilisation pattern and the social dynamics of this species in Hong Kong and the eastern section of PRE and provide the information that may likely prove fundamental to future informed conservation decisions.

6.1 Area utilisation pattern of humpback dolphins in the EPRE

To investigate the utilisation distribution of humpback dolphins in the EPRE, boat-based behaviour observation studies were conducted from 2011-2014 in Hong Kong (Chapter 2) and from 2011-2015 throughout the EPRE (Chapter 5). Spatial modelling showed that dolphins in the region are highly selective in terms of their area utilisation. Core areas were clustered around southwest Lantau Island and northern Lung Kwu Chau in Hong Kong. Outside Hong Kong, core areas were distributed around western Neilingding Island, Sanjiao Island, and its surrounding islands, eastern Qi'ao Island and southern Macau. Foraging was the most recorded behaviour and appeared to be the key determinant of the dolphins' overall distribution pattern. There is a fine-scale structure that separates behavioural core areas and ranges. All the identified core areas function as core foraging grounds and are interconnected by travelling ranges, which extend further than all other behaviours. Socialising and resting were infrequently observed, and socialising was seen more often within core foraging areas.

In general, humpback dolphins in the EPRE prefer natural, undisturbed, rocky shores. This is further supported by the mixed effect models, which indicated that distance to shore, specific locations, and year were important variables in affecting foraging probability. This suggests that foraging occurs around specific coastal areas, and their intensity may fluctuate between years. Depth is not a particularly important factor that affects foraging in the EPRE as the depth throughout the region is well within the 30 m depth preference of humpback dolphins. Outside Hong Kong, foraging probability reduces during wet season, apparently because of shift in resources towards Hong Kong during the peak discharge period of the Pearl River. In Hong Kong, foraging probability is associated with group size, and large foraging groups are formed even in the absence of fishing vessels.

This is the first study to investigate the area utilisation pattern of the whole EPRE and puts the Hong Kong waters into perspective. Spatial modelling indicated that core areas in Hong Kong are comparatively larger than those in mainland China waters. Core areas that are of primary importance in the EPRE are around southwest Lantau Island and Lung Kwu Chau in Hong Kong and western Neilingding Island and Sanjiao Island in mainland China. The core areas around eastern Qi’ao Island and southern Macau appear to be of secondary usage.

6.2 Social dynamics of humpback dolphins in Hong Kong

To study the social structure of the humpback dolphins, boat-based photo-identification surveys were conducted in Hong Kong from 2010 to 2014 (Chapter 3). Humpback dolphins in Hong Kong live in a fission-fusion society, in which associations between individuals are generally weak with mainly casual interactions.

The dolphins in Hong Kong exhibit social and spatial sub-structure within a highly interconnected society. Cluster analyses identified five social clusters, and the majority of dolphins belong to one of the three clusters. Temporal association patterns among social clusters appear to be similar and resemble the general highly dynamic pattern. While there is substantial overlap in range use among social clusters, core areas of the major social clusters are spatially segregated and collectively span from Lung Kwu Chau to southern Lantau Island. These findings revise the socio-spatial pattern proposed previously (Dungan et al. 2012), which suggested that there are two discrete communities inhabiting northern and southern Lantau waters, and instead this current study indicates multiple closely interacting clusters that have discrete core areas but overlapping ranges.

Hong Kong waters could be broadly divided into northern and southern sections based on the distribution of core areas (Chapter 2). Movement models indicated dolphins frequently move between northern and southern Hong Kong waters (Chapter 3). At the same time, some dolphins have comparatively restricted ranges and use only one of the sections.

6.3 Social dynamics of humpback dolphins under anthropogenic impacts in Hong Kong

To assess the impacts of the construction of HKZMB, associations and area utilisation patterns between social clusters were compared across the periods before and during the construction (Chapter 4). During the construction of the HKZMB in Hong Kong, utilisation patterns shifted towards the south, meaning further away from the construction site. The social clusters have restructured, and the responses differed between social clusters; those that were closer to the construction site underwent fission: one of the social clusters split more substantially and shifted its core areas more notably than the other. Social clusters that mainly utilised areas further away from the construction fused into one cluster that occupied southern Lantau Island. Sighting probability indicated that dolphins moved from north to south more decisively during the construction.

To evaluate the impacts of trawling, associations between trawler-associating and non-trawler-associating dolphins were compared before and after the trawl ban (Chapter 4). After the trawl ban, trawler-associating dolphins changed their residency in Hong Kong from a highly fluctuating pattern to a more stable emigration and reimmigration pattern, and associations between trawler-associating and non-trawler-associating dolphins increased.

6.4 Underlying factors that drive the socio-spatial pattern of humpback dolphins in Hong Kong and the EPRE

Resource distribution appears to be relatively predictable in estuarine habitats. In the EPRE, foraging grounds are clustered around rocky shores (Hung 2008; Chapter 2; Chapter 5). At the same time, fluctuation in river outflow and anthropogenic disturbances create uncertainty in the resource abundance. With no predation risk in the PRE, strong social bonds and large groups for evading and defending predators are not necessary and groupings and space use patterns are primarily regulated by resources distribution and their relative abundance. The high variability in resources in the PRE are likely the main causes for fluid associations and changing clusters among humpback dolphins in Hong Kong (Chapter 3) and can be further amplified by anthropogenic environmental change and disturbances (Chapter 4).

Humpback dolphins in Hong Kong form multiple closely interacting social clusters that have different core areas but overlapping ranges. Such divisions may be driven by individual fine-scale differences in the pattern of area use and ranging, as observed in bottlenose dolphins *Tursiops* spp. (e.g. Lusseau et al. 2006; Wiszniewski et al. 2009; Louis et al. 2015). In Hong Kong, differences in individual area utilisation patterns may relate to habitat preferences (Weiss 2006; Torres et al. 2009; Tsai and Mann 2013), ability to respond to environmental changes (Tuomainen and Candolin 2011), social preferences, and perhaps individual knowledge of habitat quality across the whole region (Bejder et al. 2009).

Large foraging groups were seen occasionally, likely related to the presence of shoaling fishes, which account a high proportion of the humpback dolphins' diet (Barros et al. 2004). The formation of large foraging groups may also facilitate social interactions and mating (Würsig 1986). In the EPRE, socialising activities appear to be found within foraging grounds (Chapter 2; Chapter 5), suggesting that humpback dolphins take advantage of the large groups at foraging areas for socialising with other individuals. Other than resource distribution and abundance, individual behavioural differences may also affect association patterns. Increased associations between trawler-associating dolphins and non-trawler-associating dolphins after the trawl ban in Hong Kong indicates that differences in foraging strategies could promote social differentiation between individuals (Chapter 4).

Although the habitat choice of the dolphins in EPRE and their general association pattern resembles that known for other humpback dolphin population, the associations between individuals appear weaker. This most likely relates to population size and openness of the area. All populations of Indo-Pacific humpback dolphins with known association patterns are smaller than the PRE population and their habitats are less diverse than that in Hong Kong (Chang 2011;

Xu et al. 2012; Dungan et al. 2015). With less individuals living in a more confined environment, the probability of encountering the same individuals may increase, and thus animals may tend to form stronger social bonds and a more connected network.

6.5 Conservation implications

While the fission-fusion social system and dynamic community structure appear to be a coping strategy for the changing environment, the humpback dolphin is a coastal species that depends on highly restricted coastal habitats; thus, they are particularly vulnerable to coastal development.

This study found that there is only a limited number of core areas in the EPRE, and the western and southern Lantau waters in Hong Kong are most likely the largest remaining core habitat in the region (Chapter 5). Core foraging areas are located off the coast of western to southern Lantau Island (Chapter 2; Chapter 5), and are frequented by several social clusters. Overall, a larger proportion of dolphins prefer western and southern Lantau waters compared to the northern waters in Hong Kong (Chapter 3). In addition, the construction of the HKZMB has led to a shift in utilisation towards the south (Chapter 4), and, in turn, this further increases the ecological importance of western and southern Lantau waters to humpback dolphins in the EPRE.

At the same time, importance of other core areas should not be underrated as individuals and social clusters display spatial preferences (Chapter 3; Chapter 4). For instance, there are individuals and social clusters that prefer northern Hong Kong waters more than the southern section. In other words, each core area is unique and utilised more by certain individuals, and thus, all core areas must be strictly protected.

Despite that very few habitats remain in the EPRE and all core areas are segregated, none of them are isolated (Chapter 2; Chapter 5), and a large proportion of dolphins move between northern and southern core areas in Hong Kong (Chapter 3). Furthermore, the social structure is highly fluid and all clusters are interconnected. As such, conservation effort should be dedicated to maintaining the connectivity between habitats. These findings highlight the need of preserving connectivity between all the core areas.

Humpback dolphins in the EPRE suffer from diminishing core habitats. The construction of the HKZMB in Hong Kong has led to a diminishing use of waters near Lung Kwu Chau and most of the northern Hong Kong waters (Hung 2016; Chapter 4). Construction of a wind farm within one of the two main core areas in mainland China waters has commenced in 2016 (Chapter 5). The exact impacts on dolphins are yet to be documented, but the construction impacts of the HKZMB provides warning insights onto dolphins' response to habitat loss in this region (Chapter 4), and shifts in area utilisation to the remaining few and limited core habitats is to be expected. Such high rate of habitat loss is likely to accelerate the population decline in the PRE (Karczmarski et al. 2017). The decline of the Yangtze finless porpoise population in response to rapid habitat loss (Huang et al. 2012b) should be taken as an example and warning sign of the challenges to the survival of the humpback dolphins in the PRE.

This study revealed that the MPA coverage of behaviourally important areas in Hong Kong and the EPRE is seriously insufficient (Chapter 2; Chapter 5). Although the MPA in mainland China is the largest protected area dedicated to humpback dolphins' protection in the PRE, its complete lack of coverage of core habitats represents a striking case of poor MPA design (Chapter 5). Such inadequacy has left critical habitats vulnerable to anthropogenic disturbances and development. A complete revision on the MPAs design in the EPRE is much needed.

Based on spatio-behavioural dynamics and distribution of humpback dolphins, this study recommends adaptive management and establishment of a large MPA that provides strict protection to the remaining core areas and limits disturbance to the travelling ranges. A hierarchical two- tier framework of marine protected area designation in Hong Kong western waters is proposed (Chapter 2; Fig. 2.5).

6.6 Recommendations for future studies

Prey distribution and abundance are considered to be the prime factors in driving the fission-fusion social system and area utilisation patterns of humpback dolphins in Hong Kong and the PRE. However, the actual prey availability in the region is unknown. To better understand the prey-dolphin distribution patterns, acoustic surveys of sonically active fish that humpback dolphins prey upon shall be conducted. In addition, stable isotopes analyses using samples taken from stranded dolphins could indicate whether there is any resource partitioning between individuals, and future studies may follow up on whether resource partitioning contributes to the social structure described in Chapter 3.

Associations between individuals are characterised by short-term affiliations (Chapter 3), but it remains uncertain whether and how factors such as age, sex, or kinship affect the social structure of humpback dolphins in the PRE, as they are known to do elsewhere. Moreover, these factors may also influence dispersal and ranging patterns and potentially contribute to the high variability in site fidelity in Hong Kong (Chapter 3). The knowledge of how these factors affect associations, ranging and the range use of humpback dolphins is limited (see Karczmarski 1999; Parra 2005; Chang 2011). Long-term photo-identification on individuals may help to construct a database of individuals' age and sex. Taking biopsy samples from live dolphins could obtain genetic and sex information. Both of these methods are highly recommended and should be applied to understand the influence of age, sex, and kinship on associations and range use of humpback dolphins in the PRE.

This study focused only on the day-light pattern of area utilisation. It remains unknown whether the distribution of the core areas are the same at night. It has been found that bottlenose dolphin activities in the Mediterranean Sea increased at night, and this appeared to be due to reduced vessel traffic (La Manna et al. 2014). Similar changes may occur in the PRE. A recent passive acoustic monitoring (PAM) study conducted in northern Hong Kong waters suggested that dolphin activities increase at night; however, the author has also warned that it could be due to sampling bias (Würsig et al. 2016). To investigate whether the area use pattern changes at night, deployment of passive acoustic monitoring (PAM) devices at different locations would be required and is much recommended.

The study area of this project was confined to Hong Kong and the eastern part of the PRE. Preliminary analyses suggested that there are more social units outside Hong Kong in the EPRE (C.K.M. Or unpublished data) but whether and to what extent these units are interconnected with other units outside the EPRE remains unknown. If discrete communities are present, a major revision on the current conservation focus and management measures would be needed. Given the importance of resolving the question of whether there are any discrete units in the PRE, expanding the study area and surveying different regions within the same study period, and expanding the scope of study to population genetics would be truly vital to better understanding of the conservation ecology of humpback dolphins in the PRE. Such work would be logistically and financially challenging, but is much needed and much recommended.

6.7 Closing remarks

Indo-Pacific humpback dolphins (*Sousa chinensis*) live in a fission-fusion society as an adaptive response to the changing environment. However, their high degree of selectivity for natural, undisturbed, rocky shores confines their core habitats to only a few locations. To ensure persistence of the population, conservation priority must be given to protecting the integrity of the remaining core habitats and maintaining the connectivity between these important areas, so that the functional socio-behavioural structure of the population can be preserved.

References

AECOM, 2012. Contract No. HY/2010/02 Hong Kong Zhuhai Macao Bridge Hong Kong Boundary Crossing Facilities Reclamation Works Quarterly EM&A Report for March 2012- May 2012. Available at http://www.enpo.com.hk/EMnA_Report/HKBCF_HY201002/Quarterly/201203/pdf/TOC.pdf. (Accessed on 1 November 2016).

Agardy, T., Di Sciara, G.N., Christie, P., 2011. Mind the gap: addressing the shortcomings of marine protected areas through large scale marine spatial planning. Marine Policy 35, 226–232.

Agriculture, Fisheries and Conservation Department (AFCD), 2012. Trawling ban to take effect tomorrow. Available at https://www.afcd.gov.hk/english/publications/publications_press/pr1816.html. (Accessed on 1 November 2016).

Airport Authority, 2014. Hong Kong Expansion of Hong Kong International Airport into a Three-runway System: EIA Report. Available at http://www.epd.gov.hk/eia/register/report/eiareport/eia_2232014/html/Master%20Content%20v1.htm. (Accessed on 1 November 2016).

Allen, M.C., Read, A.J., 2000. Habitat selection of foraging bottlenose dolphins in relation to boat density near Clearwater, Florida. Marine Mammal Science 16, 815–824.

Andrews, K.R., Karczmarski, L., Au, W.W., Rickards, S.H., Vanderlip, C.A., Bowen, B.W., Gordon Grau, E., Toonen, R.J., 2010. Rolling stones and stable homes: social structure, habitat diversity and population genetics of the Hawaiian spinner dolphin (*Stenella longirostris*). Molecular Ecology 19, 732–748.

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

ARUP, 2009a. Hong Kong-Zhuhai-Macao Bridge Hong Kong Boundary Crossing Facilities environmental impact assessment report. Available at http://www.epd.gov.hk/eia/register/report/eiareport/eia_1732009/Contents%20Page%20(PDF).htm. (Accessed on 1 November 2016).

ARUP, 2009b. Hong Kong Section of Hong Kong - Zhuhai - Macao Bridge and Connection with North Lantau Highway-Hong Kong Section of Hong Kong - Zhuhai - Macao Bridge and Connection with North Lantau Highway environmental impact assessment report. Available at http://www.epd.gov.hk/eia/register/report/eiareport/eia_1722009/Contents%20Page%20(PDF).htm. (Accessed on 1 November 2016).

Ashe, E., Noren, D., Williams, R., 2010. Animal behaviour and marine protected areas: incorporating behavioural data into the selection of marine protected areas for an endangered killer whale population. Animal Conservation 13, 196–203.

Baldwin, R. M., Collins, M., Van Waerebeek, K., Minton, G., 2004. The Indo-Pacific humpback dolphin of the Arabian region: A status review. Aquatic Mammal 30, 111–124.

Barrat, A., Barthélemy, M., Pastor-Satorras, R., Vespignani, A., 2004. The architecture of complex weighted networks. Proceedings of the National Academy of Sciences of the United States of America 101, 3747–3752.

Barros, N.B., Jefferson, T.A., Parsons, E., 2004. Feeding habits of Indo-Pacific humpback dolphins (*Sousa chinensis*) stranded in Hong Kong. Aquatic Mammals 30, 179–188.

Bartoń, K., 2014. MuMInL multi-model inference. R package version 1.12.1 Available at http://cran.mtu.edu/web/packages/MuMIn/MuMIn.pdf. (Accessed on 1 November 2016).

Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. *lme4: Linear mixed-effects models using Eigen and S4.* R package version 1.1-8. Available at http://CRAN.R-project.org/package=lme4. (Accessed on 1 November 2016)

Beale, C.M., Monaghan, P., 2004. Behavioural responses to human disturbance: a matter of choice? Animal Behaviour 68, 1065–1069.

Beissinger, S.R., 1997. Integrating behavior into conservation biology: potentials and limitations, in: Clemmons, J.R., Buchholz, R. (Eds.), Behavioral approaches to conservation in the wild. Cambridge University Press, Cambridge, United Kingdom, pp. 23–47.

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

Bejder, L., Samuels, A., Whitehead, H., Finn, H., Allen, S., 2009. Impact assessment research: use and misuse of habituation, sensitisation and tolerance in describing wildlife responses to anthropogenic stimuli. Marine Ecology Progress Series 395, 177–185.

Bejder, L., Samuels, A.M.Y., Whitehead, H.A.L., Gales, N., Mann, J., Connor, R., Heithaus, M., Watson-Capps, J., Flaherty, C., Kruetzen, M., 2006. Decline in relative abundance of bottlenose dolphins exposed to long-term disturbance. Conservation Biology 20, 1791–1798.

Best, E.C., Dwyer, R.G., Seddon, J.M., Goldizen, A.W., 2014. Associations are more strongly correlated with space use than kinship in female eastern grey kangaroos. Animal Behaviour 89, 1–10.

Blundell, G. M., Maier, J. A. K., Debevec, E. M., 2001. Linear home ranges: effects of smoothing, sample size, and autocorrelation on kernel estimates. Ecological Monographs 71, 469–489.

BMT Asia Pacific, 2013. Contract No. HY/2011/03 Hong Kong-Zhuhai-Macao Bridge Hong Kong Link Road Section between Scenic Hill and Hong Kong Boundary Crossing Facilities Quarterly EM&A Report No.1 (October 2012 to November 2012) Available at http://www.enpo.com.hk/EMnA_Report/HKLR_HY201103/Quarterly/201210/pdf/toc.pdf. (Accessed on 1 November 2016).

Bohnsack, J.A., 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? Bulletin of Marine Science 44, 631–645.

Booth, G.D., Niccolucci, M.J., Schuster, E.G., 1994. Identifying proxy sets in multiple linear regression: an aid to better coefficient interpretation. Research paper INT-470. United States Department of Agriculture, Forest Service, Ogden.

Borgatti, S.P., 2002. NetDraw Software for Network Visualization. Analytic Technologies: Lexington, KY.

Boyce, M.S., Vernier, P.R., Nielsen, S.E., Schmiegelow, F.K., 2002. Evaluating resource selection functions. Ecological modelling 157, 281–300.

Brandt, M.J., Diederichs, A., Betke, K., Nehls, G., 2011. Responses of harbour porpoises to pile driving at the Horns Rev II offshore wind farm in the Danish North Sea. Marine Ecology Progress Series 421, 205–216.

Braulik, G.T., Findlay, K., Cerchio, S., Baldwin, R., 2015. Assessment of the Conservation Status of the Indian Ocean Humpback Dolphin (*Sousa plumbea*) Using the IUCN Red List Criteria. Advances in Marine Biology 72, 119–141.

Bridge, P. D., 1993. Classification in: Fry, J. C. (Eds.) Biological data analysis. Oxford University Press, Oxford.

Burkhart, S.M., Slooten, E., 2003. Population viability analysis for Hector's dolphin (*Cephalorhynchus hectori*): a stochastic population model for local populations. New Zealand Journal of Marine and Freshwater Research 37, 553–566.

Burnham, K. P., Anderson, D. R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York.

Burnham, K.P., Anderson, D.R., 2004. Multimodel inference understanding AIC and BIC in model selection. Sociological methods & research 33, 261–304.

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65, 23–35.

Cagnazzi, D.D.B., Harrison, P.L., Ross, G.J.B., Lynch, P., 2009. Abundance and site fidelity of Indo-Pacific humpback dolphins in the Great Sandy Strait, Queensland, Australia. Marine Mammal Science 27, 255–281.

Cairns, S. J., Schwager, S. J., 1987. A comparison of association indexes. Animal Behaviour 35, 1454–1469.

Calenge, C., 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. Ecological modelling 197, 516–519.

Cañadas, A., Sagarminaga, R., De Stephanis, R., Urquiola, E., Hammond, P., 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. Aquatic Conservation: Marine and Freshwater Ecosystems 15, 495–521.

Cantor, M., Whitehead , H., 2013. The interplay between social networks and culture: theoretically and among whales and dolphins. Philosophical Transactions of the Royal Society B: Biological Science 368, 1–10.

Caro, T., 2007. Behavior and conservation: a bridge too far? Trends in Ecology and Evolution 22, 394–400.

Carr, M.H., 2000. Marine protected areas: challenges and opportunities for understanding and conserving coastal marine ecosystems. Environmental Conservation 27, 106–109.

Carr, M.H., Neigel, J.E., Estes, J.A., Andelman, S., Warner, R.R., Largier, J.L., 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. Ecological Applications, S90–S107.

Carstensen, J., Henriksen, O.D., Teilmann, J., 2006. Impacts of offshore wind farm construction on harbour porpoises: acoustic monitoring of echolocation activity using porpoise detectors (T-PODs). Marine Ecology Progress Series 321, 295–308.

CEL, 2014. Comments on the environmental impact assessment (EIA) report for the "Expansion of Hong Kong International Airport into a Three-Runway System" (EIA-223/2014): Comments on the findings pertinent to Chinese White Dolphins. Cetacean Ecology Lab, The Swire Institute of Marine Science, The University of Hong Kong. Available at http://media.wix.com/ugd/f0657f_eec9361db3de41bc89f8cdd0a3d96634.pdf. (Accessed on 1 November 2016).

Chan, S.C.Y., Karczmarski, L., 2017. Indo-Pacific humpback dolphins (*Sousa chinensis*) in Hong Kong: Modelling demographic parameters with mark-recapture techniques. PLoS ONE 12(3): e0174029. https://doi.org/10.1371/journal.pone.0174029.

Chan, S.C.Y., Karczmarski, L., 2015. Tough life of urban dolphins: skin disorders and traumatic mutilations of Indo-Pacific humpback dolphins *Sousa chinensis* in Hong Kong. In: Abstracts, International Conference on Biodiversity, Ecology and Conservation of Marine Ecosystems 2015 (BECoME 2015), Hong Kong, p. 252. Available at http://www.biosch.hku.hk/become/files/conference_booklet_all_11June.pdf. (Accessed on 1 November 2016).

Chang, W.-L., 2011. Social structure and reproductive parameters of Indo-pacific humpback dolphins (*Sousa chinensis*) off the west coast of Taiwan. Master thesis, National Taiwan University.

Chang, W.-L., Karczmarski, L., Huang, S.-L., Gailey, G., Chou, L.-S., 2016. Reproductive parameters of the Taiwanese humpback dolphin (*Sousa chinensis taiwanensis*). Regional Studies in Marine Science 8, 459–465.

Chen, B., Zheng, D., Yang, G., Xu, X., Zhou, K., 2009. Distribution and conservation of the Indo-Pacific humpback dolphin in China. Integrative Zoology 4, 240–247.

Chen, B., Zheng, D., Zhai, F., Xu, X., Sun, P., Wang, Q., Yang, G., 2008. Abundance, distribution and conservation of Chinese white dolphins (*Sousa chinensis*) in Xiamen, China. Mammalian Biology 73, 156–164.

Chen, T., Hung, S.K., Qiu, Y., Jia, X., Jefferson, T.A., 2010. Distribution, abundance, and individual movements of Indo-Pacific humpback dolphins (*Sousa chinensis*) in the Pearl River Estuary, China. Mammalia 74, 117–125.

Chen, T., Qiu, Y., Jia, X., Hung, S.K., Liu, W., 2011. Distribution and group dynamics of Indo-Pacific humpback dolphins (*Sousa chinensis*) in the western Pearl River Estuary, China. Mammalian Biology 76, 93–96.

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

Cinotech Consultants Limited (Cinotech), 2013. Contract HY/2011/09 Hong Kong-Zhuhai-Macao Bridge Hong Kong Link Road-Section between HKSAR Boundary and Scenic Hill Quarterly EM&A Report February to May 2013 Available at http://www.enpo.com.hk/EMnA_Report/HKLR_HY201109/Quarterly/201302/pdf/TOC.pdf. (Accessed on 1 November 2016).

Civil Engineering and Development Department (CEDD), 2016. Tung Chung New Town. Available at http://www.cedd.gov.hk/eng/achievements/regional/regi_tungchung.html. (Accessed on 1 November 2016).

Collins, T., 2015. Re-assessment of the Conservation Status of the Atlantic Humpback Dolphin, *Sousa teuszii* (Kükenthal, 1892), Using the IUCN Red List Criteria. Advances in Marine Biology 72, 47–77.

Connor, R. C., Wells, R. S., Mann, J., Read, A.J., 2000. The bottlenose dolphin: Social relationships in a fission–fusion society, in: Mann, J., Conner, R. C., Tyack, P. L., Whitehead, H. (Eds.), Cetacean Societies: Field studies of dolphins and whales. University of Chicago Press, Chicago, pp. 91–126.

Constantine, R., Brunton, D.H., Dennis, T., 2004. Dolphin-watching tour boats change bottlenose dolphin (*Tursiops truncatus*) behaviour. Biological Conservation 117, 299–307.

Corkeron, P.J., 1990. Aspects of the behavioral ecology of inshore dolphins *Tursiops truncatus* and *Sousa chinensis* in Moreton Bay, Australia, in: Leatherwood, S., Reeves, R.R. (Eds.) The bottlenose dolphin. Academic Press, United Kingdom, pp. 285–293.

Corner, L.A.L., Pfeiffer, D.U., Morris, R.S., 2003. Social-network analysis of *Mycobacterium bovis* transmission among captive brushtail possums (*Trichosurus vulpecula*). Preventive Veterinary Medicine 59,147–167.

Cross, P.C., Lloyd-Smith, J.O., Bowers, J.A., Hay, C.T., Hofmeyr, M., Getz, W.M., 2004. Integrating association data and disease dynamics in a social ungulate: bovine tuberculosis in African buffalo in the Kruger National Park. Annales Zoologici Fennici 41, 879–892.

Currey, R.J., Dawson, S.M., Slooten, E., 2009. An approach for regional threat assessment under IUCN Red List criteria that is robust to uncertainty: The Fiordland bottlenose dolphins are critically endangered. Biological Conservation 142, 1570–1579.

Dahne, M., Gilles, A., Lucke, K., Peschko, V., Adler, S., Krugel, K., Sundermeyer, J., Siebert, U., 2013. Effects of pile-driving on harbour porpoises (*Phocoena phocoena*) at the first offshore wind farm in Germany. Environmental Research Letters 8, 025002.

Dang, V.H., 2014. Marine Protected Areas Network in the South China Sea: Charting a Course for Future Cooperation. Martinus Nijhoff Publishers, Leiden.

Daura-Jorge, F.G., Cantor, M., Ingram, S.N., Lusseau, D. and Simões-Lopes, P.C., 2012. The structure of a bottlenose dolphin society is coupled to a unique foraging cooperation with artisanal fishermen. Biology Letters 8, 702–705.

de la Torre, S., Snowdon, C.T., Bejarano, M., 2000. Effects of human activities on wild pygmy marmosets in Ecuadorian Amazonia. Biological Conservation 94, 153–163.

Degrati, M., Dans, S.L., Pedraza, S.N., Crespo, E.A., Garaffo, G.V., 2008. Diurnal behavior of dusky dolphins, *Lagenorhynchus obscurus*, in golfo Nuevo, Argentina. Journal of Mammalogy 89, 1241-1247.

Dong, L.X., Su, J.L., Li, Y., Xia, X.M., Guan, W.B., 2006. Physical processes and sediment dynamics in the Pearl River, in: Wolanski, E. (Ed.), The Environment in Asia Pacific Harbors. Springer, Dordrecht, pp. 127–137.

Dudley, N., 2008. Guidelines for Applying Protected Area Management Categories. International Union for Conservation of Nature, Gland, Switzerland.

Dungan, S., Hung, S., Wang, J., White, B., 2012. Two social communities in the Pearl River Estuary population of Indo-Pacific humpback dolphins (*Sousa chinensis*). Canadian Journal of Zoology 90, 1031–1043.

Dungan, S.Z., Wang, J.Y., Araújo, C.C., Yang, S.C., White, B.N., 2015. Social structure in a critically endangered Indo-Pacific humpback dolphin (*Sousa chinensis*) population. Aquatic Conservation: Marine and Freshwater Ecosystems. DOI: dx.doi.org/10.1002/aqc.2562.

Edenbrow, M., Darden, S.K., Ramnarine, I.W., Evans, J.P., James, R., Croft, D.P., 2011. Environmental effects on social interaction networks and male reproductive behaviour in guppies, *Poecilia reticulata*. Animal Behaviour 81, 551–558.

Edgar, G.J., Stuart-Smith, R.D., Willis, T.J., Kininmonth, S., Baker, S.C., Banks, S., Barrett, N.S., Becerro, M.A., Bernard, A.T., Berkhout, J., 2014. Global conservation outcomes depend on marine protected areas with five key features. Nature 506, 216–220.

Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40, 677.

Elliser, C.R., Herzing, D.L., 2012. Community structure and cluster definition of Atlantic spotted dolphins, *Stenella frontalis*, in the Bahamas. Marine Mammal Science 28, E486–E502.

Elliser, C.R., Herzing, D.L., 2014. Long-term social structure of a resident community of Atlantic spotted dolphins, *Stenella Frontalis*, in the Bahamas 1991–2002. Marine Mammal Science 30, 308–328.

Environmental Protection Department (EPD) HKSAR, 2015. Marine Water Quality Data. HKSAR Environmental Protection Department. Available at http://epic.epd.gov.hk/EPICRIVER/marine/download (Accessed on: 1 November 2016).

Environmental Resources Management (ERM), 1994. Reclamation and servicing of Tuen Mun Area 38 for special industries: environmental impact assessment study – main report prepared for the Civil Engineering Department, Hong Kong Government.

Environmental Resources Management (ERM), 1998. Fisheries Resources and Fishing Operations in Hong Kong Waters. Agriculture, Fisheries and Conservation Department, Hong Kong SAR.

Environmental Resources Management (ERM), 2000. International Theme Park in Penny's Bay of North Lantau and its Essential Associated Infrastructure environmental impact assessment. Available at http://www.epd.gov.hk/eia/register/report/eiareport/eia_0412000/index.html. (Accessed on 1 November 2016).

Environmental Resources Management (ERM), 2012. Dredging, Management and Capping of Contaminated Sediment Disposal Facility to the South of The Brothers. Available at http://www.sbcmp-monitoring.com.hk/Project%20Profile.html. (Accessed on 1 November 2016).

Environmental Resources Management (ERM), 2014. Contract No. HY/2012/07 Tuen Mun – Chek Lap Kok Link – Southern Connection Viaduct Section First Quarterly Environmental Monitoring & Audit (EM&A) Report. Available at http://www.enpo.com.hk/EMnA_Report/TMCLKL_HY201207/Quarterly/201311/pdf/TOC.pdf. (Accessed on 1 November 2016).

ESRI, 2008. ArcGIS 9.3. ESRI, Redlands.

Farine, D.R., Sheldon, B.C., 2015. Selection for territory acquisition is modulated by social network structure in a wild songbird. Journal of Evolutionary Biology 28, 547–556.

Farine, D.R., Whitehead, H., 2015. Constructing, conducting and interpreting animal social network analysis. Journal of Animal Ecology 84, 1144–1163.

Fertl, D., Leatherwood, S., 1997. Cetacean interactions with trawls: a preliminary review. Journal of Northwest Atlantic Fishery Science 22, 219−248.

Fieberg, J., Börger, L., 2012. Could you please phrase "home range" as a question? Journal of Mammalogy 93, 890–902.

Frère, C. H., Krutzen, M., Mann, J., Connor, R., Bejder, L., Sherwin, W. B., 2010. Home range overlap, matrilineal and biparental kinship drive female associations in bottlenose dolphins. Animal Behaviour 80, 481–486.

Frid, A., Dill, L., 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6, 11–26.

Friday, N., Smith, T.D., Stevick, P.T., Allen, J., 2000. Measurement of photographic quality and individual distinctiveness for the photographic identification of humpback whales, *Megaptera novaeangliae*. Marine Mammal Science 16, 355–374.

Fury, C.A., Harrison, P.L., 2011. Seasonal variation and tidal influences on estuarine use by bottlenose dolphins (*Tursiops aduncus*). Estuarine, Coastal and Shelf Science 93, 389–395.

Gailey, G., Karczmarski, L., 2012. DISCOVERY: Photo-identification data-management system for individually recognizable animals (Manual). The Swire Institute of Marine Science, The University of Hong Kong, Hong Kong. Available at: http://www.biosch.hku.hk/ecology/staffhp/lk/Discovery/

Gajer, P., Kobourov, S. G., 2002. GRIP: Graph Drawing with Intelligent Placement. *Journal of Graph Algorithms and Applications 6,* 203–224.

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

Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J., Wilmers, C.C., 2007. LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. PloS ONE 2, e207.

Getz, W.M., Wilmers, C.C., 2004. A local nearest-neighbor convex-hull construction of home ranges and utilization distributions. Ecography 27, 489–505.

Gill, J.A., Norris, K., Sutherland, W.J., 2001. Why behavioural responses may not reflect the population consequences of human disturbance. Biological Conservation 97, 265–268.

Gormley, A.M., Slooten, E., Dawson, S., Barker, R.J., Rayment, W., du Fresne, S., Bräger, S., 2012. First evidence that marine protected areas can work for marine mammals. Journal of Applied Ecology 49, 474–480.

Gowans, S., Whitehead H, Hooker S.K., 2001. Social organization in northern bottlenose whales, *Hyperoodon ampullatus*: not driven by deep-water foraging? Animal Behaviour 62, 369–377.

Gowans, S., Würsig, B., Karczmarski, L., 2008. The social structure and strategies of delphinids: predictions based on an ecological framework. Advances in Marine Biology 53, 195–294.

Gray, J.S., 1997. Marine biodiversity: patterns, threats and conservation needs. Biodiversity & Conservation 6, 153–175.

Gui, D., Yu, R., He, X., Tu, Q., Chen, L., Wu, Y., 2014. Bioaccumulation and biomagnification of persistent organic pollutants in Indo-Pacific humpback dolphins (*Sousa chinensis*) from the Pearl River Estuary, China. Chemosphere 114, 106–113.

Gui, D., Yu, R., Karczmarski, L., Ding, Y., Zhang, H., Sun, Y., Zhang, M., Wu, Y., 2017. Spatio-temporal trends of heavy metals in Indo-Pacific humpback dolphins (*Sousa chinensis*) from the western Pearl River Estuary, China. Environmental Science & Technology 51, 1848–1858. DOI: 10.1021/acs.est.6b05566

Guissamulo A.T., Cockcroft, V.G., 2004. Ecology and population estimates of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Maputo Bay, Mozambique. Aquatic Mammals 30, 94–102.

Guissamulo, A.T., 2008. Ecological studies of bottlenose and humpback dolphins in Maputo Bay, southern Mozambique. Ph.D. thesis. University of Kwazulu-Natal.

Hamilton, W.D., 1964. The genetical evolution of social behavior: I and II. Journal of Theoretical Biology 7, 1–-52.

Harrison, P.J., Yin, K., Lee, J.H.W., Gan, J., Liu, H., 2008. Physical–biological coupling in the Pearl River Estuary. Continental Shelf Research 28, 1405–1415.

Hartel, E.F., Constantine, R., Torres, L.G., 2015. Changes in habitat use patterns by bottlenose dolphins over a 10-year period render static management boundaries ineffective. Aquatic Conservation: Marine and Freshwater Ecosystems 25, 701–711.

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

Hilborn, R., 1990. Determination of fish movement patterns from tag recoveries using maximum likelihood estimators. Canadian Journal of Fisheries and Aquatic Sciences 47, 635–643.

Hinde, R.A., 1976. Interactions, relationships and social structure. Man 11:1-17.

HKSAR Government, 2010. A Ban on trawling activities in Hong Kong waters. (ed.193 Bureau, FaH). HKSAR Legislative Council. Available at http://www.fhb.gov.hk/download/press_and_publications/otherinfo/101013_f_hkwaters/e_hk_waters.pdf. (Accessed on 1 November 2016).

Hoelzel, A.R., Hey, J., Dahlheim, M.E., Nicholson, C., Burkanov, V., Black, N., 2007. Evolution of population structure in a highly social top predator, the killer whale. Molecular Biology and Evolution 24, 1407–1415.

Hoffmann, C.C., 1995. The feasibility of the proposed sanctuary for the Chinese white dolphin *Sousa chinensis*, at Lung Kwu Chau and Sha Chau, Hong Kong: A report for the World Wide Fund for Nature Hong Kong. The Swire Institute of Marine Science, the University of Hong Kong, Hong Kong.

Holme, P., Park, S. M., Kim, B. J., Edling, C. R., 2007. Korean university life in a network perspective: dynamics of a large affiliation network. Physica A 373, 821–830.

Hooker, S.K., Cañadas, A., Hyrenbach, K.D., Corrigan, C., Polovina, J.J., Reeves, R.R., 2011. Making protected area networks effective for marine top predators. Endangered Species Research 13, 203–218.

Hooker, S.K., Gerber, L.R., 2004. Marine reserves as a tool for ecosystem-based management: the potential importance of megafauna. Bioscience 54, 27–39.

Hoyt, E., 2011. Marine Protected Areas for Whales. Dolphins and Porpoises: A World Handbook for Cetacean Habitat Conservation and Planning. 2nd Edition, Earthscan, London.

Huang, S.-L., Karczmarski, L., 2014. Indo-Pacific humpback dolphin: A demographic perspective of a threatened species, in: Yamagiwa, J., Karczmarski, L. (Eds.) Primates and cetaceans: Field research and conservation of complex mammalian societies. Springer Science (Primatology Monographs 9), New York – Tokyo, pp 249–272.

Huang, S.-L., Hao, Y., Mei, Z., Turvey, S.T., Wang, D., 2012a. Common pattern of population decline for freshwater cetacean species in deteriorating habitats. Freshwater Biology 57, 1266–1276

Huang, S.-L., Karczmarski, L., Chen, J., Zhou, R., Lin, W., Zhang, H., Li, H., Wu, Y., 2012b. Demography and population trends of the largest population of Indo-Pacific humpback dolphins. Biological Conservation 147, 234–242.

Huang, X., Huang, L., Yue, W., 2003. The characteristics of nutrients and eutrophication in the Pearl River estuary, South China. Marine Pollution Bulletin 47, 30–36.

Hung, S.K., 2008. Habitat use of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Hong Kong. Ph.D. Thesis, The University of Hong Kong.

Hung, S.K., 2014. Monitoring of marine mammals in Hong Kong waters (2013-14). Final report (1 April 2013 to 31 March 2014) submitted to the Agriculture, Fisheries and Conservation Department of the Hong Kong SAR Government. Available at http://www.afcd.gov.hk/english/conservation/con_mar/con_mar_chi/con_mar_chi_chi/files/FinalReport2013_14pp1_98.pdf. (Accessed on 1 November 2016).

Hung, S.K., 2016. Monitoring of marine mammals in Hong Kong waters (2015–16). Final report (1 April 2015 to 31 March 2016) submitted to the Agriculture, Fisheries and Conservation Department of the Hong Kong SAR Government. Available at https://www.afcd.gov.hk/english/conservation/con_mar/con_mar_chi/con_mar_chi_chi/files/Final_Report_2015_16.pdf. (Accessed on 1 November 2016).

Hung, S.K., Jefferson, T.A., 2004. Ranging patterns of Indo-Pacific humpback dolphins (*Sousa chinensis*) in the Pearl River estuary, People's Republic of China. Aquatic Mammals 30, 159-174.

Inger, R., Attrill, M., Bearhop, S., Broderick, A., Grecian, W.J., Hodgson, D.J., Mills, C., Sheehan, E., Votier, S.C., Witt, M.J., Godley, B.J., 2009. Marine renewable energy: potential benefits to biodiversity? An urgent call for research. Journal of Applied Ecology 46, 1145–1153.

Janik, V.M., 2014. Cetacean vocal learning and communication. Current opinion in neurobiology 28, 60–65.

Jaramillo-Legorreta, A., Rojas-Bracho, L., Brownell Jr, R.L., Read, A.J., Reeves, R.R., Ralls, K., Taylor, B.L., 2007. Saving the vaquita: immediate action, not more data. Conservation Biology 21, 1653–1655.

Jaroensutasinee, M., Jutapruet, S., Jaroensutasinee, K., 2010. Population size of Indo-Pacific humpback dolphins (*Sousa chinensis*) at Khanom, Thailand. Walailak Journal of Science and Technology (WJST) 7, 115–126.

Jefferson, T.A., 2000. Population biology of the Indo-Pacific hump-backed dolphin in Hong Kong waters. Wildlife Monographs, 1–65.

Jefferson, T.A., 2007. Monitoring of Chinese white dolphins (*Sousa chinensis*) in Hong Kong waters—biopsy sampling and population data analysis: Final report. Report submitted to Agriculture, Fisheries and Conservation Department (AFCD).

Jefferson, T.A., Curry, B.E., 2015. Humpback Dolphins: A Brief Introduction to the Genus *Sousa*. Advances in Marine Biology 72, 1–16.

Jefferson, T.A., Hung, S.K., 2004. A review of the status of the Indo-Pacific humpback dolphin (*Sousa chinensis*) in Chinese waters. Aquatic Mammals 30, 149–158.

Jefferson, T.A., Hung, S.K., Robertson, K.M., Archer, F.I., 2012. Life history of the Indo-Pacific humpback dolphin in the Pearl River Estuary, southern China. Marine Mammal Science 28, 84–104.

Jefferson, T.A., Hung, S.K., Würsig, B., 2009. Protecting small cetaceans from coastal development: Impact assessment and mitigation experience in Hong Kong. Marine Policy 33, 305–311.

Jefferson, T.A., Karczmarski, L., 2001. *Sousa chinensis*. Mammalian Species 665, 1–9.

Jefferson, T.A., Leatherwood, S., 1997. Distribution and abundance of Indo-Pacific humpbacked dolphins (*Sousa chinensis* Osbeck, 1765) in Hong Kong waters. Asian Marine Biology 14, 93-110.

Jefferson, T.A., Rosenbaum, H.C., 2014. Taxonomic revision of the humpback dolphins (*Sousa* spp.), and description of a new species from Australia. Marine Mammal Science 30, 1494–1541.

Jefferson, T.A., Smith, B.D., 2016. Re-assessment of the Conservation Status of the Indo-Pacific Humpback Dolphin (*Sousa chinensis*) Using the IUCN Red List Criteria. Advances in Marine Biology 73, 1–26.

Jones, P.J., 2002. Marine protected area strategies: issues, divergences and the search for middle ground. Reviews in fish biology and fisheries 11, 197–216.

Jutapruet, S., Huang, S.-L., Li, S., Lin, M., Kittiwattanawong, K., Pradit, S., 2015. Population Size and Habitat Characteristics of the Indo-Pacific Humpback Dolphin (*Sousa chinensis*) Off Donsak, Surat Thani, Thailand. Aquatic Mammals 41, 129–142.

Kamada, T., Kawai. S., 1989. An Algorithm for Drawing General Undirected Graphs. Information Processing Letters 31, 7–15.

Kappeler, P. M., Van Schaik, C. P., 2002. Evolution of primate social systems. International journal of primatology 23, 707–740.

Karczmarski, L., 1996. Ecological Studies of Humpback Dolphins *Sousa chinensis* in the Algoa Bay Region, Eastern Cape, South Africa. Ph.D. Thesis, The University of Port Elizabeth.

Karczmarski, L., 1999. Group dynamics of humpback dolphins (*Sousa chinensis*) in the Algoa Bay region, South Africa. Journal of Zoology 249, 283–293.

Karczmarski, L., 2000. Conservation and management of humpback dolphins: the South African perspective. Oryx 34, 207-216.

Karczmarski, L., 2015. Humpback dolphins in Hong Kong and Pearl River Delta: what to do when everything goes wrong…? Available at In: Abstracts, International Conference on Biodiversity, Ecology and Conservation of Marine Ecosystems 2015 (BECoME 2015), Hong Kong. http://www.biosch.hku.hk/become/files/conference_booklet_all_11June.pdf. p. 73.

Karczmarski, L., Cockcroft, V., 1999. Daylight behaviour of humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa. *Mammalian Biology* 64, 19–29.

Karczmarski, L., Cockcroft, V., McLachlan, A., 1999. Group size and seasonal pattern of occurrence of humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa. South African Journal of Marine Science 21, 89–97.

Karczmarski, L., Cockcroft, V., McLachlan, A., Winter, P., 1998. Recommendations for the conservation and management of humpback dolphins *Sousa chinensis* in the Algoa Bay region, South Africa. Koedoe 41, 121–129.

Karczmarski, L., Cockcroft, V.G., Mclachlan, A., 2000a. Habitat use and preferences of Indo-Pacific humpback dolphin *Sousa chinensis* in Algoa Bay, South Africa. Marine Mammal Science 15, 65–79.

Karczmarski, L., Huang, S.-L., Chan, S.C.Y., 2017. Threshold of long-term survival of a coastal delphinid in anthropogenically degraded environment: Indo-Pacific humpback dolphins in Pearl River Delta. Scientific Reports 7: 42900 | DOI: 10.1038/srep42900

Karczmarski, L., Huang, S.-L., Or, C.K.M., Gui, D., Chan, S.C.Y., Lin, W., Porter, L., Wong, W.-H., Zheng, R., Ho, Y.-W., Chui, S.Y.S., Tiongson, A.J.C., Mo, Y., Chang, W.-L., Kwok, J.H.W., Tang, R.W.K., Lee, A.T.L., Yiu, S.-W., Keith, M., Gailey, G., Wu, Y., 2016a. Humpback dolphins in Hong Kong and the Pearl River Delta: Status, threats and conservation challenges. Advances in Marine Biology 73, 26–63.

Karczmarski, L., Huang, S.-L., Wong, W.H., Porter, L., Ho, Y.W., Or, C.K.M., Lin, W., Chan, S.C.Y., Zheng, R., Chui, S.Y.S., Gailey, G., Wu, Y., 2014. The Indo-Pacific humpback dolphin (*Sousa chinensis*): Hong Kong Red List Assessment. WWF Hong Kong and Hong Kong Red List Authority. 22 pp. DOI: 10.13140/RG.2.2.16930.63684

Karczmarski, L., Huang, S-L., Wong, W-H., Chang, W-L., Chan, S.C.Y., Keith, M., 2016b. Distribution of a coastal delphinid under the impact of long-term habitat loss: Indo-Pacific humpback dolphins off Taiwan's west coast. Estuaruaries and Coasts 40, 594–603. DOI: 10.1007/s12237-016-0146-5

Karczmarski, L., Or, C.K.M., 2016. Habitat and areas for the conservation of Chinese White Dolphins in Hong Kong. Report submitted to WWF-Hong Kong. 13pp. DOI: 10.13140/RG.2.2.34756.42889

Karczmarski, L., Thornton, M., Cockcroft, V.G., 2000b. Daylight occurrence of humpback dolphins *Sousa chinensis* in Algoa Bay, South Africa. African Journal of Ecology 38, 86–90.

Karczmarski, L., Würsig, B., Gailey, G., Larson, K.W., Vanderlip, C.A., 2005. Spinner dolphins in a remote Hawaiian atoll: social grouping and population structure. Behavioral Ecology 16, 675–685.

Keith, M., Atkins, S., Johnson, A.E., Karczmarski, L., 2013. Area utilization patterns of humpback dolphins (*Sousa plumbea*) in Richards Bay, KwaZulu-Natal, South Africa. Journal of Ethology 31, 261–274.

Koper, R.P., Karczmarski, L., Preez, D., Plön, S., 2016. Sixteen years later: Occurrence, group size, and habitat use of humpback dolphins (*Sousa plumbea*) in Algoa Bay, South Africa. Marine Mammal Science 32, 490–570.

Krause, J., Ruxton, G.D., 2002. Living in groups. Oxford University Press, Oxford.

Kuczaj, S.A., Yeater, D., Highfill, L., 2012. How selective is social learning in dolphins? International Journal of Comparative Psychology 25, 221–236.

La Manna, G., Manghi, M., Sara, G., 2014. Monitoring the habitat use of common Bottlenose Dolphins (*Tursiops truncatus*) using passive acoustics in a Mediterranean marine protected area. Mediterranean Marine Science 15, 327–337.

Laver, P.N., Kelly, M.J., 2008. A critical review of home range studies. Journal of Wildlife Management 72, 290-298.

Leatherwood, S., 1975. Some observations of feeding behavior of bottle-nosed dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico and (*Tursiops cf. T. gilli*) off southern California, Baja California, and Nayarit, Mexico. Marine Fisheries Review 37, 10–16.

Lin, T.-H., Akamatsu, T., Chou, L.-S., 2013. Tidal influences on the habitat use of Indo-Pacific humpback dolphins in an estuary. Marine biology 160, 1353–1363.

Lin, W., Karczmarski, L., Xia, J., Zhang, X., Yu, X., Wu, Y., 2016. Increased human occupation and agricultural development accelerates the population contraction of an estuarine delphinid. Scientific Reports 6: 35713 | DOI: 10.1038/srep35713

Liu, J., Hills, P., 1997. Environmental planning, biodiversity and the development process: The case of Hong Kong's Chinese white dolphins. Journal of Environmental Management 50, 351–367.

Lotze, H.K., Lenihan, H.S., Bourque, B.J., Bradbury, R.H., Cooke, R.G., Kay, M.C., Kidwell, S.M., Kirby, M.X., Peterson, C.H., Jackson, J.B., 2006. Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312, 1806–1809.

Louis, M., Gally, F., Barbraud C., Beesau, J., Tixier, P., Simon-Bouhet, B., Le Rest, K., Guinet, C., 2015. Social structure and abundance of coastal bottlenose dolphins, *Tursiops truncatus*, in the Normano-Breton Gulf, English Channel. Journal of Mammalogy 96, 481–493.

Lusseau, D., 2003. The emergent properties of a dolphin social network. Proceedings of the Royal Society of London. Series B: Biological Sciences 270, 186–188.

Lusseau, D., 2004. The hidden cost of tourism: detecting long-term effects of tourism using behavioral information. Ecology and Society 9, 2.

Lusseau, D., Bain, D.E., Williams, R., Smith, J.C., 2009. Vessel traffic disrupts the foraging behavior of southern resident killer whales *Orcinus orca.* Endangered Species Research 6, 211–221.

Lusseau, D., Higham, J., 2004. Managing the impacts of dolphin-based tourism through the definition of critical habitats: the case of bottlenose dolphins (*Tursiops* spp.) in Doubtful Sound, New Zealand. Tourism Management 25, 657–667.

Lusseau, D., Newman, M.E.J., 2004. Identifying the role that animals play in their social networks. Proceedings of the Royal Society of London 271, S477–S481.

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

Lusseau, D., Wilson, B., Hammond, P. S., Grellier, K., Durban, J. W., Parsons, K. M., Barton, T. R., Thompson, P. M., 2006. Quantifying the influence of sociality on population structure in bottlenose dolphins. Journal of Animal Ecology 75, 14–24.

Macau International Airport Company Limited, 2012. Airport History. Available at http://www.macau-airport.com/en/about-us/about-mia/airport-history. (Accessed on 1 November 2016).

Madsen, P.T., Wahlberg, M., Tougaard, J., Lucke, K., Tyack, P., 2006. Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs. Marine Ecology Progress Series 309, 279–295.

Manly, B.F.J., 1995. A note on the analysis of species co-occurrences. Ecology 76, 1109–1115.

Mann, J., 2000. Unraveling the dynamics of social life: long-term studies and observational methods, in: Mann, J., Connor, R.C., Tyack, P.L., Whitehead, H. (Eds.) Cetacean Societies: Field studies of dolphins and whales. University of Chicago Press, Chicago, pp. 45–64.

Mann, J., Connor, R., Tyack, P., Whitehead, H., 2000. Cetacean societies: Field studies of whales and dolphins. University of Chicago Press, Chicago.

Mann, J., Stanton, M.A., Patterson, E.M., Bienenstock, E.J., Singh, L.O., 2012. Social networks reveal cultural behaviour in tool-using dolphins. Nature communications 3, 980.

Mao, Q., Shi, P., Yin, K., Gan, J., Qi, Y., 2004. Tides and tidal currents in the Pearl River Estuary. Continental Shelf Research 24, 1797–1808.

Marcotte, D., Hung, S.K., Caquard, S., 2015. Mapping cumulative impacts on Hong Kong's pink dolphin population. Ocean & Coastal Management 109, 51–63.

Miller P. J. O., Biassoni N., Samuels A., Tyack P. L.. 2000. Whale songs lengthen in response to sonar. Nature 405, 903.

Milligan, G. W., Cooper, M. C., 1987. Methodology review: clustering methods. Applied Psychological Measurement 11, 329–354.

Minton, G., Poh, A.N.Z., Peter, C., Porter, L., Kreb, D., 2016. Indo-Pacific Humpback Dolphins in Borneo: A Review of Current Knowledge with Emphasis on Sarawak. Advances in Marine Biology 73, 141–156.

Mitani, J.C., Call, J., Kappeler, P.M., Palombit, R.A., Silk, J.B., 2012. The evolution of primate societies. University of Chicago Press, Chicago.

Möller, L. M., Beheregaray, L. B., Harcourt, R. G., Krutzen, M., 2001. Alliance membership and kinship in wild male bottlenose dolphins (*Tursiops aduncus*) of southeastern Australia. Proceedings of the Royal Society of London, Series B 268, 1941–1947.

Morgan B. J. T., Simpson, M. J. A., Hanby, J. P., Hall-Craggs, J., 1976. Visualizing interaction and sequential data in animal behaviour: theory and application of cluster-analysis methods. Behaviour 56, 1–43.

Morton, B., 1990. The Marine Flora and Fauna of Hong Kong and Southern China II (3 vols). Hong Kong University Press, Hong Kong.

Morton, B., 1998. Hong Kong’s Marine Parks Ordinance and designation of reserve: where next? in: Morton, B. (Ed.) Proceedings of the Third International Marine Biological Workshop: The Marine Biology of the South China Sea. Hong Kong University Press, Hong Kong, pp. 541–561.

Morton, B., 2000. Coastal zone management for marine conservation in Hong Kong: the need for regional cooperation in Southern China, in: Morton, B. (Ed.) Proceedings of the Tenth International Marine Biological Workshop: The Marine Flora and Fauna of Hong Kong and Southern China. Hong Kong University Press, Hong Kong, pp. 3–33.

Newman, M. E. J., 2004. Analysis of weighted networks. Physical Review E 70, 056131.

Newman, M. E. J., 2006. Modularity and community structure in networks. Proceedings of the National Academy of Sciences of the United States of America 103, 8577–8582.

Newsome, S.D., Clementz, M.T., Koch, P.L., 2010. Using stable isotope biogeochemistry to study marine mammal ecology. Marine Mammal Science 26, 509–572.

Ng, S.L., Leung, S., 2003. Behavioral response of Indo-Pacific humpback dolphin (*Sousa chinensis*) to vessel traffic. Marine environmental research 56, 555–567.

Oizumi, K., 2011. The Emergence of the Pearl River Delta Economic Zone: Challenges on the Path to Megaregion Status and Sustainable Growth. Pacific Business and Industries 11, 2–20.

Or, C.K.M., Karczmarski, L., 2015a. What to protect in the seascape of anthropogenic pressure? Area utilization of Indo-Pacific humpback dolphins Sousa chinensis in Hong Kong. In: Abstracts, International Conference on Biodiversity, Ecology and Conservation of Marine Ecosystems 2015 (BECoME 2015), Hong Kong Available at http://www.biosch.hku.hk/become/files/conference_booklet_all_11June.pdf. pp. 198. (Accessed on 1 November 2016).

Or, C.K.M., Karczmarski, L., 2015b. The seascape of the Anthropocene: spatio-behavioural dynamics of Indo-Pacific humpback dolphins (*Sousa chinensis*) in Hong Kong. In: Abstracts, 34th International Ethological Conference, Cairns, pp. 9 Available at http://www.behaviour2015.org/assets/Behaviour-2015/Behaviour-2015ABSTRACTS.pdf. pp. 9. (Accessed on 24 August 2015).

Or, C.K.M., Keith, M., Karczmarski, L., 2013. Where to go in a highly developed area? Utilization distribution of Indo-Pacific humpback dolphins in Pearl River Estuary, Hong Kong, China. In: Abstracts, 20th Biennial Conference on the Biology of Marine Mammals, Dunedin, pp. 162.

Osbeck, P., 1765. Reise nach Ostindien und China. (Translated from the original Swedish by J.G.Georgiand J.C. Koppe) Koppe, Rostock. (in German).

PADS, 1989. Port and Airport Development Strategy 1989. Hong Kong SAR Environmental Protection Department (EPD). Available at http://www.epd.gov.hk/epd/english/environmentinhk/eia_planning/guide_ref/acp2_6.html. (Accessed on 1 November 2016).

Parks S. E., Clark C. W., Tyack P. L.. 2007. Short- and long-term changes in right whale calling behavior: the potential effects of noise on acoustic communication. Journal of the Acoustical Society of America 122, 3725–3731.

Parra, G.J., 2005. 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. Ph.D. Thesis, James Cook University.

Parra, G.J., 2006. Resource partitioning in sympatric delphinids: space use and habitat preferences of Australian snubfin and Indo-Pacific humpback dolphins. Journal of Animal Ecology 75, 862–874.

Parra, G.J., Cagnazzi, D., 2016. Conservation Status of the Australian Humpback Dolphin (*Sousa sahulensis*) Using the IUCN Red List Criteria. Advances in Marine Biology 73, 157–192.

Parra, G.J., Corkeron, P.J., Arnold, P., 2011. Grouping and fission-fusion dynamics in Australian snubfin and Indo-Pacific humpback dolphin. Animal Behaviour 82, 1423–1433.

Parsons, E.C.M., 1997. Hong Kong’s cetaceans: the biology, socioecology and behaviour of *Sousa chinensis* and *Neophocaena phocaenoides*. Ph.D. Thesis, The University of Hong Kong.

Parsons, E.C.M., 1998. The behaviour of Hong Kong's resident cetaceans: the Indo-Pacific hump-backed dolphin and the finless porpoise. Aquatic Mammals 24, 91–110.

Parsons, E.C.M., 2012. The negative impacts of whale-watching. Journal of Marine Biology 2012, 1–9.

Parsons, K.M., Durban, J.W., Claridge, D.E., Balcomb, K.C., Noble, L., Thompson, P.M., 2003. Kinship as a basis for alliance formation between male bottlenose dolphins, *Tursiops truncatus,* in the Bahamas. Animal Behaviour 66, 185–194.

Piwetz, S., Lundquist, D. and Würsig, B., 2015. Chapter Two-Humpback Dolphin (Genus *Sousa*) Behavioural Responses to Human Activities. Advances in marine biology 72, 17–45.

Powell R. A. 2000. Animal home ranges and territories and home range estimators, in: Boitani L., Fuller T. K. (Eds.) Research techniques in animal ecology: controversies and consequences. Columbia University Press, New York, pp. 65–110.

Porter, L.J., 1998. The taxonomy, ecology and conservation of *Sousa chinensis* (Osbeck, 1765) (Cetacea: Delphinidae) in Hong Kong waters. Ph.D. Thesis, The University of Hong Kong.

R Development Core Team, 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051 07-0. Available at http://www.R-project.org. (Assessed on 1 November 2016).

Ramos-Fernández, G., Boyer, D., Gómez, V.P., 2006. A complex social structure with fission–fusion properties can emerge from a simple foraging model. Behavioral ecology and sociobiology 60, 536–549.

Rayment, W., Webster, T., 2009. Observations of Hector's dolphins (*Cephalorhynchus hectori*) associating with inshore trawling at Banks Peninsula, New Zealand. New Zealand Journal of Marine and Freshwater Research 43, 911−916.

Reeves, R.R., Dalebout, M.L., Jefferson, T.A., Karczmarski, L., Laidre, K., O'Corry-Crowe, G., Rojas-Bracho, L., Secchi, E.R., Slooten, E., Smith, B.D., Wang, J.Y., Zhou, K. 2008. *Sousa chinensis*. The IUCN Red List of Threatened Species. Available at http://dx.doi.org/10.2305/IUCN.UK.2008.RLTS.T20424A9197694.en. (A ccessed on 1 November 2016).

Reynolds, T. D., Laundre, J. W., 1990. Time intervals for estimating pronghorn and coyote home ranges and daily movements. The Journal of Wildlife Management 54, 316–322.

Robin, X., Turck, N., Hainard, A., Tiberti, N., Lisacek, F., Sanchez, J.-C., Müller, M., 2011. pROC: an open-source package for R and S+ to analyze and compare ROC curves. BMC bioinformatics 12, 1.

Rodgers, A.R., Carr, A.P., Beyer, H.L., Smith, L., Kie, J.G., 2007. HRT: Home Range Tools for ArcGIS. Version 1.1. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada.

Ross, P.S., Barlow, J., Jefferson, T.A., Hickie, B.E., Lee, T., MacFarquhar, C., Parsons, E.C., Riehl, K.N., Rose, N.A., Slooten, E., 2011. Ten guiding principles for the delineation of priority habitat for endangered small cetaceans. Marine Policy 35, 483–488.

Ross, P.S., Dungan, S.Z., Hung, S.K., Jefferson, T.A., Macfarquhar, C., Perrin, W.F., Riehl, K.N., Slooten, E., Tsai, J., Wang, J.Y., 2010. Averting the baiji syndrome: conserving habitat for critically endangered dolphins in Eastern Taiwan Strait. Aquatic Conservation: Marine and Freshwater Ecosystems 20, 685–694.

Ross, G.J.B., Heinsohn, G.E., Cockcroft, V.G., 1994. Humpback dolphins *Sousa chinensis* (Osbeck, 1765), *Sousa plumbea* (G. Cuvier, 1829) and *Sousa* *teuszii* (Kukenthal, 1892), in: Ridgway, S.H., Harrison, R. (Eds.) Handbook of marine mammals, Vol. 5: The first book of dolphins. Academic Press, San Diego, pp 23–42.

Saayman, G.S., Tayler, C.K., 1979. The socioecology of humpback dolphins (*Sousa* sp.), in: Winn, H.E., Olla, B.L. (Eds.), Behavior of marine animals. Volume 3. Cetaceans. Plenum Press, New York and London, pp. 165–226

Sain, S.R., Baggerly, K.A., Scott, D.W., 1994. Cross-validation of multivariate densities. Journal of the American Statistical Association 89, 807–817.

Scheidat, M., Tougarrd, J., Brasseur, S., Carstensen, J., van Polanen Petel, T., Teilmann, J., Reijnders, P., 2011. Harbour porpoises (*Phocoena phocoena*) and wind farms: a case study in the Dutch North Sea. Environmental Research Letters 6, 025102.

Schoener, T.W., 1981. An empirically based estimate of home range. Theoretical Population Biology 20, 281–325.

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J., Gitzen, R. A., 1999. Effects of sample size on kernel home range estimates. Journal of Wildlife 63, 739–747.

Seaman, D.E., Powell R.A., 1996. An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology 77, 2075–2085.

Shane, S., Wells, R., Wursig, B., 1986. Ecology, behaviour and social organization of the bottlenose dolphin: a review. Marine Mammal Science 2, 34−63.

Shanghai Investigation, Design & Research Institute Company Limited (SIDRI), 2013. Environmental Impact Assessment: Summary.

Shumway, C.A., 1999. A neglected science: applying behavior to aquatic conservation. Environmental Biology of Fishes 55, 183–201.

Signer, J., Balkenhol, N., Ditmer, M., Fieberg, J., 2015. Does estimator choice influence our ability to detect changes in home-range size? Animal Biotelemetry 3, 16.

Sih, A., Hanser, S.F., McHugh, K.A., 2009. Social network theory: new insights and issues for behavioral ecologists. Behavioral Ecology and Sociobiology 63, 975–988.

Silk, J.B., 2007. Social components of fitness in primate groups. Science 317, 1347–1351.

Silk, J.B., Beehner, J.C., Bergman, T.J., Crockford, C., Engh, A.L., Moscovice, L.R., Wittig, R.M., Seyfarth, R.M., Cheney, D.L., 2010. Strong and consistent social bonds enhance the longevity of female baboons. Current Biology 20, 1359–1361.

Silverman, B.W., 1986. Density estimation for statistics and data analysis. Chapman and Hall, Ltd., London.

Simmonds, M.P., Hutchison, J., 1996. The conservation of whales and dolphins: Science and practice. John Wiley and Sons, Chichester.

Sims, P.Q., Hung, S.K., Würsig, B., 2012. High-speed vessel noises in West Hong Kong waters and their contributions relative to Indo-Pacific humpback dolphins (*Sousa chinensis*). Journal of Marine Biology 2012, 1–11.

Slooten, E., 2013. Effectiveness of area-based management in reducing bycatch of the New Zealand dolphin. Endangered Species Research 20, 121–130.

Slooten, E., Dawson, S.M., Whitehead, H., 1993. Associations among photographically identified hectors dolphins. Canadian Journal of Zoology 71, 2311–2318.

Smith, B.D., Mansur, R.M., Strindberg, S., Redfern, J.,Moore, T., 2015. Population demographics, habitat selection, and a spatial and photographic analysis of bycatch risk of Indo-Pacific humpback dolphins *Sousa chinensis* and bottlenose dolphins *Tursiops aduncus* in the northern Bay of Bengal, Bangladesh: International Whaling Commission Scientific Committee Report.

Stanton, M.A., Gibson, Q.A., Mann, J., 2011. When mum’s away: a study of mother and calf ego networks during separations in wild bottlenose dolphins (*Tursiops* sp.). Animal Behaviour 82, 405–412.

Stensland, E., Carlén, I., Särnblad, A., Bignert, A., Berggren, P., 2006. Population size, distribution, and behaviour of Indo-Pacific bottlenose (*Tursiops aduncus*) and humpback (*Sousa chinensis*) dolphins off the south coast of Zanzibar. Marine Mammal Science 22, 667-682.

Storz, J., 1999. Genetic consequences of mammalian social structure. Journal of Mammalogy 80, 553–569.

Sugg, D.W., Chesser, R.K., Dobson, F.S., Hoogland, J.L., 1996. Population genetics meets behavioral ecology. Trends in Ecology & Evolution 11, 338–342.

Swihart, R.K., Slade, N.A., 1985. Testing for independence of observations in animal movements. Ecology 66, 1176–1184.

Teilmann, J., Carstensen, J., 2012. Negative long term effects on harbour porpoises from a large scale offshore wind farm in the Baltic- evidence of slow recovery. Environmental Research Letters 7, 045101.

Titcomb, E.M., O’Corry-Corwe, G., Hartel, E.F., Mazzoil, M.S., 2015. Social communities and spatiotemporal dynamics of association patterns in estuarine bottlenose dolphins. Marine Mammal Science 31, 1314–1337.

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

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

Tsang, E., Milicich, M. 1999. Study on the suitability of Southwest Lantau to be established as marine park or marine reserve. An unpublished report submitted to the Agriculture, Fisheries and Conservation Department of Hong Kong SAR Government, Hong Kong.

Tuomainen, U., Candolin, U., 2011. Behavioural responses to human-induced environmental change. Biological Reviews 86, 640–657.

Turchin, P., 1998. Quantitative analysis of movement. Sinauer Associates, Sunderland, Massachusetts.

Turvey, S.T., Pitman, R.L., Taylor, B.L., Barlow, J., Akamatsu, T., Barrett, L.A., Zhao, X., Reeves, R.R., Stewart, B.S., Wang, K., 2007. First human-caused extinction of a cetacean species? Biology letters 3, 537–540.

Vanderlaan, A.S., Taggart, C.T., 2007. Vessel collisions with whales: the probability of lethal injury based on vessel speed. Marine Mammal Science 23, 144–156.

Van Winkle, W., 1975. Comparison of several probabilistic home-range models. The Journal of wildlife management 39, 118–123.

Wai Kee Holdings Limited. 2015. Quarrying. Available at http://www.waikee.com/eng/bus_quarry.html. (Accessed on 1 June 2016).

Wang, J.Y., Chu Yang, S., Hung, S.K., Jefferson, T.A., 2007. Distribution, abundance and conservation status of the eastern Taiwan Strait population of Indo-Pacific humpback dolphins, *Sousa chinensis*. Mammalia 71, 157–165.

Wang, J.Y., Yang, S.C., Fruet, P.F., Daura-Jorge, F.G., Secchi, E.R., 2012. Mark-recapture analysis of the critically endangered eastern Taiwan Strait population of Indo-Pacific humpback dolphins (*Sousa chinensis*): Implications for conservation. Bulletin of Marine Science 88, 885–902.

Wang, W., 1995. Biology of *Sousa chinensis* in Xiamen Harbor, in: Huang, Z., Leatherwood, S.,Woo, J., Liu,W. (Eds.), Conference on Conservation of Marine Mammals by Fujian, Hong Kong, and Taiwan. Specific Publication of the Journal of Oceanography in Taiwan Strait vol. 4, Xiamen, pp. 21–26. (in Chinese).

Weir, C.R., T. Collins. 2016. A review of the geographical distribution and habitat of the Atlantic humpback dolphin (*Sousa teuszii*). Advances in Marine Biology 72, 79-117.

Weir, J., Duprey, N., Würsig, B., 2008. Dusky dolphin (*Lagenorhynchus obscurus*) subgroup distribution: are shallow waters a refuge for nursery groups? Canadian Journal of Zoology 86, 1225–1234.

Weiss, J., 2006. Foraging habitats and associated preferential foraging specializations of bottlenose dolphin (*Tursiops truncatus*) mother-calf pairs. Aquatic Mammals 32, 10.

Wells, R.S., Boness, D.J., Rathbun, G.B., 1999. Behavior, in: Reynolds, J.E. III, Rommel, S.A. (Eds.), Biology of marine mammals, first ed. Smithsonian Institution Press, Washington and London, pp. 324–422.

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

Whitehead, H., 2001. Analysis of animal movement using opportunistic individual-identifications: application to sperm whales. Ecology 82, 1417–1432.

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

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

Whitehead, H., 2015. Socprog 2.6 (for Matlab 8.5.0): programs for analysing social structure. Dalhousie University, Halifax.

Whitehead, H., Dufault, S., 1999. Techniques for analysing vertebrate social structure using identified individuals: review and recommendations. Advances in the study of behavior 28, 33–74.

Whitehead, H., Rendell, L., Osborne, R. W., Würsig, B., 2004. Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. Biological Conservation 120, 427–437.

Whitfort, A.S., Cornish, A., Griffiths, R., Woodhouse, F.M., 2013. A review of Hong Kong’s wild animal and plant protection laws.: HKU KE IP 2011/12-52 Report. Available at http://www.law.hku.hk/faculty/staff/Files/130917lawreview.pdf. (Accessed on 1 November 2016).

Williams, R., Bain, D.E., Smith, J.C., Lusseau, D., 2009. Effects of vessels on behaviour patterns of individual southern resident killer whales *Orcinus orca*. Endangered Species Research 6, 199–209.

Wilson, B., Porter. L., Gordon, J., Hammond, P.S., Hodgins, N., Wei, L., Lin,W., Lusseau, D., Tsang,A., Van Waerebeek, K.,Wu, Y.P., 2008. A decade of management plans, conservation initiatives and protective legislation for Chinese white dolphin (*Sousa chinensis*): an assessment of progress and recommendations for future management strategies in the Pearl River Estuary, China. Workshop Report, 7–11 April 2008, WWF Hong Kong, Hong Kong.

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

Wiszniewski, J., Lusseau, D., Möller, L.M., 2010. Female bisexual kinship ties maintain social cohesion in a dolphin network. Animal Behaviour 80, 895–904.

World Bank, 2015. East Asia’s Changing Urban Landscape: Measuring a Decade of Spatial Growth. Available at http://www.worldbank.org/content/dam/Worldbank/Publications/Urban%20Development/EAP_Urban_Expansion_full_report_web.pdf. (Accessed on 1 November 2016).

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

Worton, B.J., 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. Journal of Wildlife Management 59, 794–800.

Würsig, B. 1986. Delphinid foraging strategies, in: Schusterman, R.J., Thomas, J.A., Wood F.G. (Eds.), Dolphin cognition and behavior: a comparative approach. Lawrence Erlbaum Associates, New Jersey, pp. 347–359.

Würsig, B., Greene, C., Jefferson, T., 2000. Development of an air bubble curtain to reduce underwater noise of percussive piling. Marine environmental research 49, 79-93.

Würsig, B., Parsons, E., Piwetz, S., Porter, L., 2016. The Behavioural Ecology of Indo-Pacific Humpback Dolphins in Hong Kong. Advances in Marine Biology 73, 65-90.

WWF-Hong Kong, 2014. WWF's submission on the Third Runway Project for the Legislative Council Panel on EconomicDevelopment on 29 September 2014. Available at http://www.legco.gov.hk/yr13-14/english/panels/edev/papers/eaedev1007cb1-1995-1-e.pdf. (Accessed on 1 November 2016).

Xu, X., Song, J., Zhang, Z., Li, P., Yang, G., Zhou, K., 2015. The world's second largest population of humpback dolphins in the waters of Zhanjiang deserves the highest conservation priority. Scientific reports 5, 8147.

Xu, X., Zhang, Z., Ma, L., Li, P., Yang, G., Zhou, K., 2012. Site fidelity and association patterns of Indo-Pacific humpback dolphins off the east coast of Zhanjiang, China. Acta Theriologica 57, 99–109.

Yamagiwa, J., Karczmarski, L., 2014. Primates and cetaceans. Field research and conservation of complex mammalian societies. Primatology Monographs 9, Springer, Tokyo.

Yeh, A.G.-O., Li, X., 1999. Economic development and agricultural land loss in the Pearl River Delta, China. Habitat international 23, 373–390.

Yin, K., 2002. Monsoonal influence on seasonal variations in nutrients and phytoplankton biomass in coastal waters of Hong Kong in the vicinity of the Pearl River Estuary. Marine Ecology Progress Series 245, 111–122.

Yin, K., Qian, P.-Y., Chen, J.C., Hsieh, D.P., Harrison, P.J., 2000. Dynamics of nutrients and phytoplankton biomass in the Pearl River estuary and adjacent waters of Hong Kong during summer: preliminary evidence for phosphorus and silicon limitation. Marine Ecology Progress Series 194, 295–305.

Yin, K., Zhang, J., Qian, P.-Y., Jian, W., Huang, L., Chen, J., Wu, M.C., 2004. Effect of wind events on phytoplankton blooms in the Pearl River estuary during summer. Continental Shelf Research 24, 1909–1923.

Zar, J.H., 2010. Biostatistical Analysis, fifth ed. Pearson Prentice Hall, Upper Saddle River, New Jersey.

Zhai, F.-F., 2006. A study on the social structure, behavior, and habitat selection of Chinese white dolphins (*Sousa chinensis*) in Xiamen waters, China. M. Sc. Thesis, Nanjing Normal University. (in Chinese).

Zhang, S., Lu, X.X., Higgitt, D.L., Chen, C.-T.A., Han, J., Sun, H., 2008. Recent changes of water discharge and sediment load in the Zhujiang (Pearl River) Basin, China. Global and Planetary Change 60, 365–380.

Zhao, H., 1990. The Evolution of the Pearl River Estuary. China Ocean Press, Beijing.

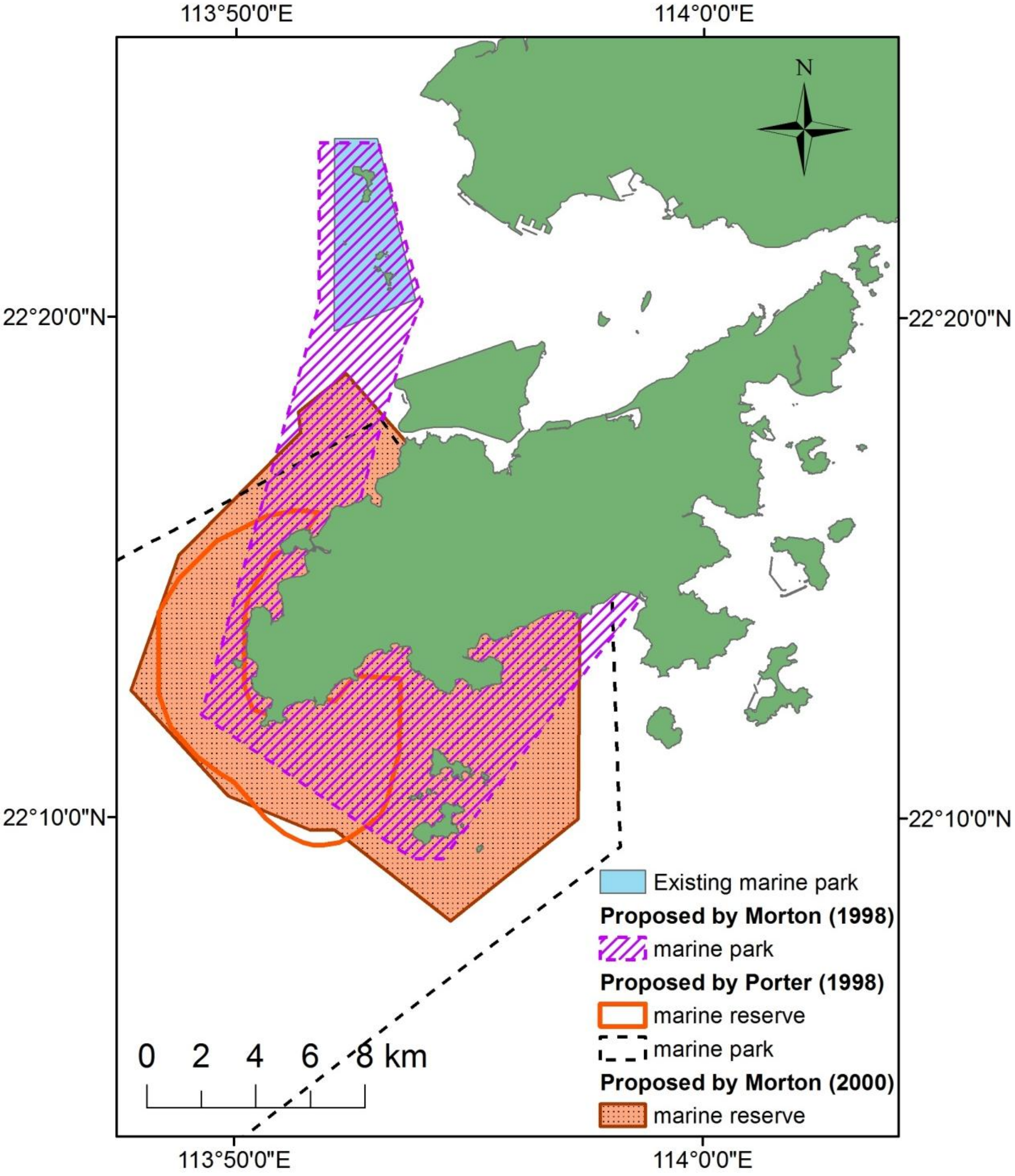
Zheng, R., Karczmarski, L., Lin, W., Chan, S.C.Y., Chang, W.-L., Wu, Y., 2016. Infanticide in the Indo-Pacific humpback dolphin (*Sousa chinensis*). Journal of Ethology 34, 299–307. DOI: 10.1007/s10164-016-0475-7

Zhou, K., Leatherwood, S., Jefferson, T.A., 1995. Records of small cetaceans in Chinese waters: a review. Asian Marine Biology 12, 119–139

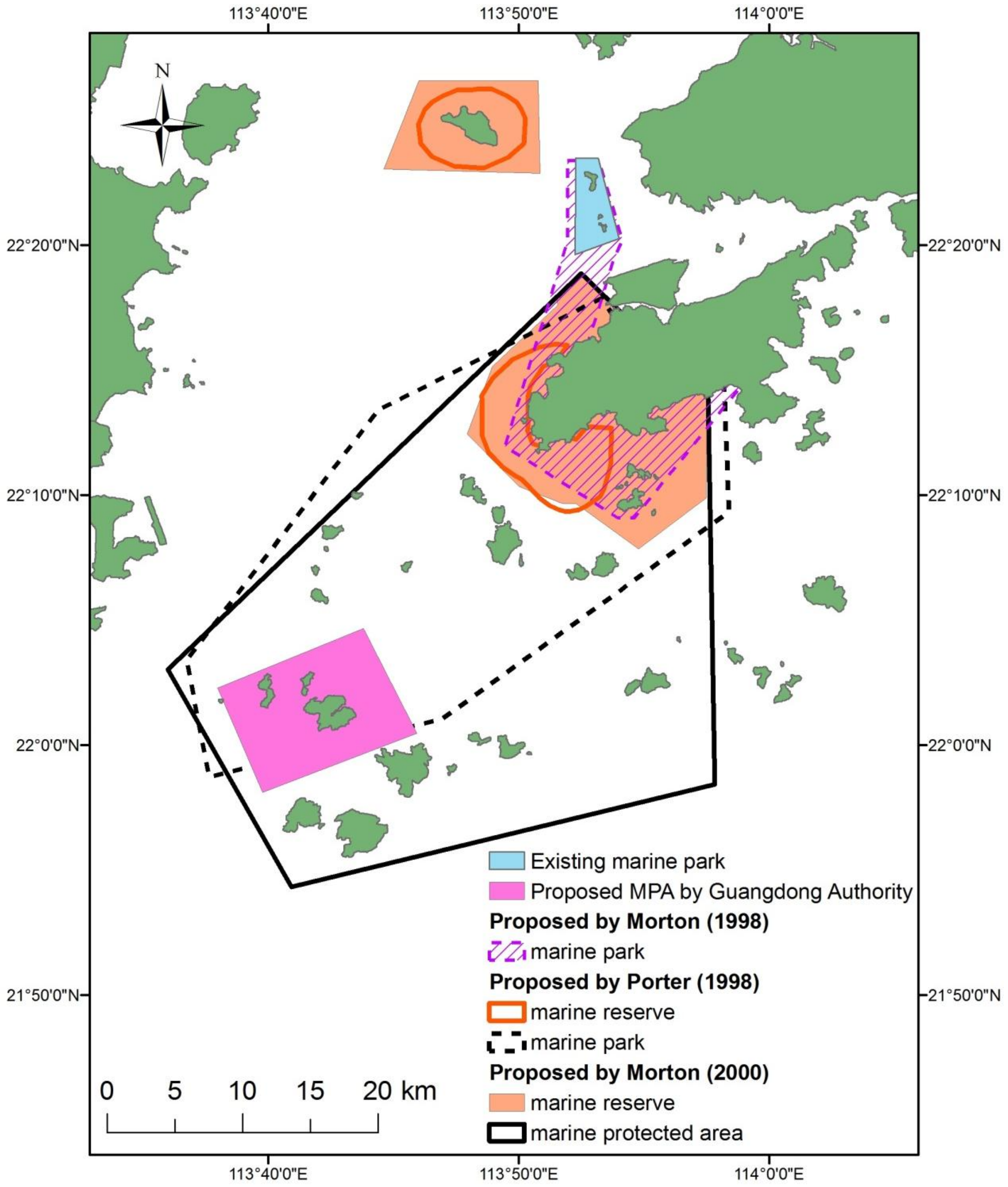
Zhou, K., Xu, X., Tian, C., 2007. Distribution and abundance of Indo-Pacific humpback dolphins in Leizhou Bay, China. New Zealand Journal of Zoology 34, 35–42.

Zuur, A. F. Ieno, E. N., Walker, N. J., Saveliev, A.A., Smith, G.M., 2009. Mixed Effects Models and Extensions in Ecology with R . Springer, New York.

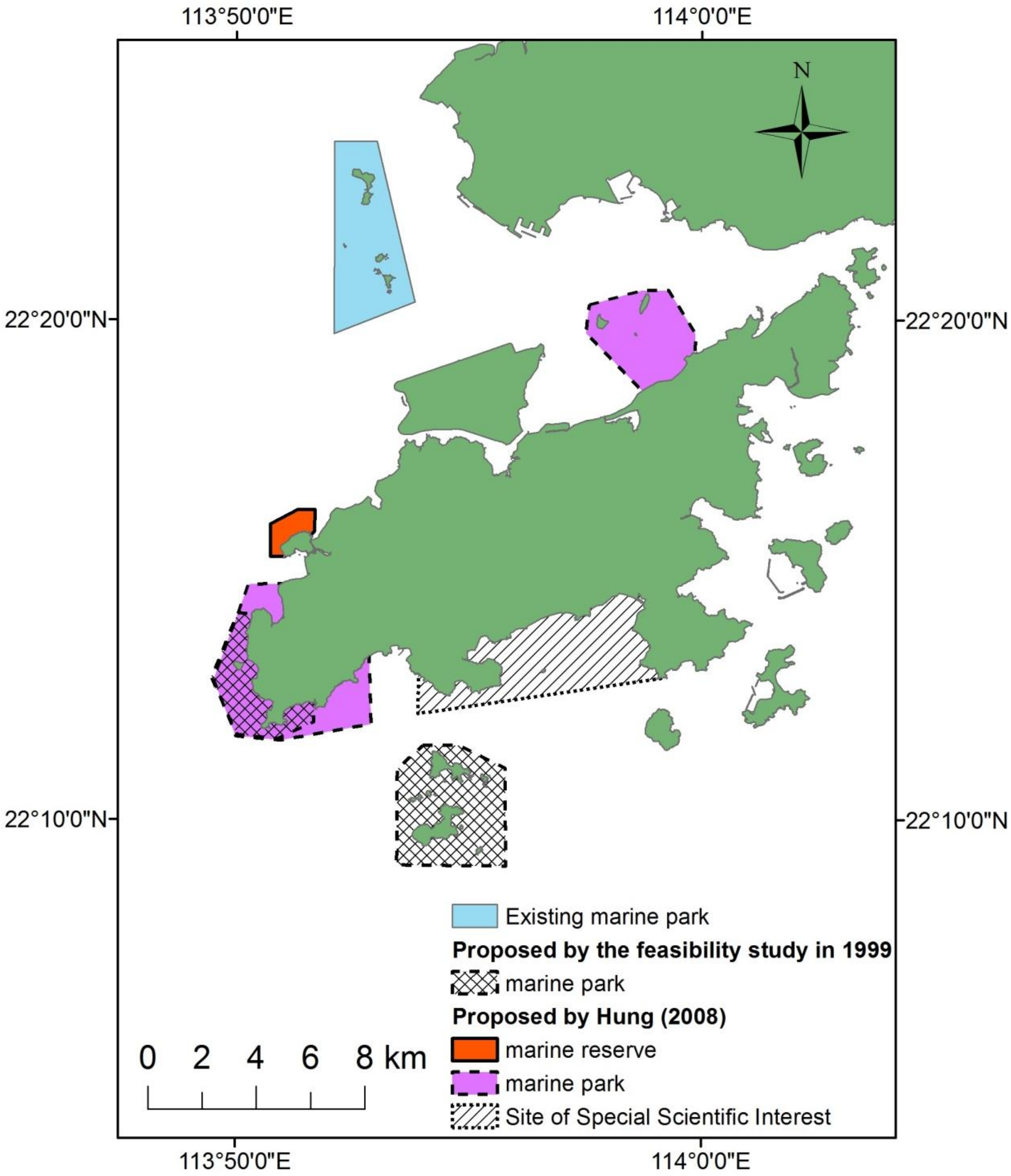
Appendices



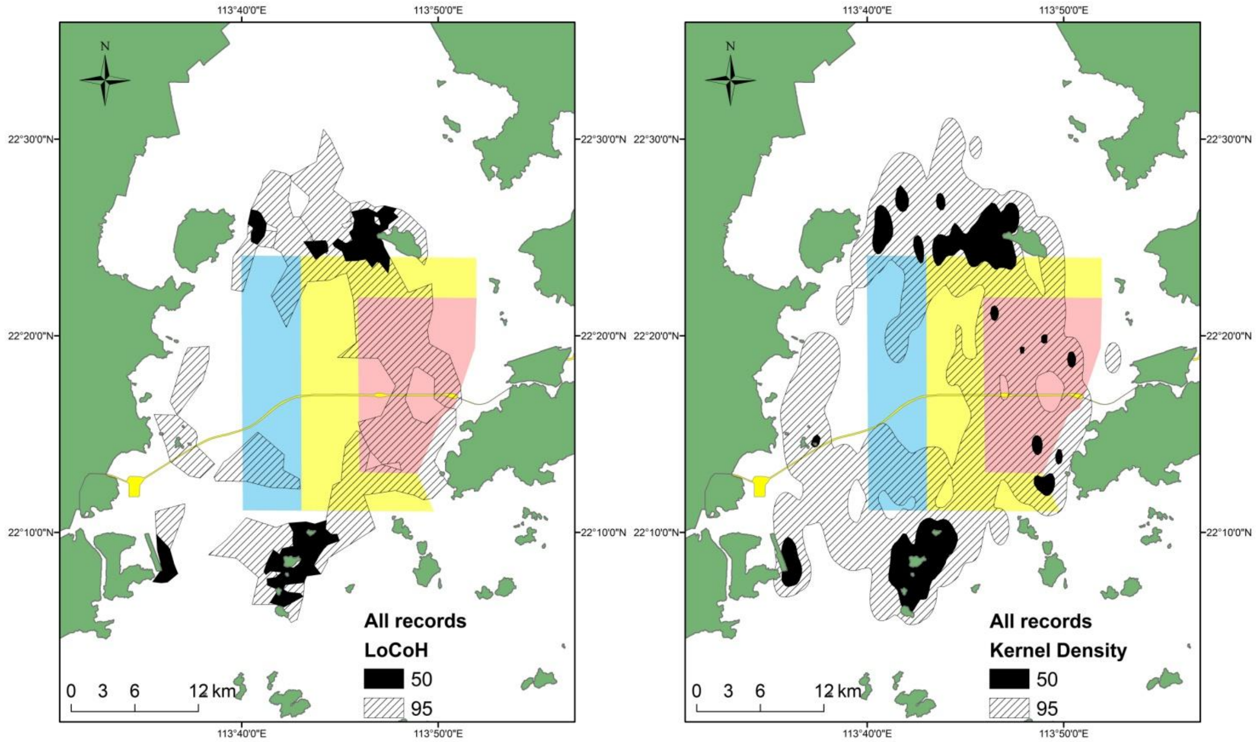
Appendix 1 Marine Protected Areas (MPAs) proposed in Hong Kong during the period between 1998 and 2000. The existing Sha Chau and Lung Kwu Chau Marine Park (12km^2) denoted by the blue background was designated in 1996. The marine park suggested by Morton (1998) is in purple hatched lines. The marine reserve and marine park proposed by Porter (1998) and extended to mainland China are indicated as enclosures by the bright orange line and black dotted line respectively. Following the study of Porter (1998), Morton (2000) revised the proposed MPAs into a single large marine reserve that covered the west to south part of Lantau Island and the Soko Islands and it is indicated by the brown polygon.



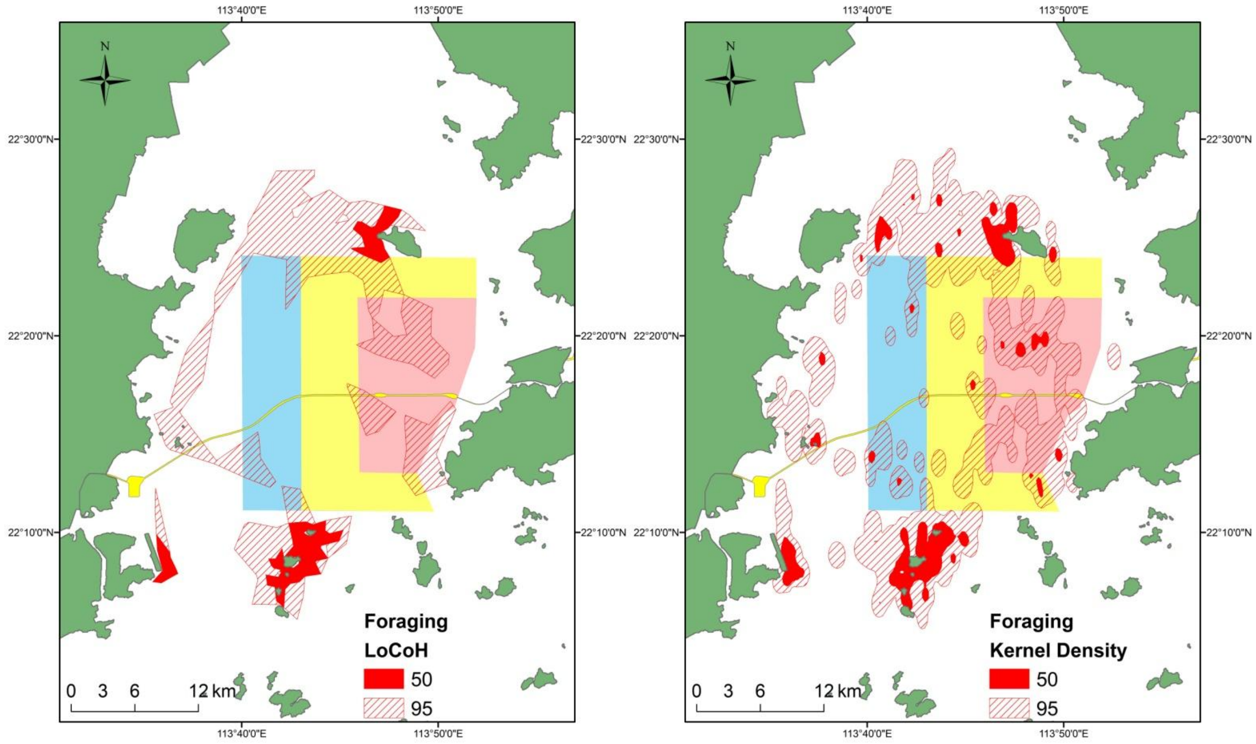
Appendix 2 Marine Protected Areas (MPAs) proposed in Hong Kong and mainland China waters between 1998 and 2000. The existing Sha Chau and Lung Kwu Chau Marine Park ($12km^2$) denoted by the blue background was designated in 1996. The marine park suggested by Morton (1998) is in purple hatched lines. The marine reserves and marine park proposed by Porter (1998) and extended to mainland China are indicated as enclosures by the bright orange line and black dotted line respectively. Following the study of Porter (1998), Morton (2000) revised the proposed MPAs and expanded the marine reserves, indicated by the brown polygon, and the marine protected area, which is denoted by black solid line. The proposed marine protected area by the Guangdong Authority is denoted in pink background and is reproduced from Morton (2000).



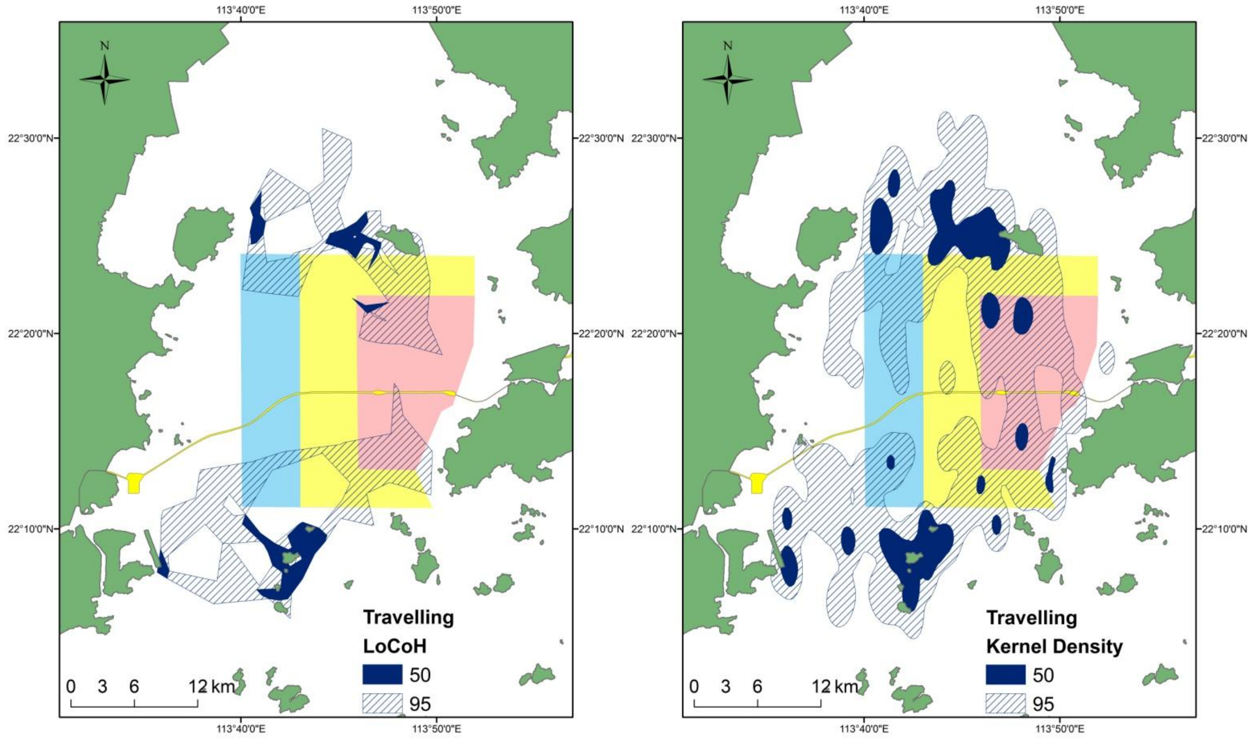
Appendix 3 Marine Protected Areas (MPAs) proposed in Hong Kong between 1999 and 2008. The existing Sha Chau and Lung Kwu Chau Marine Park (12km^2) denoted by the blue background was designated in 1996. The two marine parks proposed by the feasibility study (Tsang and Milicich 1999) are indicated in black crossed lines. These suggestions were reviewed by Hung (2008), who further proposed a marine reserve that is denoted in orange background, expansion of marine parks that are shown in purple background, and a Site of Special Scientific Interest, which is indicated in black hatched line.



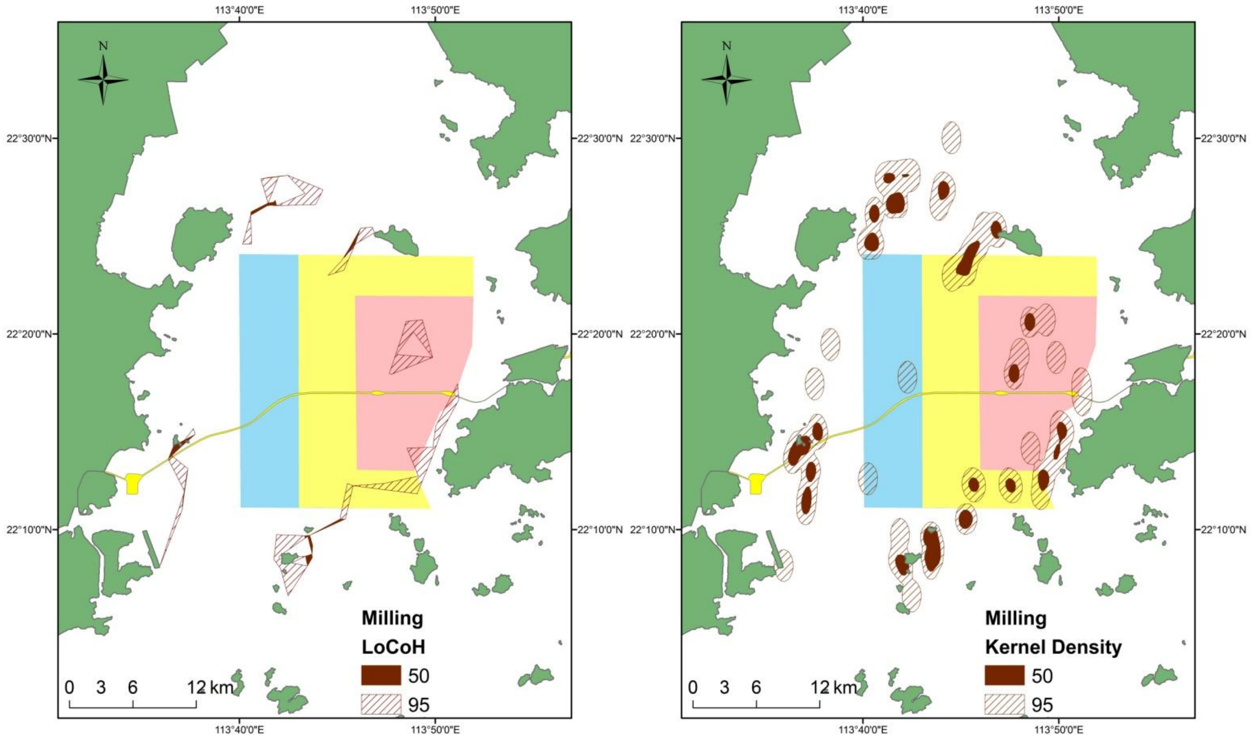
Appendix 4 Area utilisation pattern of Indo-Pacific humpback dolphins estimated with 50% and 95% isopleths of Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) for all sightings recorded during 2011–2015 in the eastern Pearl River Estuary (EPRE) excluding Hong Kong. The coloured area is the existing Marine Protected Area in mainland (i.e. Guangdong Pearl River Estuary Chinese White Dolphin National Nature Reserve) with the core area indicated in pink, the buffer area in pale yellow, and the experimental area in blue.



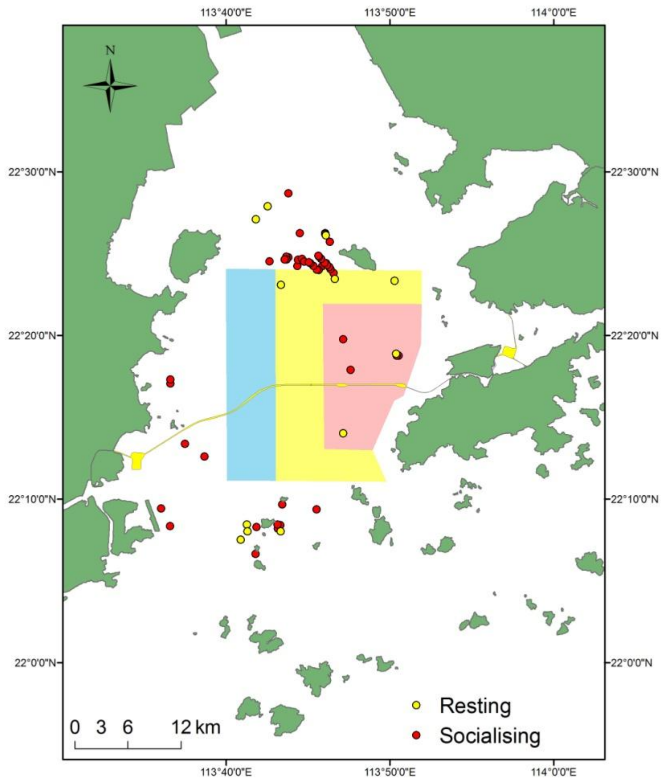
Appendix 5 Area utilisation pattern of Indo-Pacific humpback dolphins estimated with 50% and 95% isopleths of Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) for foraging recorded during 2011–2015 in the eastern Pearl River Estuary (EPRE) excluding Hong Kong. The coloured area is the existing Marine Protected Area in the mainland (i.e. Guangdong Pearl River Estuary Chinese White Dolphin National Nature Reserve) with the core area indicated in pink, buffer area in pale yellow, and experimental area in blue.



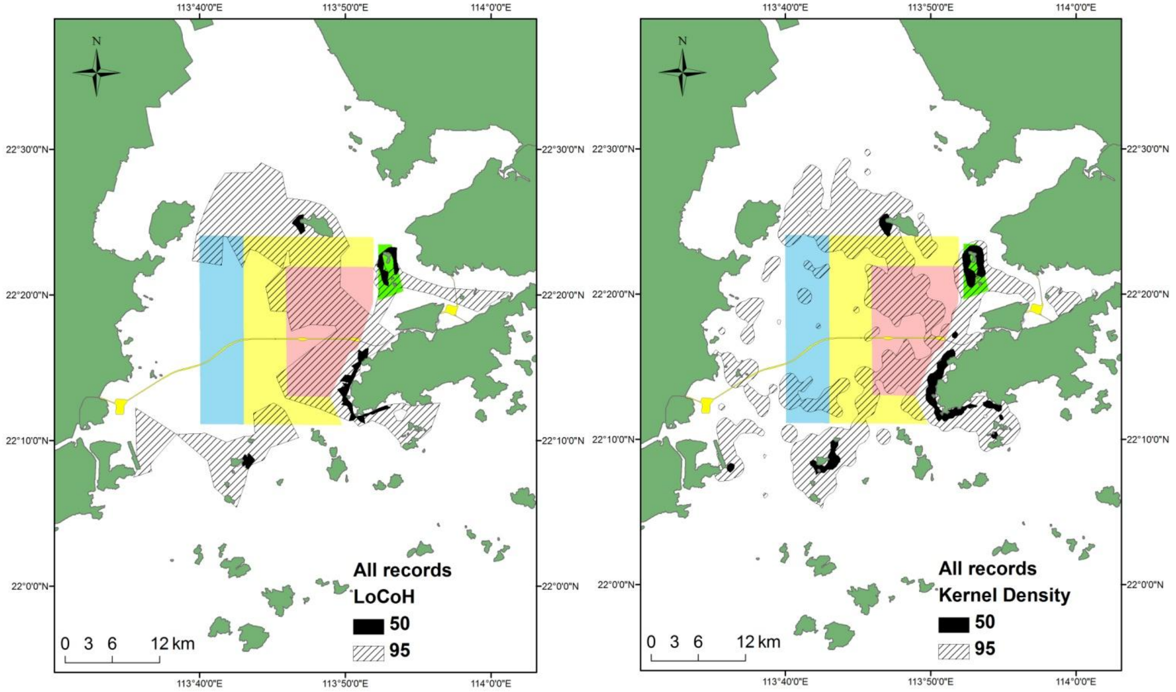
Appendix 6 Area utilisation pattern of Indo-Pacific humpback dolphins estimated with 50% and 95% isopleths of Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) for travelling recorded during 2011–2015 in the eastern Pearl River Estuary (EPRE) excluding Hong Kong. The coloured area is the existing Marine Protected Area in the mainland (i.e. Guangdong Pearl River Estuary Chinese White Dolphin National Nature Reserve), with the core area indicated in pink, buffer area in pale yellow, and experimental area in blue.



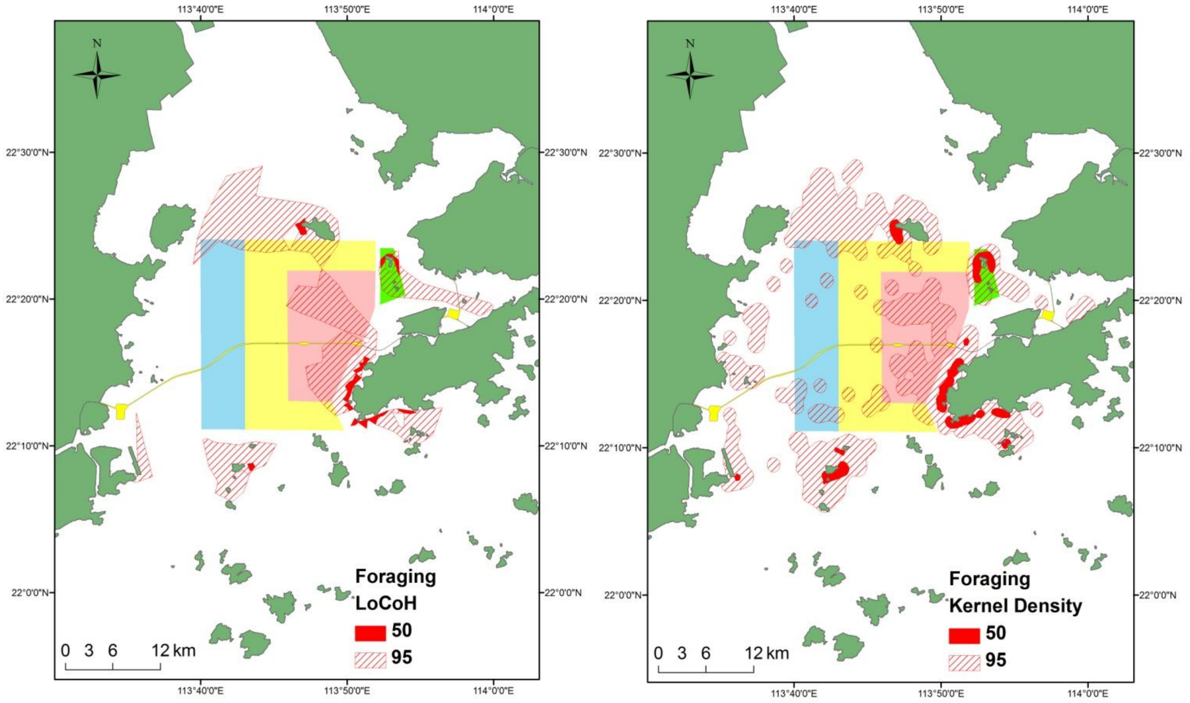
Appendix 7 Area utilisation pattern of Indo-Pacific humpback dolphins estimated with 50% and 95% isopleths of Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) for milling recorded during 2011–2015 in the eastern Pearl River Estuary (EPRE) excluding Hong Kong. The coloured area is the existing Marine Protected Area in the mainland (i.e. Guangdong Pearl River Estuary Chinese White Dolphin National Nature Reserve) with the core area indicated in pink, buffer area in pale yellow, and experimental area in blue.



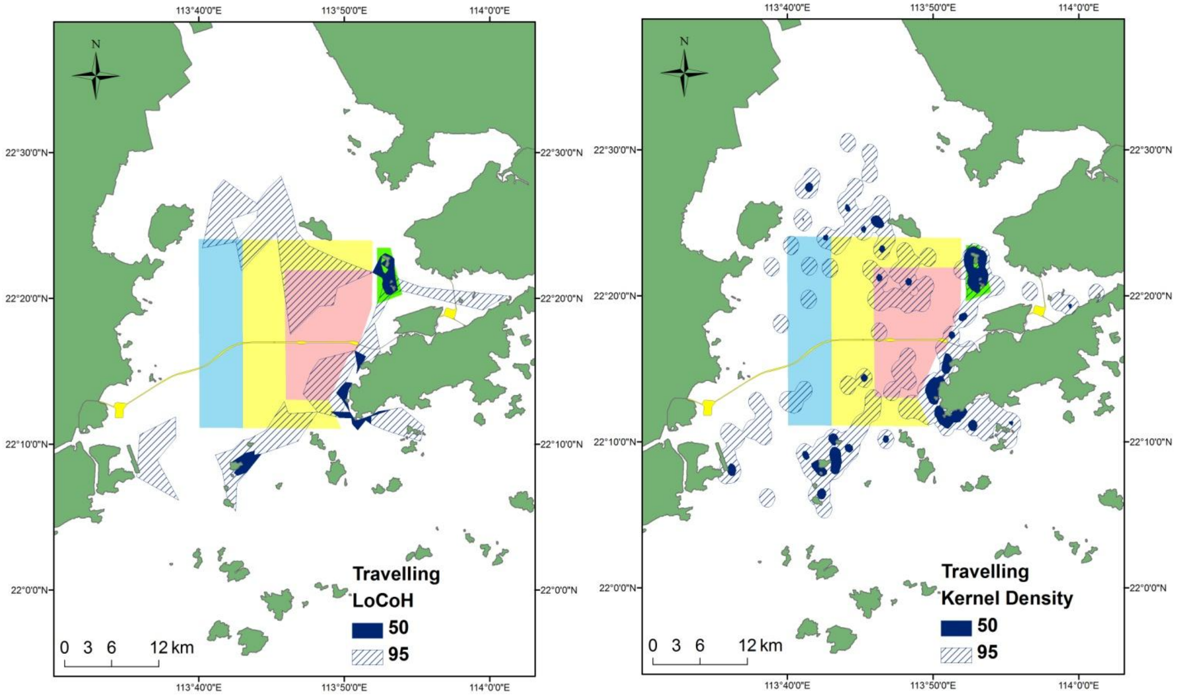
Appendix 8 Sightings of resting and socialising Indo-Pacific humpback dolphins during 2011-2015 in the eastern Pearl River Estuary (EPRE) excluding Hong Kong. The coloured area is the existing Marine Protected Area in mainland (i.e. Guangdong Pearl River Estuary Chinese White Dolphin National Nature Reserve) with the core area indicated in pink, buffer area in pale yellow, and experimental area in blue.



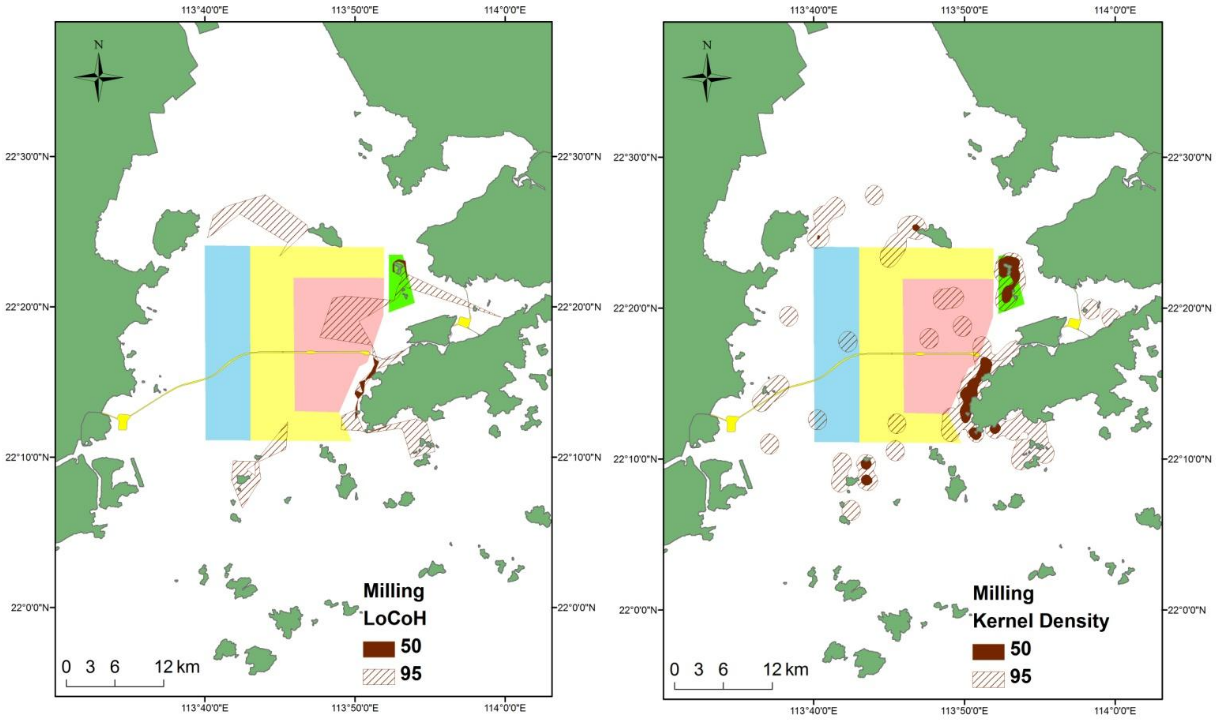
Appendix 9 Area utilisation pattern of Indo-Pacific humpback dolphins estimated with 50% and 95% isopleths of Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) for all sightings recorded during 2011–2015 in the entire eastern Pearl River Estuary (EPRE), including Hong Kong waters. The coloured areas are the existing Marine Protected Areas in Hong Kong (i.e. Sha Chau and Lung Kwu Chau Marine Park noted in bright green) and mainland (i.e. Guangdong Pearl River Estuary Chinese White Dolphin National Nature Reserve of which the core area indicated in pink, buffer area in pale yellow, and experimental area in blue).



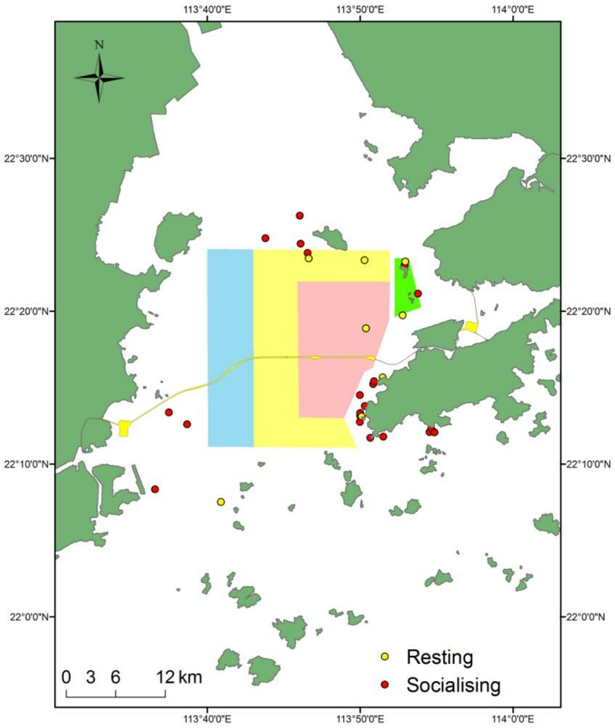
Appendix 10 Area utilisation pattern of Indo-Pacific humpback dolphins estimated with 50% and 95% isopleths of Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) for foraging recorded during 2011-2015 in the entire eastern Pearl River Estuary (EPRE), including Hong Kong waters. The coloured areas are the existing Marine Protected Areas in Hong Kong (i.e. Sha Chau and Lung Kwu Chau Marine Park noted in bright green) and the mainland (i.e. Guangdong Pearl River Estuary Chinese White Dolphin National Nature Reserve of which the core area is indicated in pink, buffer area in pale yellow, and experimental area in blue).



Appendix 11 Area utilisation pattern of Indo-Pacific humpback dolphins estimated with 50% and 95% isopleths of Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) for travelling recorded during 2011–2015 in the entire eastern Pearl River Estuary (EPRE), including Hong Kong waters. The coloured areas are the existing Marine Protected Areas in Hong Kong (i.e. Sha Chau and Lung Kwu Chau Marine Park noted in bright green) and the mainland (i.e. Guangdong Pearl River Estuary Chinese White Dolphin National Nature Reserve of which the core area is indicated in pink, buffer area in pale yellow, and experimental area in blue).



Appendix 12 Area utilisation pattern of Indo-Pacific humpback dolphins estimated with 50% and 95% isopleths of Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) for travelling recorded during 2011–2015 in the entire eastern Pearl River Estuary (EPRE), including Hong Kong waters. The coloured areas are the existing Marine Protected Areas in Hong Kong (i.e. Sha Chau and Lung Kwu Chau Marine Park noted in bright green) and the mainland (i.e. Guangdong Pearl River Estuary Chinese White Dolphin National Nature Reserve of which the core area is indicated in pink, buffer area in pale yellow, and experimental area in blue).



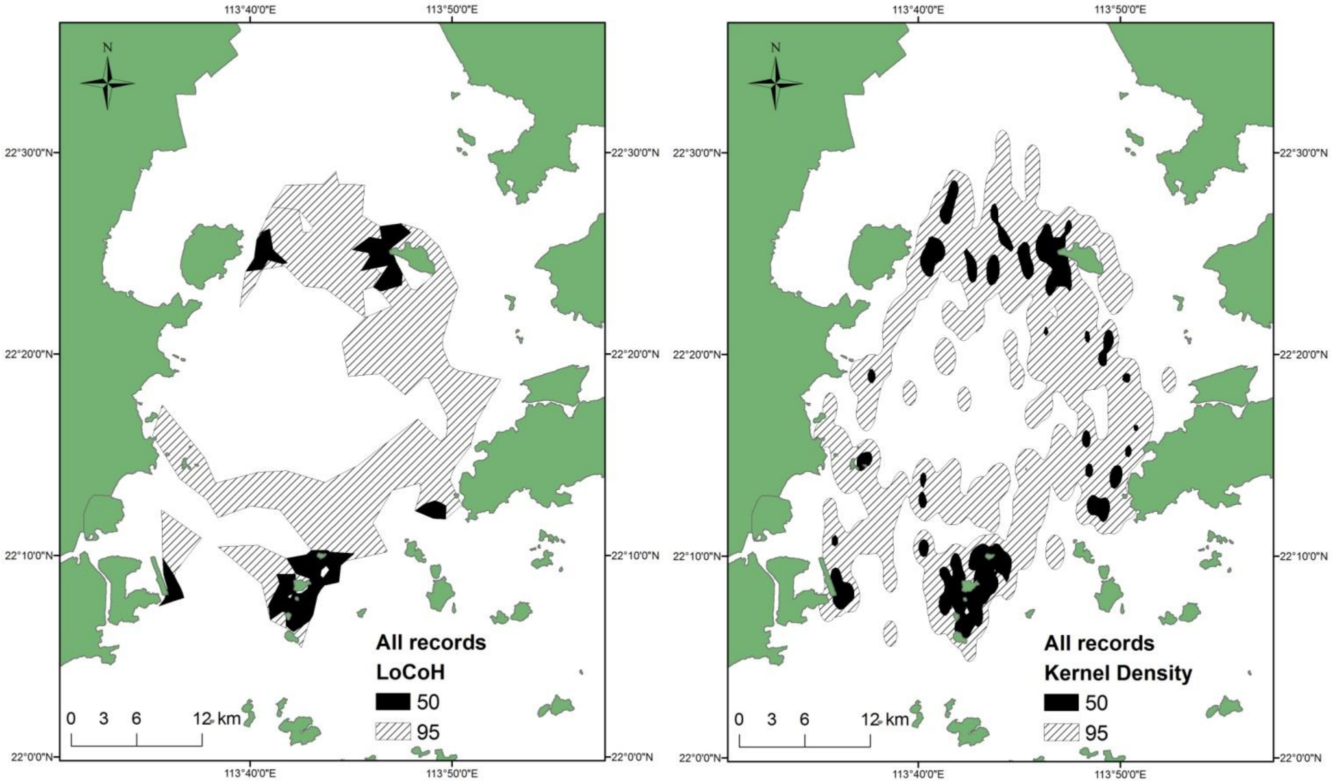
Appendix 13 Sightings of resting and socialising Indo-Pacific humpback dolphins during 2011–2015 in the eastern Pearl River Estuary (EPRE), including Hong Kong waters. The coloured area is the existing Marine Protected Area in Hong Kong (i.e. Sha Chau and Lung Kwu Chau Marine Park noted in bright green) and the mainland (i.e. Guangdong Pearl River Estuary Chinese White Dolphin National Nature Reserve of which the core area is indicated in pink, buffer area in pale yellow, and experimental area in blue).

Appendix 14 Number of GPS points of humpback dolphin behaviour recorded in the eastern Pearl River Estuary (EPRE) excluding Hong Kong during 2011–2015. Only the first GPS points of each dolphin encounter were included.

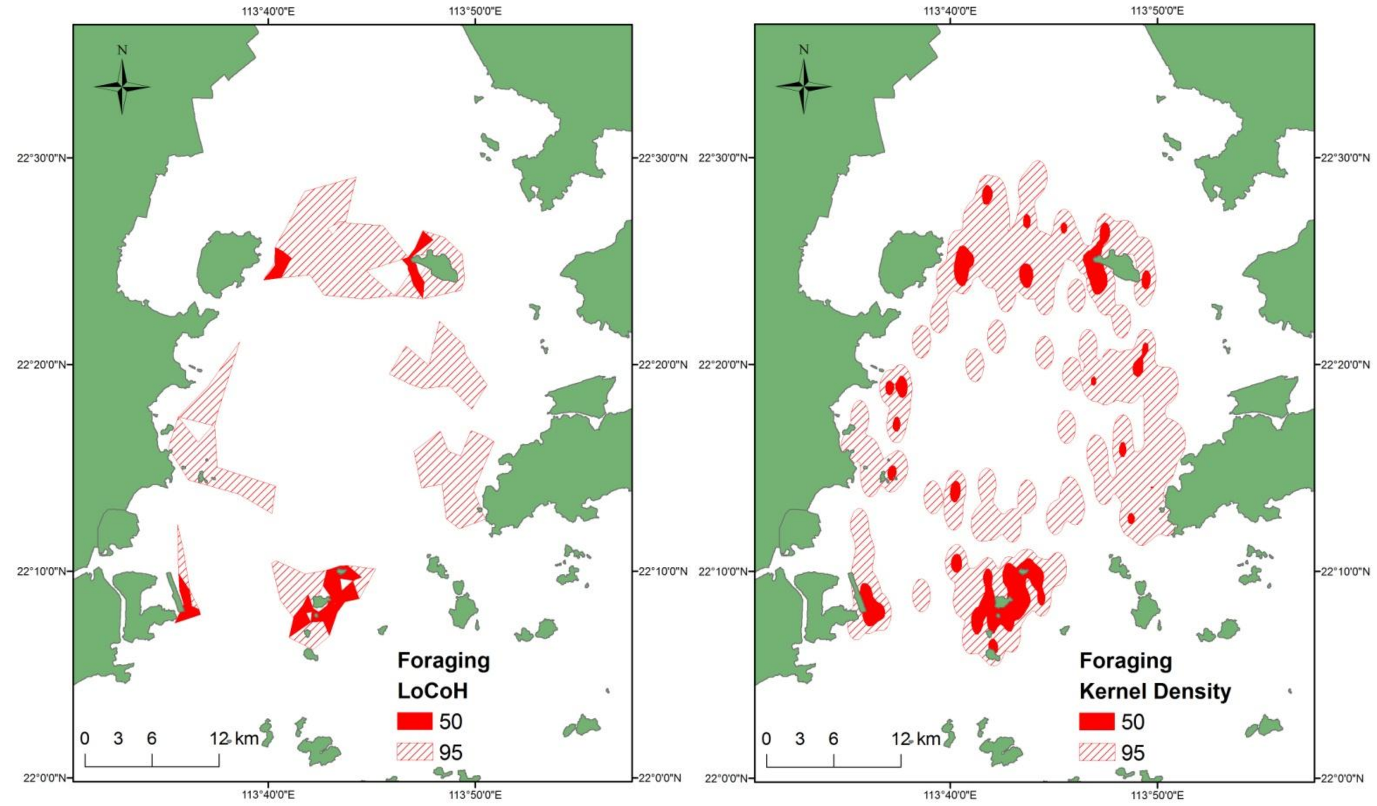
	Total	Percentage
Foraging	257	53.8
Travelling	121	25.3
Milling	39	8.2
Socialising	8	1.7
Resting	4	0.8
Foraging-Travelling	24	5.0
Foraging-Milling	10	2.1
Foraging-Socialising	2	0.4
Travelling-Milling	1	0.2
Travelling-Resting	1	0.2
Undetermined	11	2.3
Total	478	100

Appendix 15 Calculated areas (in km^2) for Local Convex Hull (LoCoH) estimates and Kernel Density estimation (KDE) at 95% and 50% utilisation distributions for the first sightings of each encounter recorded during 2011–2015 in eastern Pearl River Estuary (EPRE) excluding Hong Kong. The values of the Swihart & Slade Index > 0.6 (Swihart and Slade 1985) or Schoener Index < 1.6 or > 2.4 (Schoener 1981) indicate significant autocorrelation in the data. H_{ref} refers to the reference bandwidth of KDE and h is the bandwidth used for KDE. Sample sizes of milling, socialising, resting and mixed behaviours were too small to generate utilisation distribution estimates.

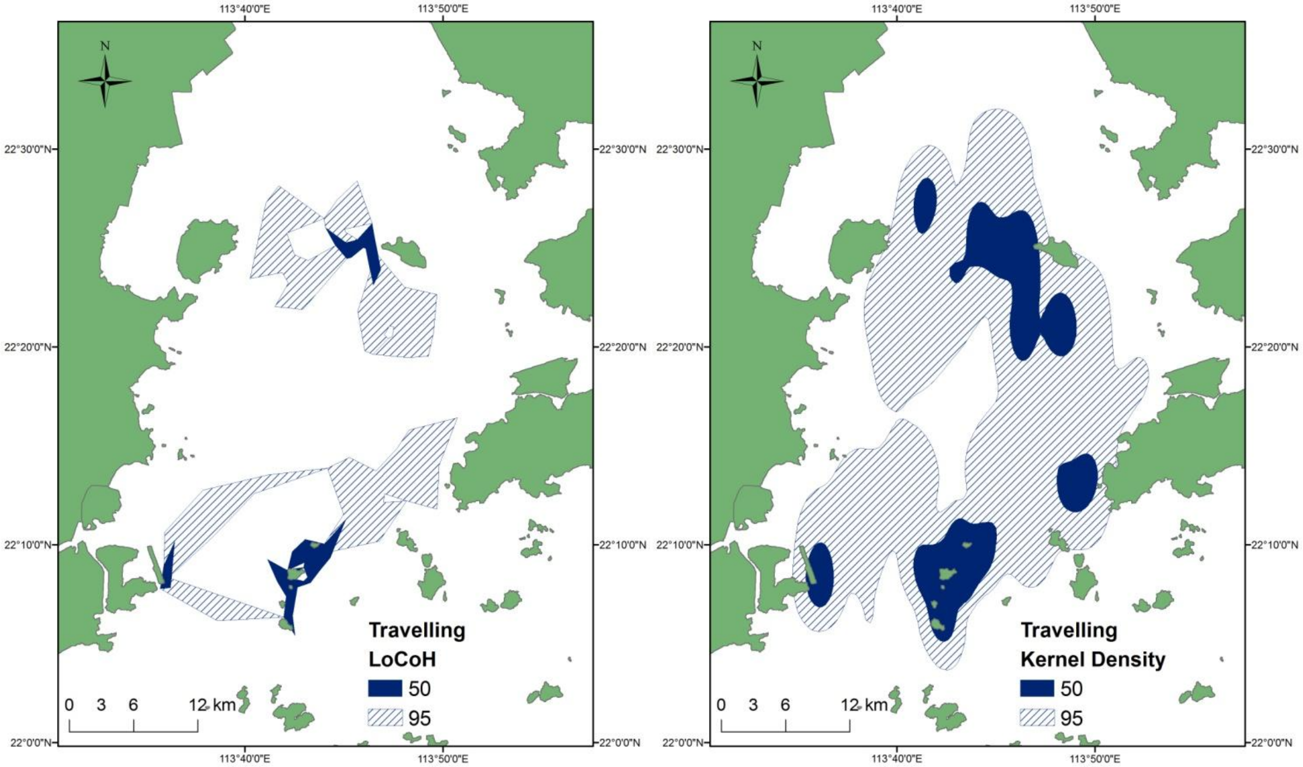
	LoCoH 50%	LoCoH 95%	KDE 50%	KDE 95%	Swihart & Slade Index	Schoener Index	h	h_{ref}	n
All records	51.74	396.79	82.04	562.26	1.31	1.00	0.05	0.36	478
Foraging	24.79	225.87	54.24	418.46	0.96	1.24	0.05	0.40	257
Travelling	28.52	244.71	154.44	815.40	0.55	1.53	0.15	0.45	121



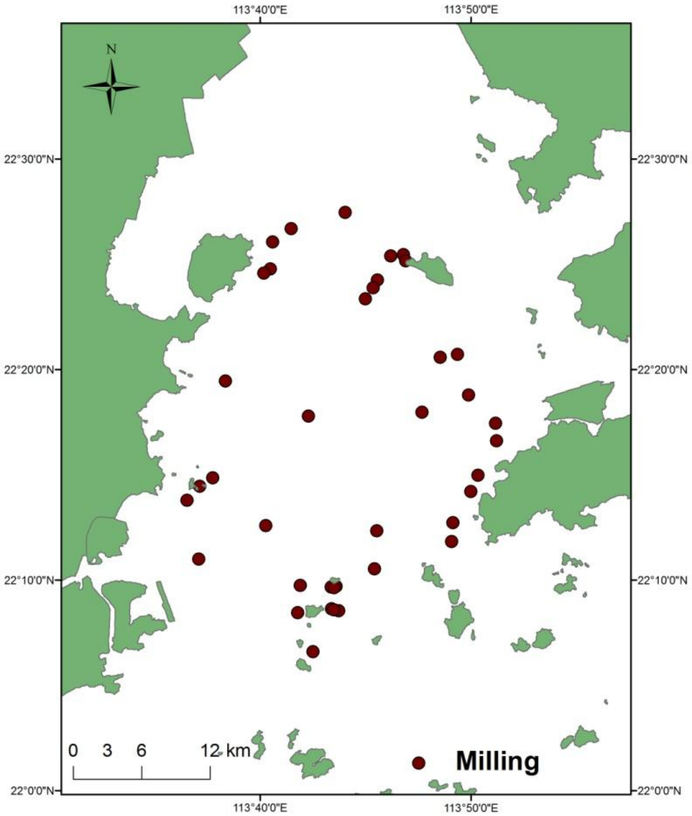
Appendix 16 Area utilisation pattern of Indo-Pacific humpback dolphins estimated with 50% and 95% isopleths of Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) based on the first sightings of each encounter recorded during 2011–2015 in the eastern Pearl River Estuary (EPRE) excluding Hong Kong.



Appendix 17 Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) with 95% and 50% isopleths utilisation distributions based on the first sightings of foraging Indo-Pacific humpback dolphins in the eastern Pearl River Estuary (EPRE) excluding Hong Kong, during 2011–2015.



Appendix 18 Local Convex Hull (LoCoH) and Kernel Density estimation (KDE) with 95% and 50% isopleths utilisation distributions based on the first sightings of travelling Indo-Pacific humpback dolphins in the eastern Pearl River Estuary (EPRE) excluding Hong Kong, during 2011–2015.



Appendix 19 First sightings of milling Indo-Pacific humpback dolphins in the eastern Pearl River Estuary (EPRE) excluding Hong Kong, during 2011–2015.