Population parameters and group dynamics of humpback dolphins (*Sousa plumbea*) in Plettenberg Bay, South Africa

by

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I, John Hon wah KWOK declare that the thesis, which I hereby submit for the degree of Master of Science (M.Sc.) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

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Project Summary

Individual photo-identification mark-recapture study was performed to estimate the demographic parameters and socio-behavioural group dynamics of the Indian Ocean humpback dolphin (*Sousa plumbea*) in Plettenberg Bay, South Africa, during April 1999 to April 2004. Apparent survival rates, recapture probabilities, and super-population size were quantified with the application of Cormack-Jolly-Seber and POPAN models. Given that the majority of identified individuals were sighted only once, transience of animals was significant and these dolphins likely travel distances exceeding the size of the Plettenberg Bay region. Higher survey intensity, however, is needed to improve the accuracy and robustness of population parameter estimations.

This study applied a comprehensive approach in the formulation of candidate models during mark-recapture model selection processes. Various effects, such as the basic time-dependent (‘t’), constant over time (‘.’), transience (‘a2’), trap-dependence (‘*m’), seasonal (‘season’) and effort (‘effort’) effects were applied to test the likelihood of factors. Incorporating and identifying these effects provided the means for more accurate and unbiased estimation of demographic parameters; e.g. separating “transient” individuals in the estimation of apparent survival rates limited the negative bias related to movement instead of true mortality, thus making the estimate closer to the true survival rates.

Socio-behavioural analyses revealed that humpback dolphins that use the coastal waters of Plettenberg Bay live in a dynamic fission-fusion society with fluid inter-individual associations. There appears to be social differentiation between dolphins transiting through the area and those that use Plettenberg Bay more frequently, perhaps on long-term basis. The transients, however, represent a predominant majority of the humpback dolphins seen in the Bay. The degree of residency of the small number of more frequently seen individuals remains undetermined.

The socio-dynamics of humpback dolphin groups in the Plettenberg Bay region meet the expectations of a recently proposed conceptual framework of delphinid social strategies, which suggests that group dynamics and ranging patterns of inshore delphinids are determined by the spatiotemporal predictability and availability of limited inshore resources. The study in Plettenberg Bay confirms that humpback dolphins represent an intermediate-ranging pattern among coastal delphinids.

Although not free from technical and analytical limitations, which are discussed, this study provides important information on demographic parameters and socio-behaviour of humpback dolphins inhabiting the Plettenberg Bay region. Such data carries considerable conservation implications and is informative to future management decision that may affect coastal waters of Plettenberg Bay and its mammalian inhabitants.

KEY WORDS: Indian Ocean humpback dolphin (*Sousa plumbea*), mark-recapture models, dynamic fission-fusion society, Plettenberg Bay.

Chapter 1. Humpback Dolphins: An Overview

1.1 Introduction

Studying cetacean ecology and behaviour presents researchers with many challenges as these animals are often inaccessible to continuous and systematic observations. They spend much of their daily activities underwater and the short periods above water are often too short to collect reliable focal observations; especially if they occur in groups. For those reasons, comprehensive field studies of cetaceans are relatively recent, dating only from the time when technological development, such as high-speed photographic gear, data loggers, etc., begun facilitating field data collection (Mann et al. 2000). In recent decades, there has been an impressive development of new research techniques (e.g. toxicology, isotopes, genetic sequencing techiques; see Boyd et al. 2010; e.g. Cammen et al. 2016) and rapid advancement in cetacean field studies and methods (e.g. Linchant et al. 2015)

Among the very first pioneering cetacean field studies was the work by Saayman and Tayler (1979) in Plettenberg Bay, South Africa. Although relatively basic, if viewed from the current perspective, this study presented foundational research of humpback dolphins (*Sousa* spp.). It was among first field studies that followed a fairly systematic and coordinated field protocol and it made valuable first steps in behavioural studies of otherwise inaccessible marine mammals. It was only many years later, when advanced photographic techniques were introduced to field studies of cetacean (e.g. Hammond et al. 1990) that new avenues of research and new prospects of field research became available.

1.2 Taxonomy and distribution

The taxonomy of the genus *Sousa* has long been unresolved (e.g. Pilleri and Gihr 1972; Ross et al. 1994; Jefferson and Karczmarski 2001; Jefferson and Rosenbaum 2014). Between one and five nominal species have been proposed; consisting initially of the Indo-Pacific form of *S. chinensis* (Osbeck 1765) and *S. borneensis* (Lydekker, 1901), the Indian Ocean form *S. plumbea* (G. Cuvier

1829) and *S. lentigenosa* (Owen 1866), and the Atlantic form *S. teuszii* (Kukenthal 1892). For the past two decades, most researchers recognized either two or three species of *Sousa* (e.g. Jefferson and Karczmarski 2001; Rice 1998; Ross et al. 1994). The three-species taxonomy distinguished *S. teuszi* off West Africa, *S. plumbea* in the western Indian Ocean, and *S. chinensis* off Southeast Asia and the western Pacific Ocean. When two-species taxonomy was considered, *S. chinensis* and *S. plumbea* were combined into one species referred to as the Indo-Pacific humpback dolphin *S. chinensis*, ranging from South Africa in the west to southeast China and northeast Australia in the east. In such a case, humpback dolphins in the central and western Indian Ocean were referred to as the "*plumbea* form" and those in the eastern Indian Ocean and western Pacific Ocean were referred to as the "*chinensis* form", based on their morphological differences.

The International Union for Conservation of Nature (IUCN) has for a long time accepted the two-species taxonomy, even though this has been challenged by some experts in the field (e.g. L. Karczmarski at Global Mammal Assessment: Cetacean Red List Assessment, IUCN Species Survival Commission, Cetacean Specialist Group, 22–26 January 2007, La Jolla, CA, USA; personal communication). For many years, the IUCN list recognised humpback dolphins in the Indian and Pacific oceans as two geographic forms of one and the same species that differ in their external morphology. Voices questioning this taxonomic classification and pointing out considerable negative conservation implications, even though well argued (e.g. Huang and Karczmarski 2014) remained unheard and overlooked for a long time.

In recent years, however, more evidence gradually accumulated indicating that the taxonomy of the genus *Sousa* required further revisions. Frère et al. (2008) suggested that the Australian Indo-pacific humpback dolphins are highly distinct from other *Sousa* species from other regions. Lin et al. (2010) also supported this suggestion with further analysis on population genetics. Further insights have been provided by a recent multi-authored study (Mendez et al. 2013) which integrated multiple lines of evidence, from morphometry to molecular genetics, to better understand the evolutionary divergence of humpback dolphins along their entire distribution range. This study led to a recent revision of the genus' taxonomy, re-describing previously suggested species and arguing acceptance of a four-species taxonomy. These new taxonomy was further summarised by Jefferson and Rosenbaum (2014), with the four species in the genus *Sousa* as follows: *S. teuszii* (the Atlantic humpback dolphin off West Africa), *S. plumbea* (the Indian Ocean humpback dolphin in the western Indian Ocean), *S. chinensis* (the Indo-Pacific humpback dolphin, from the Bay of Bengal throughout Southeast Asia), and *S. sahulensis* (the Australian humpback dolphin, off northeast Australia and southern New Guinea). This classification represents the most up-to-date currently recognised taxonomy of humpback dolphins.

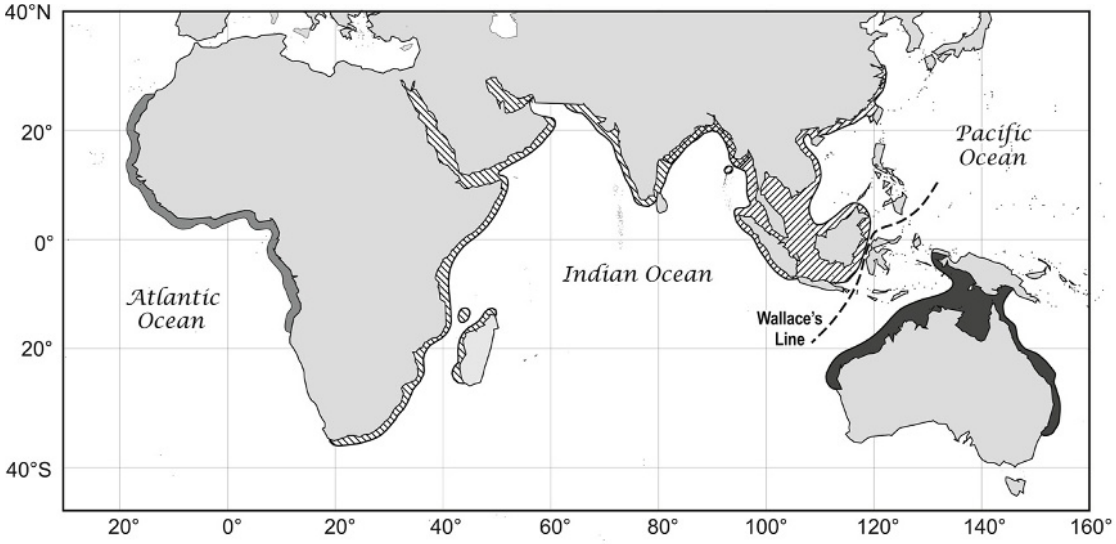

Fig. 1. Distribution range of humpback dolphins (genus *Sousa*); *S. teuszii* off West Africa (grey shading), *S. plumbea* in western Indian Ocean (left-oriented hatching), *S. chinensis* off southeast Asia and western Pacific (right-oriented hatching), and *S. sahulensis* off northeast Australia (black shading). Map source: Jefferson and Rosenbaum (2014).

The distribution of *Sousa* is presented in Fig. 1. The Atlantic humpback dolphins occur in the West African region from Morocco and Western Sahara to approximately Angola, apparently as several isolated populations (Weir and Collins 2015). The Indian Ocean humpback dolphins inhabit coastal waters from South Africa, around the rim of the Indian Ocean northwards and eastwards to at least the southern tip of India, although the range limits in the eastern part of the distribution are currently not well known (Braulik et al. 2015). The Indo-Pacific humpback dolphins are found in waters of Southeast Asia, from about Myanmar and possibly eastern India eastward to the island of Borneo, and northward to central China (Jefferson and Rosenbaum

2014). The Australian humpback dolphin occurs in the warmer waters of central and northern Australia, and the southern parts of New Guinea (Beasley et al. 2016; Parra and Cagnazzi 2016).

1.3 Morphology

Humpback dolphins have a robust body, compressed in front of the dorsal ridge laterally and increasingly compressed towards the flukes (Ross et al. 1994), with a notable small and sickle-shaped dorsal fin situated on an elevated mid-dorsal section on the back (hence the name "humpback"). There are variations of size of hump, in different environments, habitats and populations (Ross et al. 1994; Jefferson and Karczmarski 2001). In general, the "hump" is quite obvious in individuals off Queensland, Australia; and very pronounced in individuals in the western Indian Ocean and in *S. teuszii* off West Africa. However, the hump is less conspicuous in populations of Southeast Asia and western Pacific (Ross et al. 1994; Jefferson and Rosenbaum 2014).

All species of the genus *Sousa* are medium-sized dolphins, with the maximum length recorded to be 280 cm and weight of 250–280 kg (Ross et al. 1994). Average total length of specimens in north Indian Ocean was 212 cm, from south China and Australia was 213 cm, and from West Africa was 220 cm, and 223 cm from South Africa (Pilleri and Gihr 1972; Robineau and Rose 1984; Ross 1984; Ross et al. 1994; Zhou et al., 1980). A strong relationship between total length and body mass was formulated by Ross et al. (1994), with the authors concluding that the specimens collected from southern Africa waters are apparently sexually dimorphic in length (i.e. males are greater in size than females). However, the sexual dimorphism is less evident for the population in Southern China and Hong Kong waters (Jefferson 2000).

The rostrum of humpback dolphins is generally long and thin, about 6 - 10% of the total body length (Ross 1984). On the upper jaw, there are 31-38 teeth in *S. chinensis*, 33-39 teeth in *S. plumbea*, and 27-32 teeth in *S. teuszii*; and *S. plumbea* was found to have a longer and narrower skull among all *Sousa* species (Jefferson and Van Warebeek 2004). Ross (1977, 1984) reported that the blubber of humpback dolphins in South African waters is somewhat thicker than those of sympatrically occurring Indo-Pacific bottlenose dolphins (*Tursipos adancus*) from the same region.

Externally, the Atlantic humpback dolphins are similar in colour and shape to the Indian Ocean humpback dolphins (Jefferson and Rosenbaum 2014). However, the morphological differences between Indian Ocean humpback dolphins and Indo-Pacific humpback dolphins are very substantial and therefore it remains surprising that these animals were for so long (approximately two decades) referred to as two so-called "forms" of the same species. The dolphins in western Indian Ocean, currently recognised as *S. plumbea*, are uniformly gray in colour and have a well-pronounced very prominent dorsal hump. The Indo-Pacific humpback dolphins, on the other hand, are born as dark gray, becoming light gray as juveniles and white to light pink as adults, without a prominent dorsal hump but only a relatively small dorsal ridge instead (Jefferson and Rosenbaum 2014).

1.4 Age and development

Marine mammals are large-bodied and long-lived, following a typical k-selection strategy (Finley 2001; Reznick et al. 2002). The lifetime reproductive output of females is generally low, yet information of age- and sex-specific survival rates is commonly not available for free-ranging populations (Bowen and Siniff 1999).

Cetacean life history parameters are hard to obtain and there is no complete set of such parameters for any of the *Sousa* species, but they are thought to be similar between the four currently recognised species. In this respect, recent studies off Taiwan's west coast (Chang 2011; Chang et al. 2016) and in Pearl River Estuary (Jefferson et al. 2012) provide a valuable and rare contribution. Age estimation was not determined in earlier studies (e.g. Saayman and Taylor 1979), but in a subsequent work the longevity was estimated to be approximately 38 years (Crokcroft 1989; Jefferson et al. 2012). Sexual maturity of males and females is estimated at 11-13 and 9-10 years, respectively (Jefferson 2000; Jefferson et al. 2012). Courtship and mating behaviour was observed in Algoa Bay, South Africa (Karczmarski et al. 1997), with summer apparently being a primary breeding season (Karczmarski and Cockcroft 1999), which seems to be related to seasonal environmental factors (Karczmarski 1999), such as seawater temperature and abundance of inshore prey (Karczmarski 1996).

Gestation period in humpback dolphins appears to last one year (Ross 1984; Ross et al. 1994), and maternal care lasts approximately three years, as observed in waters of Algoa Bay, South Africa (Karczmarski 1996; 1999). Saayman and Tayler (1979) suggested five development stages of humpback dolphins: calf I, calf II, juvenile, grayback, and whitefin. In subsequent studies, these five stages were simplified to three stages (Karczmarski 1996; 1999) and this classification was also followed in the current study; it is summarised as follows:

Stage	**Description**	**Behaviour**
Calf	2/3 or less the length of an adult (very young calves are about 1 m long (i.e. < 8 weeks old), visible foetal folds, light gray, disproportionately large melon)	Regularly accompanying a larger animal, presumed to be the mother (head-slapping when breathing)
Juvenile	Approx. 2 m in length, visibly less robust than adults	Swim independently
Adult	Approx. 2.5 m in length, robust in form	Swim independently, well pronounced dorsal hump

1.5 Habitat preferences

Throughout their range, all species of the genus *Sousa* inhabit shallow coastal waters and are typically found in waters less than 20 m deep (Ross et al. 1994; Jefferson and Karczmarski 2001; Jefferson and Rosenbaum 2014). Their narrow habitat selectivity and year-round dependence on inshore shallow water environments was first described by Karczmarski (1996) and Karczmarski et al. (2000a) and subsequently confirmed by several other studies elsewhere (e.g. Chang et al. 2016; Guissamulo 2008; Karczmarski et al. 2016a; Keith et al. 2002; 2013; Parra et al. 2006a; 2006b; Stensland et al. 2006; Sutaria and Jefferson 2004; Van Waerebeek et al. 2004). In South Africa, humpback dolphins are seen generally less than a kilometre off the shore, usually within 250-500m from the shore, and very frequently less than 250m from the shore (Karczmarski et al. 2000a; 2000b; Keith et al. 2013; Koper et al. 2016; Saayman and Taylor 1979).

Saayman and Taylor (1979) suggested that the piscivorous diet of humpback dolphins makes them forage on reef-dwelling fish in inshore habitats where water depth remains shallow. This, given the generally small groups of humpback dolphins (see further) corresponds with the socio-ecological model of delphinid groups proposed recently by Gowans, Würsig and Karczmarski (2008). The inshore distribution can facilitate making the most of predictable, albeit limited inshore prey resources and serve as anti-predator behaviour (i.e. reduce shark predation). A relatively high shark predation on humpback dolphins was reported in both South Africa (Cockcroft 1991) and elsewhere (Cockcroft 1991; Corkeron et al. 1997).

In southern Africa, humpback dolphins inhibit variety of coastal habitats with a common feature of providing a relatively sheltered environment, such as enclosed protected bay, coastal lagoons, areas with extensive seagrass meadows, coastal rocky reefs, coral reef habitats, and estuarine system (Atkins et al. 2004; Durham 1994; Guissamulo 2008; Guissamulo and Cockcroft 2004; Karczmarski 1996; Karczmarski et al. 2000a; Keith et al. 2013). They do not show any particular preference for turbid or clear water but seem to use these coastal areas based on the environmental features that facilitate natural aggregation of their prey and provide shelter (Karczmarski et al. 2000a; Keith et al. 2013). Areas that lack such features, such as long stretches of exposed sandy shores, are very seldom visited by these dolphins (Karczmarski 1996; Karczmarski et al. 2000a).

Systematic monitoring of humpback dolphin distribution and numbers along with other relevant ecological parameters of their habitat are rare. In that context, a long term effort by researchers from Taiwan represents a notable and valuable exception, where both the data on dolphin numbers and distribution are collected along with data on their prey species and relevant environmental characteristics of their habitat (Chou 2007; 2009; Chou and Chen 2011; Chou and Lee 2010; Chou et al. 2011), which then can be used for a broader assessment of long-term impact of habitat degradation (Karczmarski et al. 2016a).

1.6 Behaviour and behavioural ecology

Humpback dolphins display a distinguishable diurnal foraging pattern (Karczmarski and Cockcroft 1999; Karczmarski et al. 2000b; Saayman and Taylor 1979) that peaks in the morning but decrease gradually through the day and increases again shortly before sunset (Karczmarski and Cockcroft 1999). In Algoa Bay, on the Eastern Cape coast, their feeding pattern varies little with season and tidal stage (Karczmarski and Cockcroft 1997). In Maputo Bay, Mozambique, their feeding pattern seems to be related to the tidal cycle (Guissamulo 2008), similarly as it was suggested to be the case in Hong Kong waters (Parsons 1998). Consequently, it is very likely that the specifics of local environmental conditions (e.g. the openness of the coastal habitat in Algoa Bay *vs*. enclosure of the habitat and very large tidal difference in Maputo Bay) may determine the daily foraging patterns of these dolphins. In open coastal habitat of Algoa Bay, humpback dolphins were reported to forage individually and with very little or no co-operation (Karczmarski et al. 1997), whereas cooperative foraging (strand feeding) was seen by Peddemors and Thompson (1994) in coastal environment on Bazaruto Archipelago, Mozambique; and area characterised by large tidal difference and gently sloping sandy inlets. To date, nocturnal behaviour of these dolphins remains unknown.

In waters off Eastern Cape, South Africa, humpback dolphins are reported to display seasonal variation in abundance and group size, likely a result of migration, or perhaps seasonal shift in the range use pattern, that may follow seasonal differences in the distribution of their prey (Karczmarski and Cockcroft 1999; Karczmarsju et al. 1999b). The extent of individual ranges remain poorly known, but occasional movement exceeding 110 km (Karczmarski 1996) and up to 150 km (Keith et al. 2002) were reported in waters off Eastern Cape and KwaZulu-Natal, respectively. Sighting rates of humpback dolphins reported to date (Atkins et al. 2014, Karczmarski 1996, Keith et al. 2002) are generally low, indicating low site fidelity. In Algoa Bay, only about 10% of the population displayed slightly higher affinity to this specific site (Karczmarski 1999).

Grouping patterns of humpback dolphins indicate a generally fluid social system, with variable group membership (Karczmarski 1999). Bonding between individuals, at a level other than mother-calve pair, appears to be generally weak, and fluid group membership represents the general pattern for these dolphins in both South African and Hong Kong waters (Karczmarski 1999; Jefferson 2000; Keith et al. 2002). In Algoa Bay, South Africa, group size was reported to vary between 3 and up to 24 individuals, with majority of groups numbering less than six individuals (Karczmarski 1999; Karczmarski et al. 1999b); similarly, as described in earlier studies in Plettenberg Bay (6-7 individuals per group) by Saayman and Tayler (1979). Elsewhere, a predominant group size of 2-4 individuals was reported for Hong Kong waters (Jefferson 2000; Parsons 1998) and Moreton and Cleveland Bay, Australia (Cockeron et. al 1997 and Parra 2005, respectively); and less than 3 individuals per group in waters off the Goa coast, India (Parson 1998). However, larger groups were also seen, albeit infrequent, reaching 13 individuals off Madagascar (Razafindrakoto et al. 2004) and 15 individuals in Maputo Bay (Guissamulo and Cockcroft 2004). Occasional sighting of large groups numbering 50-100 individuals are known from the Persian region (Baldwin et al. 2004), and may represent a temporal aggregation of several smaller groups, as know also from Hong Kong waters (personal observation).

The demand of motherhood may influence the grouping pattern of nursing female humpback dolphins, as suggested by Karczmarski (1999) and, subsequently, it may affect the social and sexual strategies of males. Saayman and Tayler (1979) reported that in Plettenberg Bay, groups were generally more cohesive if included mother-calf pair than non-calf group. Karczmarski (1996; 1999) indicated that maternal care lasts 3-4 years and calving interval approximates 3 years, and that the ranging pattern of females and their site fidelity may differ with their reproductive status. Furthermore, there were indications, albeit preliminary, of temporal segregation of sex- and age-group of humpback dolphins off the Eastern Cape coast, suggesting that mate-searching behaviour may be applied in male reproductive strategies (Karczmarski 1999). However, a more stable social system of humpback dolphin was observed in more protected inshore waters of Maputo bay, Mozambique (Guissamulo and Cockcroft 2004), which indicates likely environmental influence group dynamics. However, due to very limited information of predation risk, foraging and ranging behaviour of this species, the current understanding of their social structure remains far from conclusive.

Unlike other behaviours, resting has been directly observed only on a few occasions, and was described as remaining in an area without obvious feeding or any socializing interactions (Saayman and Tayler 1979). Socializing and play may consist of various vigorous behaviours, with frequent body-contact, leaping, breaching, surfing, and high-speed chasing (Karczmarski et al. 1997; Saayman and Tayler 1979). Several other behaviours observed in earlier studies include courtship and mating, allo-maternal grouping, various interactions with bottlenose dolphins, and their avoidance of motor-powered boats, which indicates their susceptibility anthropogenic disturbance (Karczmarski et al. 1997; Stensland et al. 2006).

1.7 Population estimates

In South African ocean, humpback dolphin population numbers have been estimated in Algoa Bay and Richards Bay, on the Eastern Cape and KwaZulu-Natal coast, respectively, and seem to be in the range of few hundred; *ca.* 450–480 in the Algoa Bay region (Karczmarski et al. 1999b) and *ca.* 240–260 in Richards Bay (Atkins et al. 2004). Elsewhere in the region, the numbers are thought to be lower; *ca.* 105 individuals estimated in Maputo Bay, Mozambique (Guissamulo and Cockcroft 2004), and further north, off the south-east coast of Zanzibar, the population is estimated to number *ca*. 58-65 (Stensland et al. 2006).

Very few population estimates are known from other regions. In Asia, *ca.* 76-86 humpback dolphins are estimated in coastal waters of Ximen, China (Chen et al. 2008 and 2009) and a population of less than 100 individuals is reported off Taiwan's west coast (Wang et al. 2007; 2012; Yu et al. 2010). Indo-Pacific humpback dolphins inhabiting the Pearl River Estuary (mainland China/Hong Kong region) are thought to represent the world's largest population of the genus *Sousa*, numbering *ca.* 2500 individuals (Chen et al. 2010), although these estimates are derived from a very simplistic approach and should be viewed cautiously (as discussed in Karczmarski et al. 2016b). This population, however, has undergone a dramatic decline and may soon approach the threshold of its demographic stochasticity (Huang et al. 2012; Karczmarski et al. In Press). Elsewhere, known population numbers are generally in the range of few tens to few hundred; *ca.* 120 individuals in Moreton Bay, Australia (Cockeron et al. 1997), slightly over 60 individuals in Cleveland Bay, Australia (Parra 2005) and *ca.* 150 individuals in Great Sandy Strait, Queensland Australia (Canazzi et al. 2009). However in most cases, accurate estimates of population parameters other than just population size are rare, with the recent work by Chan and Karczmarski in Hong Kong representing a rare exception (Chan and Karczmarski, In Press).

1.8 Human impacts

The narrow habitat-selectivity of humpback dolphins puts them in direct threat due to many human activities in the coastal waters. In some areas, they are incidentally killed as result of fishery by-catch (Beadon 1991; Gallagher 1991; Papstavrou and Salm 1991; Read and Murray 2000; Salm 1992). In the past, in some regions, they were directly hunted for human consumption (Alling 1983; Baldwin and Salm 1994; Gallagher 1991; Leatherwood and Reeves 1983; Papastavrou and Salm 1991; Ross et al. 1994), although this apparently is less so at present (Karczmarski 2000).

One of the better known cases of such human-caused mortality is the incidental entanglements in shark nets, such as those in Richards Bay, South Africa. Originally set to reduce the number of shark attacks, the nets have resulted in major casualties for humpback dolphins and several other species of marine macrofauna (e.g. Atkins et al. 2004; 2013; Cockcroft 1990, 1994; Keith 2002; Pedemors et al. 1997). Similar impacts are also known from Australia, along the coasts of Queensland and New South Wales where the use of anti-shark nets originated (Heinsohn 1979; Parra *et al.* 2004; Ross *et al.* 1994). In South Africa, it is estimated that approximately 4% of the population of humpback dolphins is killed as by-catch in shark nets annually (Atkins et al. 2004; Cockcroft 1990), which is reported to be double the annual sustainable mortality rate

(International Whaling Commission 1994). Recently, Atkins et al. (2013) reported that there are on average 6.8 humpback dolphins (203 individuals over 30 years, 1980-2009) caught as by-catch in shark nets in South African waters per annum, raising concerns about sustainability of small populations.

Humpback dolphins are susceptible to the influence of heavy boat traffic (Baldwin 1995; Parson and Jefferson 2000), dolphin watching operations (e.g. Parra et al. 2004), and other recreational water craft (Karczmarski et al. 1997; Koper et al. 2016), especially when these activities overlaps with preferred dolphin foraging areas. Intensive marine traffic is a major component of under-water noise disturbance. Noise are reported to lead to behavioural changes, and can lead to displacement from core areas (Weilgart 2007). A further aspect of boat traffic, it may cause direct kills by boat collisions, especially in urbanised regions (e.g. in Hong Kong waters, at least three humpback dolphins were killed by boat strikes during 1993-1998, equivalent of 14% of all humpback dolphin stranding cases in Hong Kong during that period; Parsons and Jefferson 2000).

Their restricted inshore distribution and narrow habitat selectivity makes humpback dolphins highly susceptible to the degradation of inshore habitats (Huang et al. 2014; Karczmarski 1999; 2000; Karczmarski et al. 2016a; 2016b; Jefferson 2000; Koper et al. 2016; Parra and Cagnazzi 2016). Alterations of these habitats, depletion of their natural biological resources, discharge of pollutants, and degradation or destruction of entire habitat patches due to human activities always affects humpback dolphins and in some cases the severity of such impacts may reach beyond reversible levels (Karczmarski 2000; Karczmarski et al. 2016a; 2016b; Jefferson et al. 2009; Ross et al. 2010). In many such cases, the overall state of the environment is likely a major factor in determining the fate of local populations (e.g. Huang and Karczmarski 2014). Consequently, the conservation of humpback dolphins has to begin with an appropriate understanding of their population ecology and effective protection of their critical habitats.

Chapter 2. Overview of Research Techniques

2.1 Photographic identification

Estimation of population parameters is probably one of the most difficult tasks for marine mammal scientists. However, the most practical and widely applied method is estimating the population size at a particular point in time (Caughley 1977) via photographic identification (photo-ID) and Capture-Mark-Recapture (CMR) techniques (Begon 1979; Seber 1982). In photographic individual identification, the photograph of the upper body and identifiable dorsal fin of a dolphin constitutes the marking/recapture event. The photographic methods do not require a physical restraint and capture/marking of an animal but existing natural marks that already exists, are reliably used to distinguish one individual from another. This approach is effectively used in studies of many species of marine mammals and provides a powerful technique to study population structure and social dynamics, and variety of population parameters (e.g. Hammond et al. 1990).

There have been various developments in the practical application of photo-ID data collection and analyses, but the general principle remains consistent with the broad summary given by Würsig and Jefferson (1990). One of the notable steps in the application of the photo-ID technique to small cetaceans was made by Defran et al. (1990), who proposed coding of dorsal fins of bottlenose dolphin (*Tursiops truncatus*) by calculating a dorsal fin ratio based on the position of the largest notches on the trailing edge of dolphins' dorsal fins. In South Africa, Karczmarski and Cockcroft (1998) developed a matrix photo-ID approach to grade and code the photographs using several more recognizable external features of both humpback dolphins (*Sousa plumbea*, at the time referred to as *S. chinensis*) and indo-Pacific bottlenose dolphins (*Tursiops aduncus*, at the time referred to as *T. truncatus*). This approach includes using features such as the shape of dorsal fin, colour patterns, wound marks and various scars, to identify individual animals. This approach has been also applied in the present study described in this thesis (see later for more detail).

An important development in photo-ID data processing was the application of strictly defined criteria for the assessment of image quality and the distinctiveness of an individual, introduced first by Friday et al. (2000). It helped minimizing unequal catchability related biases, and facilitated greater consistency and comparability among photo-ID studies. This approach is nowadays commonly applied across various photo-ID studies (e.g. Ansmann et al. 2013; Cantor et al. 2012; Chan and Karczmarski In Press; Karczmarski et al. 2005; Silva et al. 2009; Smith et al. 2013).

In general, modern photo-ID requires to use Digital Single Lens Reflex (DSLR) (or Single Lens Reflex (SLR) formerly) camera with a large zoom lens, 70-300 mm or 100-400 mm are the most commonly used. The researcher has to take photographs for every dorsal fin and upper body of a dolphin, perpendicularly to the dolphins' longitudinal axis. Every identifiable individual is then catalogued and the ID-catalogue is continuously updated, reviewed and cross-referenced, allowing identification of new individuals and re-identification of recurring individuals. Attempts are made to include left/right side images of each identified individual.

2.2 Mark-recapture analyses

Capture-Mark-Recapture method (CMR) (Begon 1979; Seber 1982) is believed to be originally used to estimate the mortality rate due to an outbreak of plague by John Graunt in 1662 (Hald 2003), and was used to estimate population size of France (LaPlace 1786). The application of CMR was then greatly expanded in studies of fish and wildlife populations since 1950s. The basic principal of CMR is that a portion of a population being captured, marked and released is subsequently recaptured at the next capture occasions. It is assumed that the proportion of marked individuals among the recaptured sample should be the same as the proportion of first captured individuals in the entire population (Begon 1979; Seber 1982). This approach is very useful in the estimation of the size of a population when it is not possible to count all the individuals in the population.

As to the assumption of a closed population; there should be no additions to the population neither through recruitment nor immigration, and no removals/losses due to mortality or emigration. Only then can closed population models (e.g. Lincoln-Peterson estimator) be used for CMR analyses (Begon 1979; Seber 1982). Where these assumptions cannot be met, e.g. study period is relatively long and/or the population is changing, then the open population model, such as Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965) and POPAN model (Schwarz and Arnason 1996) would be more appropriate for the estimations of population parameters, survival rates and re-capture probability. However, it is often not easy to distinguish recruitment from immigration, or mortality from emigration even in open population models. Moreover, during the application of open population models, goodness-of-fit (GOF) tests, such as U-CARE (Choquet et al. 2009), bootstrap and median-ĉ, are used to examine if the models sufficiently fit the mark-recapture data and to identify the appropriate starting model before the estimation of parameters.

Program MARK (White and Burnham 1999) has been extensively used for mark-recapture analyses in many studies of various dolphins species, for example common bottlenose dolphins (*Tursiops truncatus*) off the Azores archipelago (Silva et al. 2009), Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in the Algoa Bay region, South Africa (Reisinger and Karczmarski 2010), Indian Ocean humpback dolphins (*Sousa plumbea*) off Algoa Bay, South Africa (Karczmarski et al. 1999a), Indo-Pacific humpback dolphins (*Sousa chinensis*) in Hong Kong waters (Chan and Karczmarski, In Press), melon-headed whales (*Peponocephala electra*) off the main Hawaiian Islands (Aschettino 2011), Guiana dolphins (*Sotalia guianensis*) off northern Brazilian coast (Cantor et al. 2012) and many others. In this study, program MARK was also used for the estimation of the population parameters and size of Indian Ocean humpback dolphins in Plettenberg Bay, South Africa.

2.3 Socio-behavioural analyses

To better understand social dynamics of group living animals, one has to quantify the patterns of interactions between individuals. Contrary to many terrestrial species, for marine mammals the type and nature of interactions are frequently impossible to discern as the animals spend only a brief moments of time at the water surface. Consequently, adopting the principle that animals interact spatially while also interacting with one another socially, by quantifying the frequency of interactions we can describe the strength and stability of inter-individual associations (Whitehead and Dufault 1999; Whitehead 2008). A useful tool for doing so with the application of individual photo-identification technique is a computerized program "SOCPROG" (Whitehead 2008; 2009; 2014), which has in recent years been widely used for analysing social structure of variety of mammalian taxa (e.g. Chang 2011; Gowans et al. 2001; Karczmarski et al. 2005; Wittemyer and Getz 2007; Gero et al. 2015).

Generally, it is either as 'presence in the same group' or as 'nearest-neighbours' within a larger group, that defines associations between pairs of individuals (Whitehead 1995, 1997, 1999). This pattern of associations can be documented with photo-ID techniques during sampling occasions (photo-ID encounters) indexed by time, and can be measured using Association Indices (Cairns & Schwager 1987, Ginsberg & Young 1992) which range between 0 and 1 (where 0 indicates individuals that were never seen together and 1 indicates individuals that are always seen together). Such a field sampling approach, if performed frequently across a sufficiently long study period, can provide a reliable measure of social stability within and between groups of studied animals (Whitehead 1995). A comprehensive conceptual overview of this research approach is given by Whitehead (2008).

Temporal analyses, which are methodologically challenging and were seldom performed prior to the introduction of SOCPROG, apply likelihood models to estimate the probability of certain behavioural patterns across a time scale. The "lagged association rates" represent an estimate of the probability that two individuals associated at a particular time are still associated a certain time (time lag) later. Mathematical models of the temporal permanence of relationships can be fitted to the observed pattern (collected data) and can be tested against one another with time interval as a variable. Furthermore, they can be tested against the null association rate (null model) which represents the expected values of associations if the associations were by chance alone. The fit of models to the observed data can be measured with Akaike Information Criterion (AIC), while the standard error for each model parameter is generally calculated using Jackknife procedure (Whitehead 2008; 2009; 2014).

Temporal pattern on individual movement can also be quantified to determine individual residence rate as a measure of site fidelity. If studies are conducted across several research sites, spatial and temporal movement within and between photo-sampling locations can be quantified to determine individual transition probabilities between locations and gain greater insights into the movement patterns (Whitehead 2001). In such studies, calculating lagged identification rates is very useful as these rates represents the probability that an individual identified at any particular time will be identified again in the study area a certain time unit (time lag) later (Whitehead 2001; 2008). Subsequently, models of residency can be fitted to the observed data with maximum likelihood and AIC methods used to determine the best model; and Jackknife techniques can be used to calculate 95% confidence intervals and standard errors for each model parameter. In the study described in this thesis, only individual residence rates were calculated as a measure of individual site fidelity, as the data was collected from a single study area.

Chapter 3. Study Area

The location of the field data collection was Plettenberg Bay (34^{o}03’S, 23^{o}29’E), on the south coast of South Africa; administratively within the Western Cape Province but on the borderline with Eastern Cape. The area has a mild maritime temperate climate with few rainfall or temperature extremes. The bay is defined on the southern end by the Robberg Peninsula (a location off Robberg Nature Reserve), which separates the bay from the open Indian Ocean. The estuary of Keurbooms River, in the central section of the bay's coastline, forms a protected shallow-water lagoon.

Figure 1. The Plettenberg Bay (34^{o}00’S, 23^{o}29’E) area which formed part of the research site, on the Eastern Cape coast, South Africa (Source: Google map).

The marine ecoregion of Plettenberg Bay falls within the Agulhas Bank Bioregion, specifically within the Agulhas inshore ecozone. A considerable diversity of marine species is supported by deep water upwelling which brings cold water into the bay, and warm water eddies that originate from the Agulhas current offshore. There are many pelagic birds in the area as well as the endangered African oystercatcher (*Haematopus moquini*) which live along the shores.

The Robberg Peninsula is home to a large Cape fur seal (*Arctocephalus pusillus pusillus*) colony, which attracts great white sharks (*Carcharodon carcharias*). Among cetaceans, Southern right whales (*Eubalaena australis*) are a common sight in the bay during their breeding season from July to December. Bryde's whales (*Balaenoptera brydei*) can be seen throughout the year, but seem to be most frequent during the summer months. Humpback whales (*Megaptera novaeangliae*) migrate past the Bay during July and December. Killer whales (*Orcinus orca*) and sei whales (*Balaenoptera borealis*) are occasionally sighted. Two coastal species of dolphins can be seen throughout the year, the Indo-Pacific bottlenosed dolphin (*Tursiops aduncus*) and Indian Ocean humpback dolphin (*Sousa plumbea*). Common dolphins (*Delphinus capensis*) appear to be more seasonal.

Terrestrial vegetation varies from Cape Fynbos to Knysna-Amatola montane forests further inland. The gully of the Keurbooms River hosts one of the best examples of the original indigenous forest, which is home to Knysna Loerie (*Tauraco corythaix*). Robberg Peninsula is a well known Fynbos reserve.

Chapter 4. Population Parameters of Humpback Dolphins (*Sousa plumbea*) in Plettenberg Bay

4.1 Introduction

In their early pioneering work, Saayman and Tayler (1979) began the first systematic shore-based surveys of humpback dolphins at two vantage points from peninsular cliff on Robberg peninsula in Plettenberg Bay, on southern Eastern Cape coast of South Africa. The observation sites were 450m above the sea level, and the study was performed from November 1970 to July 1973. It furnished the first published behavioural and ecological information on humpback dolphins based on systematic multi-year field research.

Following this early research by Saayman and Tayler, there have been no dedicated field studies of humpback dolphins up until early-mid 1990s in Algoa Bay, to the east of Plettenberg Bay, on the Eastern Cape coast (Karczmarski 1996), which applied individual photo-identification (photo-ID) technique as the primary research approach. However, it took several more years, through to the end of 1990s, before any further field research returned to the region of Plettenberg Bay. In 1999, twenty years after the classic publication by Saayman and Tayler (1979), a research team led by V.G. Cockcroft initiated boat-based photo-ID field surveys which were, with varied intensity, continued for several years. The work presented in this chapter covers the study period from the inception of the field research in early 1999 through early 2004. It applies photo-ID mark-recapture techniques to investigate population parameters and estimate the population size of humpback dolphins inhabiting the Plettenberg Bay region.

4.2 Materials and Methods

4.2.1 Study Area and Data collection

Field data collection was performed by a research team led by V.G. Cockcroft in Plettenberg Bay (34°03'S, 23°29'E), on the Eastern Cape coast, South Africa (Chapter 3, Fig. 1). Field surveys covered approximately 22km of coastline, from the rocky shores of Robberg peninsula, along the sandy shoreline of the Bay to the estuarine area of the Keurbooms River estuary.

Boat-based photo-ID surveys were conducted from April 1999 to April 2004, weather permitting, with sea state ≤ 3 in Beaufort scale. In search of dolphins, the survey boat moved at a constant speed of 5-8 knots per hour, with observers scanning the coastal waters with naked eye and with the aid of binoculars. Once a dolphin or group of dolphins was sighted, the animals were approached at low speeds to a parallel position, and dolphins were photographed aiming at their dorsal fins and upper body, using Canon Single Lens Reflex (SLR) and digital SLR (DSLR) cameras with 70-300mm telephoto zoom lenses. A conscious effort was made to photo-capture all group members regardless of the characteristics of individuals or the side of fins.

4.2.2 Photo-identification

When processing the ID-images, the image quality was assessed using on 1-100 scale (similarly as in Karczmarski et al. 2005), taking into account the focus of the image, contrast, parallax, and exposure of the fin above the water. All identifiable individuals were catalogued based on individually distinctive features on dorsal fins and upper bodies (dorsal humps), including the shape, number and position of notches as well as scars and other natural markings on the body. To ensure the correct identification of individuals, only photos scored ≥80 were included in the database for further mark-recapture analyses (see Karczmarski et al. 2005)

4.2.3 Mark-Recapture

For mark-recapture analyses, two annual seasons were defined following Karczmaski et al. (1999), when May-October is distinguished as "dry" season and Nov-Apr as "wet" season. We undertook a seasonal analysis to investigate if Sousa present seasonal behaviours or movement as well as to allow for comparisons with other studies (Karczmaski et al. 1999; Wang et al. 2016). The individual sighting histories were summarized and pooled to 6-month seasonal occasions using Microsoft Excel spreadsheet. Subsequently, the sighting histories were analysed using program MARK (version 8.0; White and Burnham 1999).

Due to the relatively long study period and the geographic area (potentially demographically openness of study population), open population models were used in this study. The Cormack-Jolly-Seber (CSJ) model (Cormack 1964; Jolly 1965; Seber 1965) was applied for the estimation of apparent survival rate (ϕ) and recapture probability (c). The POPAN formulation of Jolly-Seber model (Schwarz and Arnason 1996) was used to provide the super population size estimates (N), in which both models follow several standard assumptions that:

1. the marks are not lost or changed frequently, and all marked or unmarked animals have the same probability of being captured (here: photographed) at any occasions (i.e. equal capture probability),
2. all marked animals have the same survival probability at any time intervals, and
3. sampling is instantaneous, so that immigration and emigration of the animals are allowed.

Goodness-of-fit (GOF) tests were performed to confirm that the starting models sufficiently fit the data. GOF TEST.2 as well as TEST.3 of Programs RELEASE and U-CARE (Choquet et al. 2009) were used to examine the heterogeneity of apparent survival rates (Test.2) and capture probabilities (Test.3) in the data. A number of methods, including RELEASE, U-CARE, bootstrap and median-ĉ, were used to estimate the variance inflation factor (ĉ) as a measurement of overdispersion of data. Candidate models were built with various effects, namely time dependent (‘t’), constant over occasions (‘.’), seasonal variation (‘season’), survey intensity (‘effort’) and transient effect (or 2-class time-since marking, TSM) (‘a2’). Model selection was achieved by arranging all candidate models in ascending order of the corrected Akaike Information Criterion (AICc), or quasi-likelihood AICc (QAICc) if overdispersion was significant (ĉ > 1), where the best fitted models were selected with the lowest AIC values. If there was considerable model uncertainty (i.e. without a dominant candidate model), model averaging was applied to average the parameter estimates across candidate models by the relative corrected AIC (AICc) weights.

Total population sizes (N_T) were projected from the proportion of marked population by the equation: $N_T = N/\theta$, where N is the mark-recapture super-population estimate and θ is the mark-ID ratio. The mark-ID ratio was not available in this study, and instead the ratio estimated previously by Karczmarski *et al.* (1999) for the same species in a neighbouring site, Algoa Bay, was adopted ($\theta = 0.92 \times 0.63 = 0.58$). The variance of total population size was estimated following Wilson et al. (1999) as:

$\mathrm{var}(N_T) = N_T^2 \ (\mathrm{var}(N)/N^2 + (1-\theta)/n\theta \ )$,

where n is the total number of dolphins from which θ was calculated. The lower and upper log-normal 95% confidence intervals were calculated by

$N_{T,lower} = N_T/C$ and $N_{T,upper} = N_T \times C$ respectively, where

$C = \exp (1.96 \sqrt{(\ln (1+ (\sqrt{(\mathrm{var}(N_T))}/N_T)^2))})$ according to Burnham et al. (1987).

4.3 Results

4.3.1 Individual sighting histories

Over the five-year study, more than 20,000 digital photographs were taken. A total of 155 humpback dolphins were identified over 61 encounters during April 1999 to April 2004. The cumulative number of catalogued individuals continued to increase in a steady rate throughout the study period, with no signs of reaching a asymptote/plateau of discovering new individuals (Fig. 1). The individual sighting rates (recaptures) were generally low (Fig. 2), with 72.9% (113/155) of all catalogued individuals seen only once; although the most frequently seen animal was photographed 14 times.

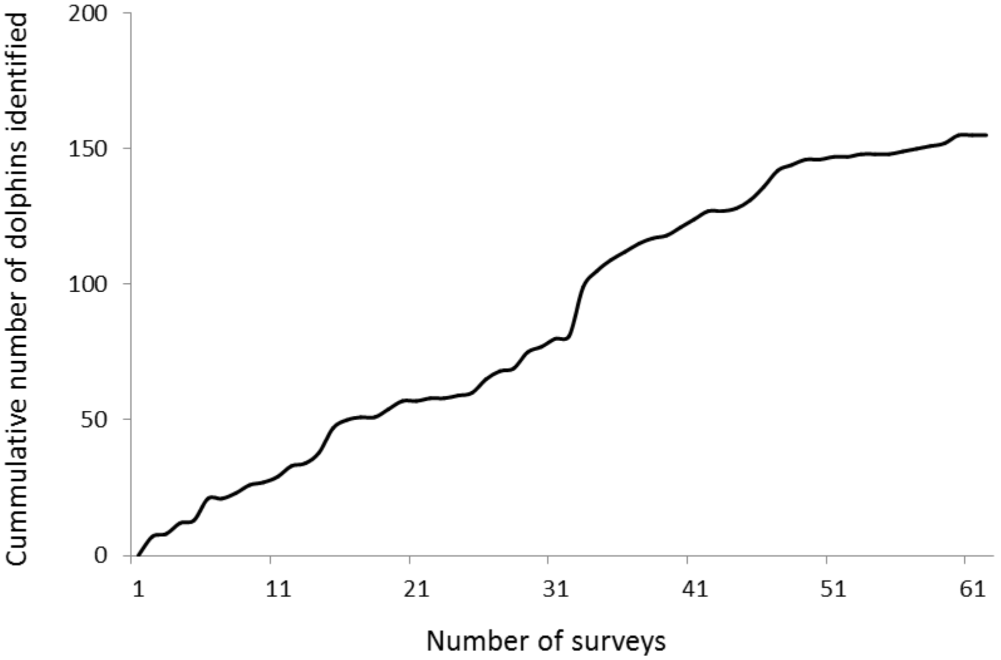

Figure 1. Discovery curve, the cumulative number of humpback dolphins identified in Plettenberg Bay during 61 field surveys from April 1999 to April 2004.

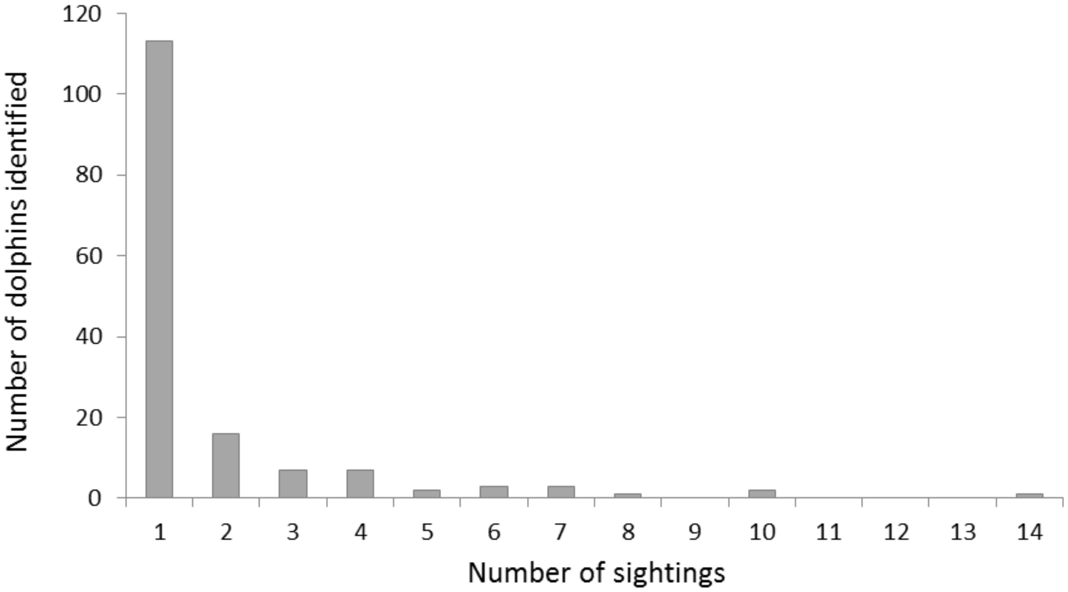

Figure 2. Sighting frequency distribution of humpback dolphins identified in Plettenberg Bay during 61 field surveys from April 1999 to April 2004.

Sighting histories of all identified individuals were pooled into 6-month periods which resulted in nine sampling occasions, as no surveys were conducted during the period November 2001 – April 2002 (Table 1). The first sampling occasion was kept as a 7-month period, to include the first survey of this study in April 1999, the only survey in this month. The pooling of sampling occasions corresponded to the definition of “wet” and “dry” seasons (see earlier). Consequently, the database consisted of three types of seasonal intervals, namely "dry to wet" (e.g. occasion 1 to 2), "wet to dry" (e.g. occasion 2 to 3) and "dry to dry" (occasion 5 to 6). The length of intervals was adjusted accordingly, while running the mark-recapture database on program MARK (Cooch and White 2014).

Table 1. Summary of field surveys conducted in Plettenberg Bay from April 1999 to April 2004.

No. of occasion	Seasonal sampling	No. of sampling occasions	No. of identified dolphin	No. months of sampling	Season
1	Apr 1999 – Oct 1999	13	41	5	Dry
2	Nov 1999 – Apr 2000	2	15	2	Wet
3	May 2000 – Oct 2000	1	5	1	Dry
4	Nov 2000 – Apr 2001	7	13	5	Wet
5	May 2001 – Oct 2001	4	11	3	Dry
6	May 2002 – Oct 2002	13	86	6	Dry
7	Nov 2002 – Apr 2003	15	85	5	Wet
8	May 2003 – Oct 2003	2	14	2	Dry
9	Nov 2003 – Apr 2004	4	15	4	Wet

4.3.2 Model selection for CJS model

GOF TEST 2 of both RELEASE and U-CARE (Choquet et al. 2009) indicated that heterogeneity in recapture probability (trap dependence effect) was not significant, while TEST 3 of U-CARE suggested heterogeneity of apparent survival rates (transient effect) was significant; however, the same test of RELEASE was slightly higher than the significant level (based on a nominal $\alpha = 0.05$ level) (Table 2). Trap dependence effect was negligible and therefore not included in further analytical treatments.

Table 2. Goodness-of-fit test using programs RELEASE and U-CARE (Choquet et al. 2009) for the humpback dolphin database in Plettenberg Bay.

RELEASE GOF test					
Test 2	χ^2	1.470	Test 3	χ^2	19.618
	d.f.	6		d.f.	12
	p value	0.962		p value	**0.075**
Not significant with trap-dependent effect			**Marginal significance with transient effect**		
U-CARE GOF test					
Test 2	χ^2	3.466	Test 3	χ^2	21.977
	d.f.	11		d.f.	12
	p value	0.983		p value	**0.038**
Not significant with trap-dependent effect			**Significant with transient effect**		

Variance inflation factors (ĉ) for transient model and full time-dependent model ranged 0.30-3.09 and 0.82-2.98 (Table 3), respectively, for various methods. As a precautionary approach, to accomodate for overdispersion in data (Cooch and White 2014), the largest ĉ value for transient model by Bootstrap simulation method (ĉ=3.09) was used to adjust QAICc values in the following process of model selection.

Table 3. Estimation of variance inflation factor (ĉ) by RELEASE, U-CARE (Choquet et al. 2009), bootstrap and median-ĉ methods for the humpback dolphin database from Plettenberg Bay.

	RELEASE	U-CARE	Bootstrap	Median-ĉ
(Transient model) ϕ(a2-t/t)p(t)	--	0.30	**3.09**	0.98 (SE 0.019)
(Full time-dependent model) ϕ(t)p(t)	1.172	1.11	2.98	0.82 (SE 0.054)

A total of 25 candidate CJS models were generated for model selection arranged in ascending order of QAICc as shown in Table 4. The initial incorporation of effort effect to capture probability to the starting transient model (24th model) greatly improved QAICc from 25.158 to 12.127 and ranked at 11th. Incorporating the constant-over-time effect for both the TSM classes of apparent survival rates further improved the model performance to become the most parsimonious model. Consequently, the 8th to 25th candidate models had essentially no support (ΔQAICc > 10), while the 5th to 7th candidate models received very little support (ΔQAICc > 7). Moreover, the 1st candidate model comprised about 66% of the total support, which was slightly over 4 times and 5 times than the 2nd and 3rd models, respectively. The most parsimonious CJS candidate model (1st model) therefore received majority of support, indicating a strong influence of transience effect for apparent survival rate and survey effort for capture probability.

Table 4. Model selection of 25 candidate models for Cormack-Jolly-Seber (CJS) model with QAICc arranged in ascending order, to estimate apparent survival rate (ϕ) and recapture probability (p) with variance inflation factor ($\hat{c}$ = 3.09).

No.	MODEL	QAICc	ΔQAICc	QAICc Weight	Model Likelihood	No. of parameters	QDEVIANCE
1	ϕ(a2-./.)p(effort)	120.335	0.000	0.657	1.000	4	28.359
2	ϕ(a2-./season)p(.)	123.314	2.979	0.148	0.226	3	33.417
3	ϕ(t)p(effort)	123.803	3.469	0.116	0.177	6	27.607
4	ϕ(a2-season/season)p(.)	126.420	6.086	0.031	0.048	5	32.345
5	ϕ(a2-./t)p(effort)	128.087	7.752	0.014	0.021	6	31.890
6	ϕ(a2-t/.) p(effort)	129.112	8.778	0.008	0.012	9	26.425
7	ϕ(a2-season/t) p(.)	129.393	9.058	0.007	0.011	7	31.054
8	ϕ(.)p(.)	130.500	10.166	0.004	0.006	2	42.663
9	ϕ(a2-t/season)p(.)	130.603	10.268	0.004	0.006	8	30.101
10	ϕ(a2-./.)p(t)	131.054	10.719	0.003	0.005	10	26.158
11	ϕ(a2-t/t)p(effort)	132.462	12.127	0.002	0.002	11	25.336
12	ϕ(a2-./t)p(t)	132.502	12.168	0.002	0.002	11	25.376
13	ϕ(season)p(.)	132.514	12.180	0.001	0.002	4	40.538
14	ϕ(a2-t/t)p(.)	132.961	12.626	0.001	0.002	10	28.065
15	ϕ(a2-./season)p(t)	133.109	12.775	0.001	0.002	11	25.984
16	ϕ(season)p(season)	135.756	15.421	0.000	0.000	6	39.559
17	ϕ(.)p(t)	137.180	16.846	0.000	0.000	9	34.493
18	ϕ(a2-season/season)p(t)	137.281	16.946	0.000	0.000	13	25.626
19	ϕ(t)p(.)	137.692	17.357	0.000	0.000	8	37.190
20	ϕ(a2-season/t)p(t)	138.934	18.600	0.000	0.000	14	24.979
21	ϕ(a2-t/season)p(t)	140.175	19.840	0.000	0.000	15	23.896
22	ϕ(a2-t/.)p(t)	140.628	20.294	0.000	0.000	15	24.350
23	ϕ(season)p(t)	141.480	21.145	0.000	0.000	11	34.354

24	ϕ(a2-t/t)p(t)	141.492	21.158	0.000	0.000	16	22.866
25	ϕ(t)p(t)	145.798	25.463	0.000	0.000	14	31.843

4.3.3 Survival and recapture parameters

The apparent survival rate of humpback dolphins of the first time-class in the TSM model, as the mixture of transient and resident individuals, was estimated to be 0.142 (SE = 0.069) constant across occasions. For the individuals from the second time-class composed of only resident individuals, the apparent survival rate was estimated to be 0.847 (SE = 0.142).

There was no heterogeneity of recapture probability between individuals, since trap dependence effect was insignificant by GOF tests. The estimates of recapture rate for humpback dolphins at different occasions ranged from 0.219 ± SE=0.081 to 0.672 ± SE=0.148 (Table 5).

Table 5. Recapture probability of humpback dolphins in Plettenberg bay during April 1999 - April 2004.

Number of occasion	Recapture probability	Standard Error (SE)
2	0.245	0.081
3	0.219	0.081
4	0.397	0.094
5	0.301	0.083
6	0.607	0.138
7	0.672	0.148
8	0.245	0.081
9	0.272	0.082

4.3.4 Model selection for POPAN model

Two time-classes (a2) transient effect and the trap dependent effect model were not applicable in POPAN formulation of Jolly-Seber model. As a result, there were thirteen POPAN candidate models with different effects formulated as shown in Table 6. The 6th to 12th POPAN candidate models received no support in explaining the data (ΔQAICc >10); and the 3rd to 5th models were poorly supported as their ΔQAICc are larger than 7. The ΔQAICc values between the 1st and the 2nd POPAN candidate model was 0.457 (i.e. less than 2), and these two models comprised slightly over 54% and 43% QAICc weight in data respectively. It indicated that both the 1st and the 2nd POPAN candidate models had similarly strong support in data, and hence the model averaging method was used for the estimation of population parameters for the sampled humpback dolphins in this study.

Table 6. Model selection of 12 candidate models for POPAN with QAICc arranged in ascending order, to estimate overall super population size with variance inflation factor ($\hat{c}$ = 3.09)

No.	POPAN MODEL	QAICc	ΔQAICc	QAICc Weight	Model Likelihood	No. of parameters	QDEVIANCE
1.	ϕ(.)p(.)pent(t)N	157.341	0.000	0.543	1.000	7	-113.272
2	ϕ(season)p(.)pent(t)N	157.797	0.457	0.432	0.796	9	-117.142
3	ϕ(t)p(.)pent(t)N	165.140	7.800	0.011	0.020	14	-120.986
4	ϕ(.)p(t)pent(t)N	165.991	8.651	0.007	0.013	16	-124.762
5	ϕ(t)p(t)pent(t)N	166.274	8.933	0.006	0.012	17	-126.828
6	ϕ(season)p(t)pent(t)N	170.353	13.012	0.001	0.002	18	-125.120
7	ϕ(t)p(t)pent(.)N	17368.784	17211.443	0.000	0.000	14	17082.659
8	ϕ(t)p(.)pent(.)N	17397.556	17240.216	0.000	0.000	4	17133.285
9	ϕ(.)p(.)pent(.)N	17427.869	17270.528	0.000	0.000	3	17165.672
10	ϕ(season)p(t)pent(.)N	22856.403	22699.063	0.000	0.000	10	22579.269
11	ϕ(.)p(t)pent(.)N	22872.616	22715.275	0.000	0.000	9	22597.676
12	ϕ(.)p(t)pent(.)N	22879.262	22721.922	0.000	0.000	12	22597.676

4.3.5 Population parameters

The super-population size (N) of marked humpback dolphins was weight-averaged and estimated at 267 individuals (CV=16.12%; 95% CI=177-357). By adopting the mark-ID ratio from Algoa Bay, the total super-population size including unmarked individuals was estimated at 461 dolphins (CV=17.51%; 95% CI=328-648).

4.4 Discussion

4.4.1 Goodness-of-fit test

The variance inflation factor $\hat{c}$ was estimated at 3.09 using Bootstrap simulation, indicating there was considerable level of overdispersion of data. Although it was slightly over the threshold of $\hat{c} = 3$ suggested by Lebreton et al. (1992), it was necessary to incorporate a transient effect for apparent survival parameters in the starting CJS model, since it was significant in the results of the GOF TEST 3 (Table 2). On the other hand, the results of both RELEASE and U-CARE (Choquet et al. 2009) GOF tests suggested trap-dependent effect for recapture parameters (p) was insignificant. This affirmed the photo-identification surveys in this study did not have any behavioural responses on the dolphins.

4.4.2 Apparent survival rate

Apparent survival rates, which consider both true survival of animals and their permanent emigration, differed greatly between the two TSM classes. Since the CJS model cannot differentiate between emigrations from mortality, individuals seen only once, would lower the estimation of the survival parameter. While almost three quarters of all identified animals were photographed once only throughout the study period (Fig. 2), the apparent survival rate of the first TSM class ($\phi = 0.142$), which includes all individuals seen only once, was considerably underestimated. In contrast, by stratifying TSM classes and separating the more frequently seen dolphins to the second TSM class, the apparent survival rate ($\phi = 0.847$) was relatively unbiased.

A similar pattern of different survival estimates between TSM classes was also observed in other coastal dolphin populations with considerable movement in and out the study areas, albeit to smaller extent (e.g. Silva et al. 2009; Chan and Karczmarski, In Press). This corresponds to the results of GOF tests in this study, and reaffirms the importance of transience in the structure of the humpback dolphin population in Plettenberg Bay. Humpback dolphins in a nearby Algoa Bay are known to exhibit long-range travel along the Eastern Cape coast (Karczmarski et al. 1999a; 1999b). With a very similar topography of a narrow band of shallow inshore waters, it is very likely that humpback dolphins in Pletternberg Bay also undergo frequent and long-distance travel beyond the range of the study site. At the same time, however, some individuals photo-identified in Plettenberg Bay were seen more frequently, up to 14 times, which suggests they may be more resident than most others. Although the sexes of the animals could not be photographically confirmed, it can be hypothesized that the more resident humpback dolphins could be nursing females which seem to prefer more protected shallow areas and reduce the extent of their along-shore travel, as suggested based on a study in Algoa Bay by Karczmarski (1999). By incorporating the various measures and undertaking the various GOF tests, we were able to obtain a better understanding as to which variables influenced the models and the related outcomes for the demographic parameters.

4.4.3 Recapture probability

Although there was a considerable variation of individual sighting frequencies between resighted dolphins (Fig. 2), individual heterogeneity of recapture probability was insignificant according to GOF tests. One plausible reason is that the majority of identified humpback dolphins were seen only once, leaving only a small portion of individual sighting history for the analysis. On the other hand, the recapture rates varied substantially across seasons and were closely correlated to the intensity of survey effort. With the exception of 6th and 7th occasions with more surveys, the recapture probabilities remained low throughout the study period. This result, together with the low resighting frequency, indicates the survey intensity was insufficient in most seasons. More research efforts will be needed to better understand individual site fidelity.

4.4.4 Population estimate

The total super-population size (N) was estimated to be 461 individuals, representing the minimum number of humpback dolphins that use Plettenberg Bay as part of their range during the course of this study. This estimate is similar to the population size estimate in Algoa Bay, South Africa (466 individuals; Karczmarski et al. 1999a). However, given the non-asymptotic discovery curve (Fig. 1) and low resighting frequency (Fig. 2), it is very likely that only a portion of the population was sampled. Moreover, considering the transience and movement pattern of humpback dolphins (see earlier discussion), it is possible that the dolphins sighted in Plettenberg Bay are part of a larger, and possibly interacting biological unit along the South African coast, which was also suggested by Karczmarski et al. (1999a), and the true population size of this larger biological unit/population may be larger than the mark-recapture estimate in Plettenberg Bay. This hypothesis of true population unit, however, cannot be verified at this stage without a robust database cross-referenced between study areas.

Chapter 5. Group Dynamics of Humpback Dolphins (*Sousa plumbea*) in Plettenberg Bay

5.1 Introduction

In studies of delphinid behavioural ecology, as in studies of other group-living animals, descriptors such as group size, group structure and stability, and any potential relations of those with the animal behaviour (e.g. ranging pattern *vs*. group size *vs*. group structure) represent important priority topics to investigate, because such information can facilitate further and more detailed socio-ecological investigations (Gowans et al. 2008), many of which carry considerable conservation implications (Karczmarski 2000; Prange et al. 2004; Strier 1997). However, even though group sizes can be relatively easily estimated for inshore dolphins, such as humpback dolphins that occur generally in small groups (e.g. Karczmarski 1999), and such estimates can be reliably done from shore-based vantage points (e.g. Saayman and Tayler 1979), in order to describe patterns of intra-group dynamics such as group structure and stability (or instability), a reliable data on group membership is needed and such data should cover a substantial temporal scale (e.g. Cagnazzi et al. 2009; Chang 2011; Karczmarski et al. 2005; Wells et al. 1987).

In their early work in Plettenberg Bay, Saayman and Tayler (1979) suggested that the maximum group size of the social unit for humpback dolphin is approximately 25 individuals, comprising different sex and age classes. However, most of the groups observed by Saayman and Tayler were considerably smaller and, consequently, although the authors did not address this issue directly, a fission-fusion pattern of group dynamics was likely; as subsequently documented by Karczmarski (1999) in Algoa Bay. Based on occasional recognition and re-sighting of a few distinctively coloured individuals, Saayman and Tayler (1979) suggested that the dolphins are most likely resident in the coastal waters of Plettenberg Bay. This notion remained unchallenged for many years, up until a more recent study by Karczmarski (1996) revealed a very different pattern in Algoa Bay, only a few hundred kilometres to the east of Plettenberg Bay.

Saayman and Tayler did not have the ability to reliably document the membership of the dolphin groups they observed, due to the technological limitations at the time of their research. These limitations have now been mostly overcome thanks to the frequently used boat-surveys as the platform for data collection and major advances in high-speed professional photographic equipment. Furthermore, recent advances in computer assisted socio-behavioural modelling (e.g. Whitehead 1995; 2007; 2008; 2009; 2014) enable in-depth quantitative analyses of individual-identification data, which opens analytical insights that was not possible during previous studies. This chapter reports on the data, albeit still preliminary, obtained through the application of current photographic field and analytical techniques, and investigates the socio-dynamics of humpback dolphin groups in the coastal waters of Plettenberg Bay.

5.2 Materials and Methods

5.2.1 Study Area, data collection and photo-identification procedure

Field data was collected in coastal waters of Plettenberg Bay, along approximately 22km of coastline between Robberg peninsula and Keurbooms River estuary, during the time period from April 1999 and April 2004. A conscious effort was made to photo-capture all group members regardless of the characteristics of individuals or the side of fins. The field protocol and subsequent data processing followed the same procedures and assessment criteria as described in Chapter 4. All identifiable individuals were catalogued based on individually distinctive features on dorsal fins and upper bodies, including the shape, number and position of notches, scars and other natural markings on the body (Karczmarski and Cockcroft 1998). Only high quality images were used in all subsequent analyses.

5.2.2 Data analyses

5.2.2.1 Measure of associations

To evaluate the strength of social association between dyads of individuals, Association Index was calculated too. In this study, a half-weight index (HWI, Dice 1945) was applied to measure the strength of relationship between two individuals:

$$\text{HWI} = \frac{x}{x + \frac{y_A + y_B}{2}}$$

where x = the number of groups that contained both individuals *A* and *B*, y_A = the number of groups in which only *A* was identified, y_B = the number of groups in which only B was identified. The index ranges from 0 (when *A* and *B* were never seen together) to 1 (when *A* and *B* are always seen together in the same group). Further analyses made use of the software program SOCPROG 2.4 (Whitehead 2009; 2014) that statistically tests the fit of socio-behavioural models to the observed data. The observed pattern of associations between individuals was analyzed based on their strength and temporal stability.

5.2.2.2 Grouping pattern

To determine whether the patterns of associations between individuals were significantly different from random, and to test associations between individual dyads against random, the observed association matrix was permuted following the Manly/Bejder et al. procedure (Bejder et al. 1998, Manly 1995). Average-linkage hierarchical cluster analysis was performed to construct a dendrogram illustrating the grouping pattern of individuals (Morgan *et al.* 1976, Milligan and Cooper 1987). To test how well the dendrogram represented the data, the cophenetic correlation coefficient (CCC) was calculated (Bridge 1993). The CCC ranges from 0 to 1 with 0 representing no relationship and 1 representing and ideal fit. A CCC value > 0.8 indicates that the dendrogram model has a sufficiently good fit (Bridge 1993).

5.2.2.3 Lagged identification rate (LIR)

The residence rate of individuals and patterns of site fidelity were measured by calculating lagged identification rates (Whitehead 2001) and models of residency were fitted to the observed data, with Akaike Information Criterion (AIC) methods used to determine the best model. The lagged identification rate (*R(τ)*) is defined as the probability of seeing an individual in an area after *τ* unit time (Whitehead 2001). It indicates the residence of an individual in a given region;

$$R(\tau)=\frac{\sum\limits_{j,k|(t_k-t_j)=\tau} m_{jk}}{\sum\limits_{j,k|(t_k-t_j)=\tau} n_j * n_k}$$

where t_j = the time of sampling period *j*, n_j = the number of individuals identified in period *j*, m_{jk} = the number of individuals identified in both periods *j* and *k*.

As recommended by Whitehead (2007), the best models of lagged identification rate were selected using Akaike Information Criterion value (AIC), where the lowest value of AIC indicates the best fit model;

$$\text{AIC} = -2 * L' + 2 * K$$

where *K* = the number of estimated parameters plus one, and *L'* equals the sum of log-likelihoods.

5.2.2.4 Standardized lagged association rate (LAR)

To quantify temporal stability of associations, lagged association rates between individuals were calculated (Whitehead 1995). Models of the temporal permanence of relationships were fitted to the data and were tested against one another with time interval as a variable and against the null association rate that represents the expected values if the associations were by chance alone.

The standardized lagged association rate (*g'(τ)*) was adopted following the procedures of Whitehead (1995). The standardized association value was used, which is recommended when some individuals may be missing from the photo-ID record of the group membership as photographed at sea;

$$g'(\tau)=\frac{\sum_{j,k|(t_k-t_j)=\tau}\sum_{A}\sum_{B\neq A}a_j(A,B)*a_k(A,B)}{\sum_{j,k|(t_k-t_j)=\tau}\sum_{A}(\sum_{B\neq A}a_j(A,B))*(\sum_{B\neq A}a_k(A,B))}$$

where $a_j(A, B)$ equals 1 if individuals *A* and *B* were associated in time period *j*; and $a_j(A, B)$ equals 0 if these two individuals were not associated (not seen in the same group) during the sampling period. The standardized lagged association rate ranges from 0 (when *A* and *B* are never seen together) to 1 (when *A* and *B* are always in the same group).

Models of the temporal permanence of associations were fitted to the observed data. Following the recommendations of Whitehead (2007), the best models of standardized lagged association rate were selected using Quasi Akaike Information Criterion value (QAIC), where the lowest value of QAIC indicates the best fit model;

$$\text{QAIC} = -(2 * L' / \hat{c}) + 2 * K$$

where $\hat{c}$ is the variance inflation factor for the most general compared models, and K is the number of parameters plus one, while L' represents the sum of log-likelihoods. Jackknife procedures were used to calculate the standard error for each model parameter.

5.3 Results

5.3.1 Data base

As stated in Chapter 4, there were 61 encounters across the study period (April 1999–April 2004), with over 20,000 digital images taken and 155 individual humpback dolphins identified. The discovery curve of the cumulative number of catalogued individuals continued to increase throughout the study (Chapter 4, Fig. 2) and individual sighting frequencies were generally low (Chapter 4, Fig. 3). The majority of individuals (72.9%) were seen once only. Although 42 individuals (27.1%) were photographed on more than one occasion and the most frequently recorded dolphin was photo-captured 14 times, very few individuals were photographed and identified more than five times (Chapter 4, Fig. 3).

5.3.2 Pattern of associations

Sightings ranged from a solitary individual to groups of 14 individuals, with a mean group size of five. For dolphins sighted > 1 time, the range and mean group size were 1-6 and average of 4 individuals, respectively. The maximum value of half-weight association index per dyad was 0.09 across all individuals, but increased to 0.53 for dolphins sighted more than once. However, the mean association indices for all individuals and those sighted > 1 were 0.03 and 0.07, respectively. Permutation test with 1000 trials showed that SD and CV values of the observed data were greater than the relevant random values (Table 1).

Table 1. Test statistics of permutation test for humpback dolphins seen in Plettenberg Bay between April 1999 and April 2004. HWI - Half-weight association index, SD = standard deviation, and CV = coefficient of variation.

	Mean HWI	**Max HWI**	**Observed SD**	**Observed CV**	**1-sided p**	**Random SD**	**Random CV**
Sighted > 1 time	0.07	0.53	0.133	4.709	0.999	0.005	0.005
			i.e. preferred association				
All individuals	0.03	0.09	0.112	1.590	1.000	0.000	0.002
			i.e. preferred association				

The coefficient of variation (CV) of true association indices, using Poisson approximation method for all individuals and dolphins sighted >1 was estimated to be 1.533 and 0.551, respectively. The correlation between true and estimated association indices using Poisson approximation method for all individual dolphins sighted >1 was estimated at 0.416 and 0.373, respectively; indicating that the data is acceptable for further analyses, but has to be treated with caution.

5.3.3 Site fidelity

Lagged identification rates (LIR) declined throughout the study. Although humpback dolphins appeared to use the study area relatively frequently for a duration exceeding 100 days, as the time lag increased the identification rates notably declined. All models examined for the site fidelity analyses are presented in Table 2.

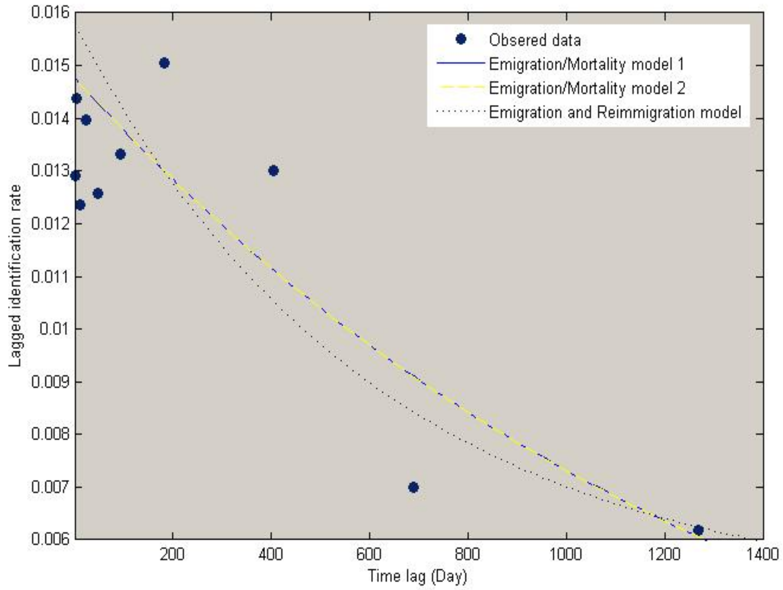

Figure 1. Lagged identification rate of humpback dolphins identified in Plettenberg Bay between April 1999 and April 2004 along with three best models (as indicated in Table 2). The best models include two models of "Emigration/Mortality" (blue line and yellow broken line) and "Emigration and remigration" (black dotted line).

Both the 1st and 2nd model with the minimum QAIC values, indicating that these models are most parsimonious, did not differ substantially in the ΔQAIC value from the 3rd model, suggesting that all three models are similarly well fit to the observed data. The 1st and 2nd models were basically the same, both representing emigration/mortality but differently formulated, whereas the 3rd model depicts emigration and reimmigration (Table 2). Candidate models 6th to 8th had essentially no support in the data, whilst models 4th and 5th had only moderate support (Table 2). As models with the ΔQAIC values between models 0 and 2 are similarly supported by the data (e.g. Burnham and Anderson 2002), all three candidate models, the 1st, 2nd and 3rd were selected for further LIR analyses.

The Lagged identification rates with best fit models for all individuals seen in Plettenberg Bay and for the individuals sighted more than once are shown in Fig. 1 and 2, respectively. Both lagged identification rates of all individuals and those seen in Plettenberg Bay more than once indicate considerably low site fidelity, even though the probabilities of resighting of an individual were relatively high within the initial 100+ days. In both cases, the best fit models were "Emigration/Mortality" and "Emigration and remigration."

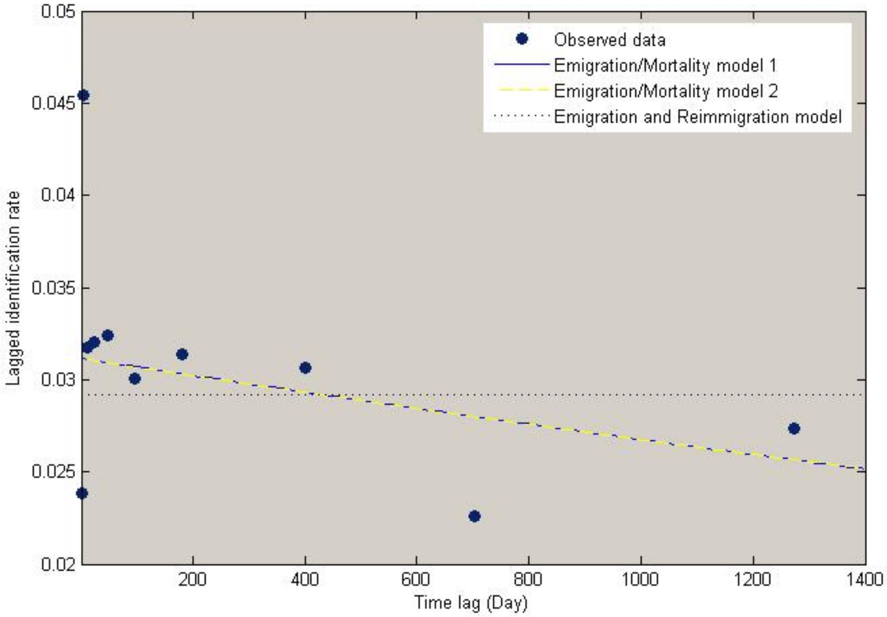

Figure 2. Lagged identification rate for humpback dolphins identified in Plettenberg bay between April 1999 and April 2004 and sighted >1 time. The best models include "Emigration/mortality" (blue line and yellow broken line) and "Emigration and remigration" (black dotted line).

Table 2. Model selection for lagged identification rates (LIR) analyses of humpback dolphins photo-identified in Plettenberg Bay between April 1999 and April 2004, with QAIC arranged in ascending order.

No.	**Model**	**QAIC**	**ΔQAIC**	**Summed Log Likelihood**	**No. of parameter**	**GOF χ^2 (df)**	**p**
1	Emigration/mortality (a1=emigration rate; 1/a2=N)	3157.270	0	-2286.997	2	49.382 (36)	>0.05
2	Emigration/mortality (a1=N; a2=Mean residence)	3157.270	0	-2286.997	2	49.396 (36)	>0.05
3	Emigration + reimmigration (a1=N; a2=Mean time in study area; a3=Mean time out of study area)	3157.417	0.15	-2285.654	3	46.034 (34)	>0.05
4	Emigration + reimmigration + mortality	3161.124	3.85	-2286.891	4	49.288 (34)	<0.05
5	Emigration + reimmigration + mortality (a1=N; a2=Mean time in study area; a3=Mean time out of study area; a4=Mortality rate)	3161.270	4.0	-2286.997	4	49.396 (34)	<0.05
6	Closed (1/a1=N)	3182.922	25.65	-2307.039	1	81.049 (40)	<0.05
7	Closed (a1=N)	3182.922	25.65	-2307.039	1	80.901 (39)	<0.05
8	Closed: Emigration + reimmigration	3186.912	29.64	-2307.032	3	80.997 (38)	<0.05

Although the overall site fidelity was low, there was a notable difference between the pattern of all individuals and the pattern displayed by individuals sighted more than once. The latter indicated a higher affinity to the study area, although the number of these individuals was very low.

5.3.4 Group dynamics

All models examined for temporal group dynamics analyses are presented in Table 3. The ΔQAIC values between the 1st candidate model and the other seven models ranged from 2 to 22813, the 1st candidate model ("Rapid disassociation + Casual acquaintances") was considered to be the best supported by the data.

Table 3. Model selection for lagged association rate (LAR) of humpback dolphins identified in Plettenberg Bay between April 1999 and April 2004 with QAIC arranged in ascending order.

No.	Model	QAIC	ΔQAIC	Summed Log Likelihood	No. of parameter	GOF χ2 (df)	p
1	Rapid dis + Casual acquaintances	424.237	0	-1025.107	2	**132.497 (d.f.=28)**	<0.05
2	Two levels of Casual acquaintances	426.237	2	-1025.107	3	**132.488 (d.f.=27)**	<0.05
3	Rapid dis + two levels of Casual acquaintances	427.258	3.021	-1022.732	4	**131.101 (d.f.=27)**	<0.05
4	Rapid dis + Preferred companions	430.013	5.776	-1043.985	1	**169.082 (d.f.=27)**	<0.05
5	Preferred companions + Casual acquaintances	432.013	7.776	-1043.985	2	**169.082 (d.f.=26)**	<0.05
6	Rapid dis + Preferred companions + Casual acquaintances	433.520	9.283	-1042.788	3	**164.514 (d.f.=25)**	<0.05
7	Casual acquaintances	838.033	413.796	2034.578	1	**2261.623 (d.f.=28)**	<0.05
8	Closed	22813.281	22389.04	-55390.987	0	**169.677 (d.f.=29)**	<0.05

The temporal pattern of group dynamics for all photo-identified humpback dolphins is presented in Fig. 3. There was no indication of temporal group stability and there was no evidence of long-term social bonds. Associations appeared short lasting, with individuals associating and disassociating frequently, suggesting a considerable fluidity of their social system. Both the observed lagged association rates and the model projection approached the level of random associations after approximately 1000 days.

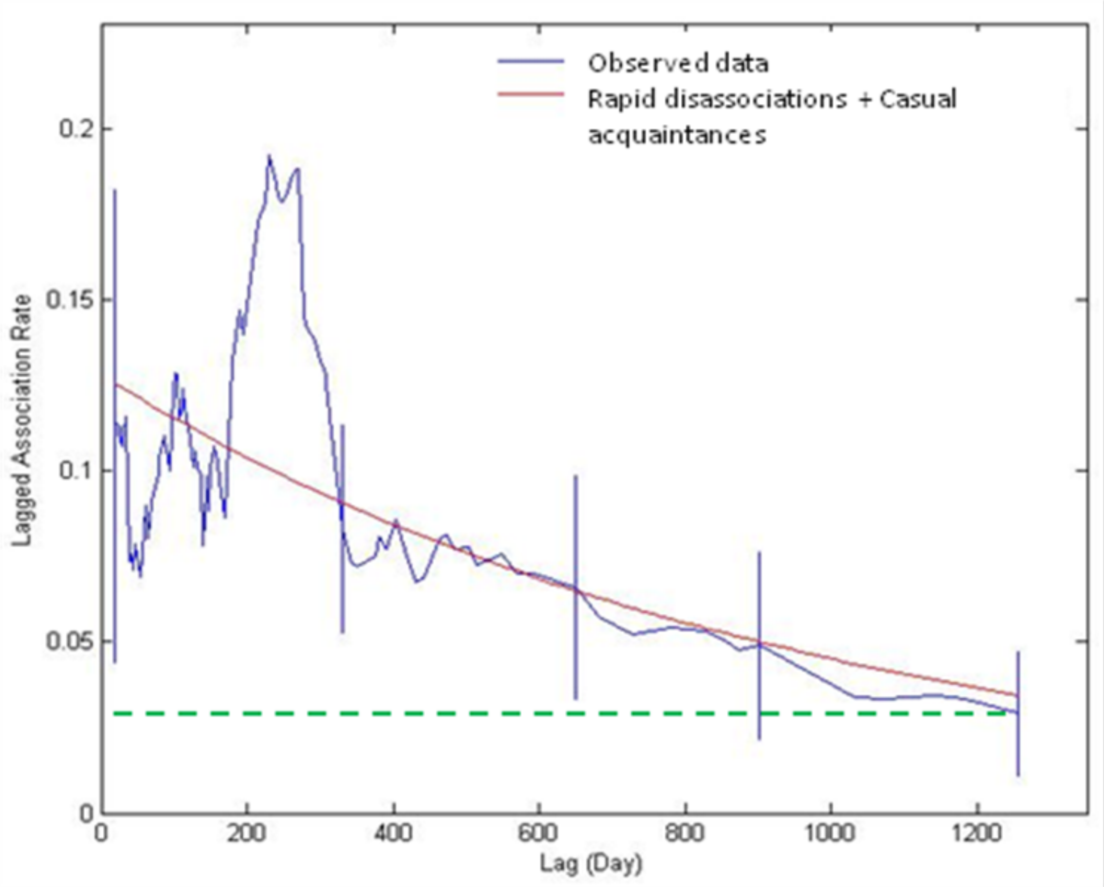

Figure 3. Lagged association rate of humpback dolphins identified in Plettenberg Bay between April 1999 and April 2004. The red line indicates the best fit model, "Rapid disassociation + Casual acquaintances" which was best supported by the data. The green broken line represents null model (random associations).

All models examined for temporal group dynamics analyses of humpback dolphins seen in Plettenberg Bay more than once are given in Table 4. The number of models that met the criteria for testing were less than in the case of all photo-identified dolphins. The ΔQAIC values between the 1st and 2nd candidate model indicated that both these models ("Two levels of Casual acquaintances" and "Casual acquaintances") were well supported by the data. Both these models had identical graphical representation (overlapping cure, Fig. 4). The remaining two models (Table 4) received no support.

Table 4. Model selection for standardised lagged association rate (LAR) of humpback dolphins identified and seen more than once in Plettenberg Bay between April 1999 and April 2004 with QAIC arranged in ascending order.

No.	MODEL	QAIC	ΔQAIC	Summed Log Likelihood	No. of parameter	GOF χ^2 (df)	p
1	Two levels of Casual acquaintances	3346.561	0	-1669.281	4	80.232 (d.f.=27)	<0.05
2	Casual acquaintances	3346.689	0.128	-1671.344	2	82.812 (d.f.=28)	<0.05
3	Preferred companions	3366.582	20.021	-1682.291	1	100.407 (d.f.=31)	<0.05
4	Preferred companions + Casual acquaintances	3367.905	21.344	-1680.853	3	97.176 (d.f.=28)	<0.05

The temporal pattern of group dynamics for dolphins sighted more than once was similar to that of all photo-identified individuals, albeit the best fit models indicate somewhat stronger associations. Nevertheless, there was no obvious temporal group stability. Although the lagged association rates appeared to stabilise after 530 days, they hovered only slightly above the null (random association) model. Furthermore, error around the data were substantial, indicating that even though the models generated by the current data may be indicative of the overall pattern, they have to be viewed cautiously as there is a considerable level of uncertainty due to the current limited sample size.

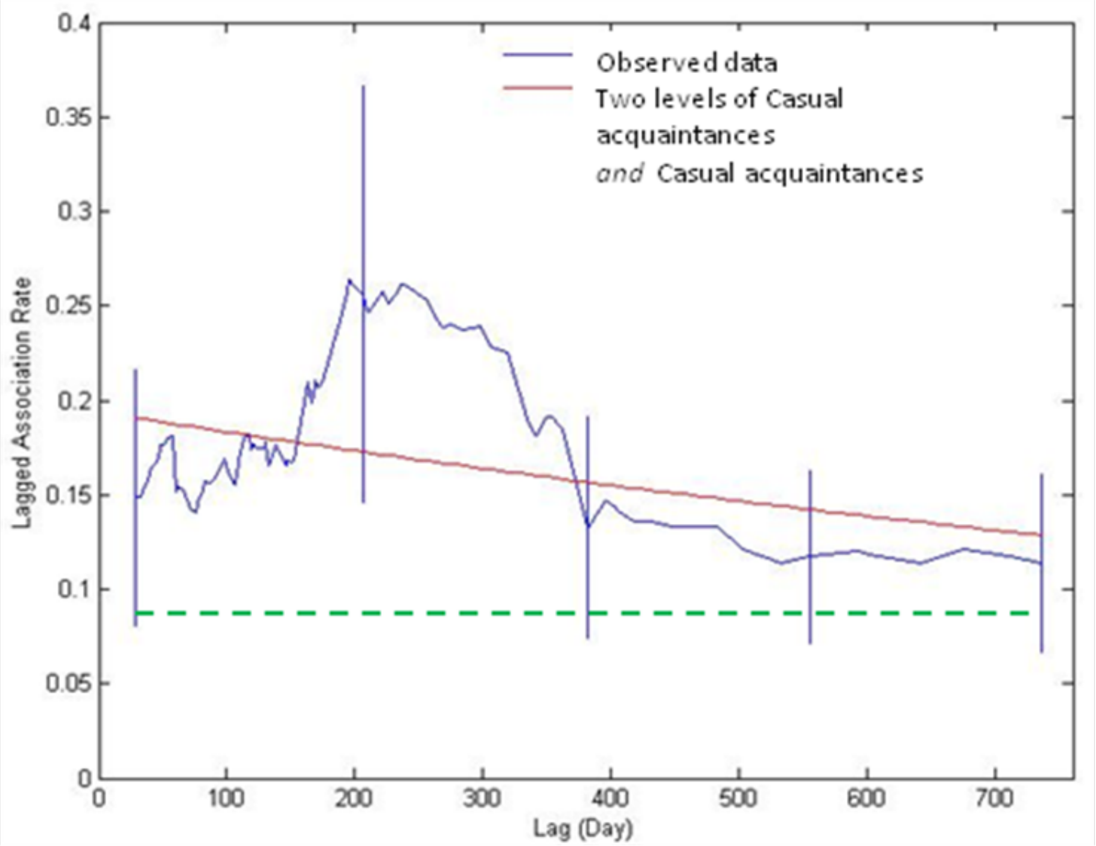

Figure 4. Lagged association rate of humpback dolphins identified in Plettenberg Bay between April 1999 and April 2004 and sighted >1 time. Two models ("Two levels of Casual acquaintances" and "Casual acquaintances") were similarly well supported by the data and the curves indicating these two models fully overlapped (shown as red line). The green broken line represents null model (random associations).

Hierarchical cluster analyses were performed for humpback dolphins sighted in the study area >1 time. The cophenetic correlation coefficient (CCC) was 0.79 which is right on the border line of the threshold value 0.8 which generally indicates that the model has a sufficiently good fit to the data. The pattern displayed by the dendrogram (Fig. 5) indicates a dyadic relationship between individuals, with no indications of obvious structure at the community level.

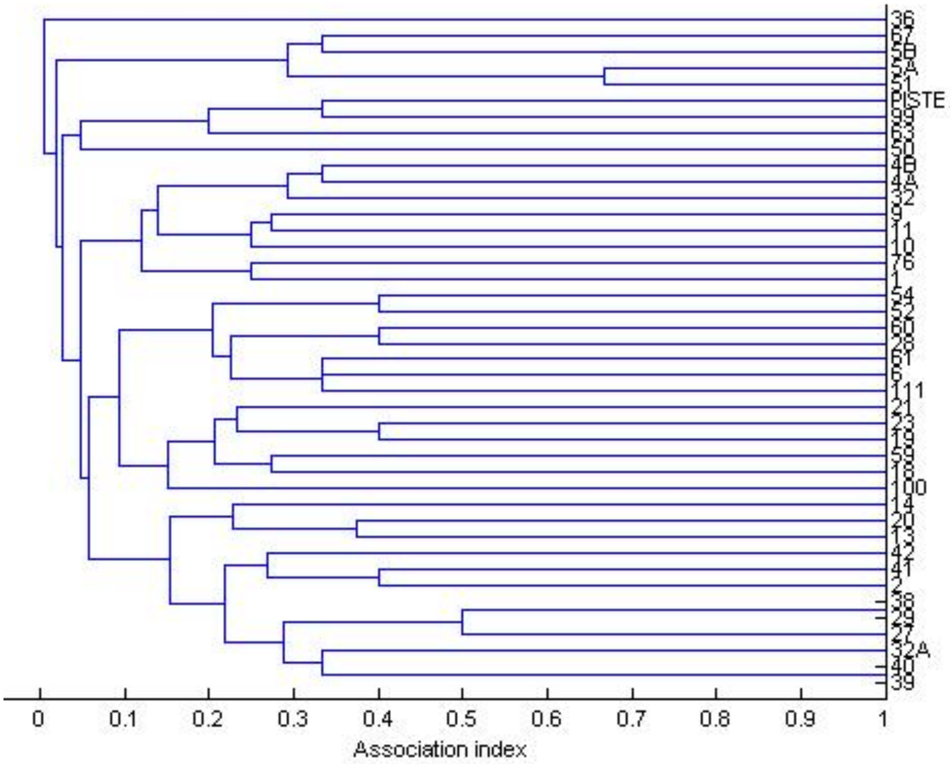

Figure 5. Dendrogram of associations of humpback dolphins photo-identified and seen more than once in Plettenberg Bay between April 1999 and April 2004.

5.4 Discussion

The results of socio-behavioural analyses indicate that humpback dolphins in Plettenberg Bay live in a fluid society of casual acquaintances, typical of the dynamic fission-fusion mammalian social systems (e.g. Gowans et al. 2008). The dolphins display generally weak site fidelity, although a small number of the animals that use Plettenberg Bay as part of their range have a seemingly higher affinity to this area. This supports the findings of Chapter 4, which suggested that although many humpback dolphins seen in Pletternberg Bay are transiting through the area, some of the animals are considerably more resident. These results conform to other population studies (e.g. Karczmarski 1996, Atkins et al. 2004). However, the degree of residency (i.e. short-term fidelity or long-term residence) remains undetermined as the intensity of field surveys and the quantity of the data collected during this study was not sufficient to provide reliably robust analyses; i.e.

the correlation test between true and estimated association indices using Poisson approximation method was in a mid-range. this result suggest that the data set was a moderately useful representation of the social structure but has to be treated with caution (Whitehead 2014).

Despite the relatively long time-span of this study, the indications of socio-behavioural dynamics of humpback dolphins generated by the current dataset remain preliminary due to the paucity of surveys and resulting small sample size. This is a common obstacle faced by opportunistic studies that make advantage of ongoing sea operations but have to follow the field protocol, survey schedule and survey intensity as facilitated by the sea operations that host the research or for example citizen science run research (Cohn 2008). In particular, the irregular schedule and large time gaps between field surveys made the analyses of LIR and LAR challenging. Above all, the sample size remains low, especially given the overall duration of the data collection period. As social analyses are dependent on large datasets, the results presented in this chapter have to be viewed as preliminary only and interpreted with caution (Whitehead 2014).

Adopting the principle that animals clustered spatially are interacting with one another socially (Whitehead 1995, 1997, 1999), membership of the same cluster (presence in the same group) defines associations between pairs of individuals. When such data are collected during sampling periods indexed by time, the strength of association and can be measured using Association Indices (Cairns & Schwager 1987, Ginsberg & Young 1992), which then can be further investigate for their temporal stability (Whitehead 1995, 1997, 1999). In this study, the lagged association rate, for any time lag *t*, was representative of an estimate of the probability that two individuals which associated at a particular time are still associated *t* time units later. This is consistent with other studies of vertebrate social structure, reviewed by Whitehead and Dufault (1999).

In a similar way, the residence rate of individuals, which is indicative of their site fidelity, was measured by calculating lagged identification rates representing the probability that an individual identified at any particular time will be identified again in the study area *t* time units later (Whitehead 2001).

There was a degree of uncertainty in the temporal analyses of movement and site fidelity, as the 1st and 2nd models (which represented a somewhat different formulation of the same pattern, "emigration/mortality") had a similar fit to the data as 3rd ("emigration and reimmigration") model (ΔQAIC = 0.15). Burnham and Anderson (2002) suggested if the ΔQAIC values between models are within a range of 0 and 2, all these models can be seen as similarly supported by the data. In this study, all three selected models generated a very similar projection. The overall low site fidelity, when projected for all individuals seen in Plettenberg Bay, is evidently due to a large number (~73%) of transient individuals, as suggested also in Chapter 4, which masks a higher site fidelity of the small number of more frequently seen individuals.

The results of permutation test with 1000 trials, where the standard deviation (SD) and coefficients of variation (CV) values of the observed real data were both greater than the random permuted values (Table 3), indicate that humpback dolphins seen during this study had preferred companionship. These companionships may be of dyadic nature, as displayed by the dendrogram in Fig. 5. The low mean association indices, however, for all seen individuals as well as those seen more than once (0.03 and 0.07, respectively) indicate the preferred companionships were short term (Whitehead 2014). Consequently, it remains unknown whether these apparent companionships are a true representation of the dolphins' social dynamics or perhaps an artefact of the small sample size. With low number of resightings, some associations can be easily overestimated, especially if they involve individuals that happen to occur in the same group but were seen very few times. Given the pattern of the lagged association rates, it appears that the latter is the more likely case and fluidity rather than stability is the norm for humpback dolphin's social system, as suggested by Karczmarski (1996; 1999) in his studies in Algoa Bay.

The CV of true association indices (AI) with the application of Poisson approximation method (estimated at 1.533 and 0.551 for all individuals and individuals seen more than once, respectively) indicated the social structure of the dolphins seen in Plettenberg Bay was dynamic and socially differentiated. Whitehead (2014) suggests that when CV of true AI is > 0.5 but < 2.0, the society is likely highly differentiated. This differentiation has to be in between the individuals seen once only and those seen more than once, as the pattern of associations of dolphins seen $>$ 1 time, as displayed in the dendrogram in Fig. 5, indicates dyadic relationship between individuals with no obvious structure at the community level. Consequently, the social differentiation suggested by CV of true AI has to be at the level between individuals seen only once and more than once. This further affirms the conclusions of Chapter 4, suggesting that the majority of the individuals seen during this study were mostly transient, with the small number of more frequently seen and socially differentiated individuals. These data conform with overall trends of what is reported for other populations along the southern African coast (Karczmarski 1996, Keith et al. 2002).

This pattern reported here, differs from what Saayman and Tayler (1979) reported 20 years earlier. However, as Saayman and Tayler based their conclusions on a small number of individuals they could identify and re-identify from a cliff-top, which represented a very small proportion of the overall number of dolphins they observed, it is possible that these few individuals were those few that actually use the area of the Bay more frequently, perhaps even in the long-term. Consequently, the finding of this current study does not necessarily contradict the suggestions by Saayman and Tayler (1979) but rather refines them. Admittedly though, both the intensity of the field surveys reported here and current sample size used in this study are insufficient to formulate a conclusive answer to this issue.

Chapter 6. General Conclusions

Mark-recapture analyses with photo-identification technique were been used to estimate the demographic parameters of the Indian Ocean humpback dolphin in Plettenberg Bay during April 1999 to April 2004. Apparent survival rates, recapture probabilities, and super-population size were quantified with the application of Cormack-Jolly-Seber and POPAN models. Given that the majority of identified individuals were sighted only once, transience of animals was significant and these dolphins are likely to travel along the South African coast for distances exceeding the size of the Plettenberg Bay region (see Karczmarski 1996). More structured, and increased survey intensity, however, is needed to improve the accuracy and robustness of population parameter estimations from the current study.

This study demonstrated a comprehensive approach in the formulation of candidate models during mark-recapture model selection processes. Various effects, other than only the basic time-dependent ('t') and constant over time ('.') effects, as in most other similar studies (e.g. Meekan et al. 2006; Parra et al. 2006; Guissamulo 2008; Aschettino 2010; Pusineri et al. 2014), were applied to test the likelihood of factors, including transience ('a2'), trap-dependence ('*m'), seasonal ('season') and effort ('effort') effects. Incorporating and identifying these effects provides the means for more accurate and unbiased estimation of demographic parameters. For example, separating "transient" individuals in the estimation of apparent survival rates limited the negative bias related to movement instead of true mortality, thus making the estimate closer to the true survival rates.

Socio-behavioural analyses revealed that humpback dolphins that use the coastal waters of Plettenberg Bay live in a dynamic fission-fusion society with fluid inter-individual associations. There appears to be social differentiation between dolphins transiting through the area and those that use Plettenberg Bay more frequent, perhaps on long-term basis. The transients, however, represent a majority of the humpback dolphins seen in the Bay. The degree of residency of the small number of more frequently seen individuals remains undetermined.

The findings of the socio-behavioural analyses, albeit preliminary, are in agreement with mark-recapture analyses and therefore, even if not fully conclusive, they are likely indicative of the actual behavioural pattern of humpback dolphins in the Plettenberg Bay region. The socio-dynamics of humpback dolphin groups described in this chapter correspond with the conceptual model of delphinid social strategies (Gowans et al. 2008), which suggests that group dynamics and ranging patterns of inshore delphinids are determined by the spatiotemporal predictability but also limited quantity of inshore resources (food, shelter, etc.). According to this conceptual model, the Plettenberg Bay humpback dolphins appear to represent an intermediate-ranging pattern, with at least some of individuals ranging over longer (although still undetermined) distances, which could facilitate a gene exchange between different humpback dolphin groups off the South African coast, as previously suggested by Karczmarski (1996, 1999).

In summary, this study provides important demographic parameters and socio-behavioural group dynamics of humpback dolphins inhabiting the Plettenberg Bay region. Reliable data on population size and structure, demographic parameters, socio-behavioural dynamics and ranging pattern are important in conservation management of free-ranging wildlife population. All these topics have been addressed in the present study, but the limitation of the current dataset has to be acknowledged. Although mark-recapture analyses and the estimation of demographic parameters could take advantage of a sophisticated model selection protocol to make the most of the available data, the socio-behavioural analyses were able to deliver only preliminary data. These analyses are highly sensitive to sample size, which in the case of this study is a function of survey intensity (frequency) and thoroughness of the photographic coverage of each encountered group. With 61 encounters across the study period, the current dataset was not large enough for a robust conclusive analysis of socio-behavioural group dynamics. Further field research, with rigorous survey plan and intensity, is therefore highly recommended. The general trends in socio-behavioural group dynamics is in line with that of what is known of the southern African humpback dolphin populations (Karczmarski 1996).

The Plettenberg Bay population has not received in-depth and dedicated research, such as the Algoa Bay area and other areas. A greater understanding of population connectivity (genetic study), habitat preference and use (spatial ecology study) along with more conclusive data on ranging and socio-behavioural pattern would be highly informative to any management decisions (such as coastal development or tourism management) that may affect humpback dolphins either directly (e.g. affecting their residence pattern) or indirectly (e.g. affecting areas used by the dolphins). Longer study period, higher intensity of surveys, larger annual sample size, and more regular sampling schedule are recommended to improve the accuracy of analyses in future studies.

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