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Trish Franklin
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# The social and ecological significance of Hervey Bay Queensland for eastern Australian humpback whales (*Megaptera novaeangliae*)

## PATRICIA FRANKLIN


**Bachelor of Arts (Honours)**

**A thesis submitted to the School of Environmental Science and Management in fulfillment of the requirements for the degree of**

**Doctor of Philosophy**


## SOUTHERN CROSS UNIVERSITY


## September 2012

# *DECLARATION*

I certify that the work presented in this thesis is, to the best of my knowledge and belief, original, except as acknowledged in the text, and that the material has not been submitted, either in a whole or in part, for a degree at this or any other university.

I acknowledge that I have read and understood the University's rules, requirements, procedures and policy relating to my higher degree research award and to my thesis. I certify that I have complied with the rules, requirements, procedures and policy of the University (as they may be from time to time).

Print Name…….

Signature…….

Date…….

# *ABSTRACT*

This study provides the first detailed research on the seasonal pod characteristics, seasonal social behaviour and temporal segregation of different reproductive and maturational classes of humpback whales in Hervey Bay (Queensland, Australia). Vessel-based surveys for this study were conducted for 9 weeks in 1992 and for 10 weeks each year between 1993 and 2009. A total of 4,506 humpback whale pods were recorded in Hervey Bay between 1992 and 2005, and photo-identification data were obtained for 2,821 individually identified humpback whales in Hervey Bay during the period 1992 to 2009. The data obtained during these surveys were used to analyse and model the variability, both within and between seasons, of pod characteristics, social behaviour in terms of pod associations, competitive groups and non-agonistic social behaviour pods. The data were also used to investigate temporal segregation of different classes of humpback whales. The overall aim of this research was to investigate the importance of Hervey Bay for particular classes of humpback whales, and to assess whether social factors influenced seasonal pod characteristics, social behaviour and temporal segregation.

Pods of humpback whales in Hervey Bay ranged in size from one to nine individuals. Pairs (1,344, 29.8%) were the most frequent pod type, followed by mother-calf alone (1,249, 27.7%), trios (759, 16.8%), singletons (717, 15.9%), and 4+ whales (437, 9.7%). Of the 4,506 pods, calves were present in 1,804 (40%), and 487 (10.8%) had one or more escorts present. Of the 1,804 pods observed with calves present, 1,251 (69.4%) were mothers alone with their calves. The size and composition of pods in Hervey Bay varied significantly as the season progressed. Pods with calves present were rarely sighted early in the season but dominated later in the season. A significant increase was recorded over years in the frequency of groups of 3+ whales, which may be related to social and behavioural changes as the eastern Australian population expands. The increasing proportion of socially active and interacting immature and mature males and females as the population increases, combined with the density and movement of humpback whale aggregations within and around Hervey Bay, may be contributing to the formation of larger groups over years.

While under observation 22.7% of pods or singletons associated with other whales to form larger newly associated pods, which ranged in size from 2 to 14 whales. The rate of formation of newly associated pods was significantly higher in the first four weeks of the season

compared with the last six weeks of the season. Non-agonistic social behaviour was also observed more frequently earlier in the season when immature and mature males and females predominated and pods with calves were rarely observed. In contrast, competitive groups were observed more frequently later in the season when mother-calf pods predominated and increased significantly towards the end of the season as pod size and composition changed. Competitive groups and non-agonistic social behaviour were more frequently observed in both larger and newly associated pods. Competitive behaviour was observed in 249 (6.3%) of pods, whereas non-agonistic social behaviour was observed in 465 (11.8%) of pods.

Using long-term observations of 361 individual whales identified photographically between 1992 and 2009, the study investigated the temporal segregation of different reproductive and maturational classes of humpback whales in Hervey Bay. Mature non-lactating females occurred mainly during August. Lactating females occurred in September and October with peak density occurring in late September, an average of thirty-two days after that for mature non-lactating females. There was no significant difference in the peak density and observations by day within season of immature males and females and mature non-lactating females. There were very few mature males observed in August, with the main concentrations occurring in September and October; the occurrence of this class overlapped with that of non-lactating females but more so with lactating females. Furthermore, the data suggest that both non-lactating and lactating females interact with immature and maturing males and females to a greater extent than previously reported, and show that social factors influence pod dynamics and behaviour of humpback whales in Hervey Bay. The observed temporal segregation pattern of humpback whales in Hervey Bay is fully consistent with the results reported by Dawbin (1966, 1997) from whaling catches made between the 1930s and 1960s. The results indicate that temporal segregation is a constant and cohesive feature of the social organisation of migrating humpback whales, which provides a predictable social framework for individuals moving through various maturational and reproductive stages as they age.

Hervey Bay is neither a terminal destination nor a calving or breeding area but rather a stopover early in the southern migration. This research has shown that Hervey Bay is an important habitat for different maturational and reproductive classes of whales. This is particularly true for females and their calves later in the season; for non-lactating and early pregnant females together with immature males and females early in the season; and for mature males seeking to maximize mating opportunities in mid- to late season. However, human activities including increased boat traffic, pollution, aquaculture development and

habitat degradation are increasing rapidly in Hervey Bay, coinciding with the increasing humpback whale population. Therefore, it is important that long-term monitoring of this population and its use of the Hervey Bay habitat continues into the future. It is also vital that the effects of human activities are monitored and managed effectively to ensure the long-term viability of Hervey Bay as a habitat important to the social development and reproductive success of these eastern Australian humpback whales.

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# *Chapter 1*

# General Introduction

## 1.1 HUMPBACK WHALES (*Megaptera novaeangliae*, Borowski 1781)

Humpback whales are found in all oceans of the world and are a large baleen whale distinguished by long pectoral fins, distinctive tubercles on the rostrum and unique ventral surface pigmentation patterns and unique serrations on the trailing edge of the tail flukes (True 1904, Katona and Whitehead 1981, Clapham and Mead 1999). They are noted for their exuberant surface behaviours and are the focus of a global whale-watching industry (Clapham 2000, O'Conner *et al*. 2009).

## 1.2 TAXONOMY AND MORPHOLOGY

### *1.2.1 Taxonomy*

Humpback whales belong to the Order Cetacea (now included in Order Cetartiodactyla), Suborder Mysticeti Family Balaenopteridae (Clapham and Mead 1999). Historically the species was described as several different populations, which were considered to vary in size and pigmentation. However the variations among populations described did not warrant subspecies differentiation, as the general agreement was that they were all referable to the same species (True 1904, Clapham and Mead 1999). *Megaptera novaeangliae* was first described from a specimen on the coast of New England by Borowski (1781) and remains the current and accepted taxonomic classification of humpback whales; the genus is considered mono-typic (Clapham and Mead 1999).

### *1.2.2 Species Morphology*

True (1904), noted that the morphological feature that distinguishes *Megaptera novaeangliae* from other balaenopterids and any other cetacean, is the large pectoral fins measuring one third of their body length. The anterior surface of the pectoral fins have a number of large protuberances unlike the anterior edge in any other species of Cetacea, and in contrast to the medial ridge of other balaenopterids, rounded tubercles are present on the upper and lower jaws and rostrum (True 1904, Clapham and Mead 1999). The morphology of the pectoral fins and the placement of the leading edge tubercles are reported to have a hydrodynamic form and function that provides enhanced lift at high angles of attack for high maneuverability associated with feeding behaviour (Whitehead 1981, Fish and Battle 1995, Miklosovic *et a*l. 2004). The colouration of the dorsal surface is black and the ventral surface varies from all black to all white (Rosenbaum *et al*. 1995, Clapham and Mead 1999).

In some populations the white ventral surface of some humpback whales can extend considerably up the flanks towards the dorsal fin (Kaufman *et al*. 1987). The black and white patterns on the ventral surface of the tail flukes also vary in combinations of the two pigmentations and together with the characteristic serrated posterior margin of the flukes, each caudal fin is individually distinctive (Katona and Whitehead 1981). The utilisation of those individual pigmentation patterns and the ventral fluke serrations has been the basis of many long-term studies of identified individual humpback whales (Clapham and Mead 1999). The dorsal fin is also highly variable in shape and ranges from low-set and rounded to high-set and falcate (Katona and Whitehead 1981, Clapham and Mayo 1990).

As in all balaenopterids, the ventral grooves expand during feeding, allowing considerable enlargement of the mouth cavity. The baleen plates, which function as a filtering curtain, are mainly black except along the front 30.5 cm where they are partly white on the anterior (True

1904). Compared to all other baleen whales the humpback whales have relatively few throat grooves, 14 to 22, which are approximately 10 to 13 cm wide, while all other rorqual whales have 38 to 100 throat grooves (True 1904, Clapham and Mead 1999).

The most distinctive characteristic distinguishing female humpback whales from males is the presence of a hemispherical lobe at the posterior terminus of the genital slit, which is absent in males (True 1904, Glockner 1983).

Chittleborough (1965) analysed the mean lengths of 2,031 male and 1,605 female humpback whales and reported that for physically mature males and females the mean lengths were 13.0 m and 13.9 m, respectively; 9.9 m and 9.7 m for males and females at the age of one year; and 11.8 m and 11.9 m in length at the average age of sexual maturity. He also reported that the mean body length of females is approximately 1-1.5 m longer than males.

Of the many body lengths data recorded from commercial whaling sources, True (1904) reported that the largest humpback whale male was 16.2 m and the largest female was 15.7 m. In comparison, the whaling stations at Moss Landing and Trinidad, California, between 1919 and 1926 reported that the largest individual humpback whales were 17.4 m for males and 18.6 m for females (Clapham *et.al.* 1997); however, it is not clear whether these were measured in a straight line from the tip of the rostrum to the notch of the flukes, or using a curvilinear method along the body (which gives an inaccurate and larger measurement). The largest humpback whales among several thousand measured by Chittleborough (1965) from Antarctic and Australian catches, were 14.3 m for males and 15.5 m for females. Clapham and Mead (1999, p.2) cautioned that “although the extreme values of sizes appear questionable it must be remembered that many subsequent measurements were recorded from heavily exploited populations from which the largest individuals had been removed, and that

while humpback whales of 17 to 18 m long seem unlikely, it is conceivable that pristine populations could contain a few individuals of this size."

## 1.3 LIFE HISTORY

### *1.3.1 Birth, growth and maturity*

Humpback whale calves are born after a gestation of between 11 and 12 months (Chittleborough 1958a, Clapham 2000) and although there have been some twin fetuses recorded from whaling carcasses (Chittleborough 1958a, 1965; Slijper 1962; Mikhalev; 1997), there are no reliable records of a humpback whale giving birth to twins. Although no birth event has been observed in this species the abundance of females with young calves in sub-tropical and tropical waters during the winter makes it clear that the majority of calves are born in low latitudes (Matthews 1937, Chittleborough 1965, Clapham 2000). Weaning is approximately at age 10-12 months and independent feeding can occur at six months, with a few calves remaining with their mothers at some point during the second winter (Chittleborough 1958a; Baker and Herman 1984b; Clapham and Mayo 1987, 1990; Glockner-Ferrari and Ferrari 1990; Baraff and Weinrich 1993; Clapham 1993).

The peak birth month in the Southern Hemisphere, as determined from fetal birth length, is early August (Matthews 1937; Chittleborough 1958a, 1965). Studies in the breeding grounds in the Northern Hemisphere suggest that the peak birth month is February (Herman and Antinoja 1977, Whitehead 1981). The mean length of calves at birth is between 13 and 15 feet (3.96 to 4.57 m) (Clapham *et al*. 1999). Calves are precocious: they may begin the migration to the mother's high-latitude feeding grounds when only a few weeks old and probably learn

from their mothers the migratory routes to the feeding areas and back to the breeding grounds (Clapham and Mayo 1987, Clapham 2000).

In the Northern Hemisphere, calving intervals were found to be between one and five years, although two to three years appear to be most common (Wiley and Clapham 1993, Barlow and Clapham 1997, Steiger and Calambokidis 2000). In the Southern Hemisphere, most information on humpback population characteristics and life history was obtained from whaling data from the early 1900s to the 1960s (Clapham and Baker 2008). Reported average annual birthing rates from whaling data of 0.37 (Western Australia: Chittleborough 1965) are comparable to the measure of 'calves per mature female per year' reported from some long-term studies, including 0.37 for Alaska (Baker *et al*. 1987); 0.41 for the Gulf of Maine (Clapham and Mayo 1990, Clapham 2000) and 0.48 for the Hawaiian Islands (Herman *et al*. 2011). Post-partum ovulation has been reported (Chittleborough 1965) and inter-birth intervals of a single year have occasionally been recorded (Clapham and Mayo 1987, Glockner-Ferrari and Ferrari 1990, which may be a consequence of early calf mortality or the fitness of the female (Lockyer 1984, Clapham and Mayo 1987, Gabriele *et al*. 2001. The annual survival rate of calves in the Southern Hemisphere is unknown (Fleming and Jackson 2011).

In the North Atlantic Gulf of Maine feeding grounds and the North Pacific Hawaiian Islands breeding grounds, adult mortality of humpback whales has been estimated to range between 0.049 and 0.037 (Barlow and Clapham 1997, Mizroch *et al*. 2004). In Hervey Bay, eastern Australia in the Southern Hemisphere, adult survival of humpback whales has been estimated at 0.966 (95% CI: 0.87 to 1.00 (Chaloupka *et al*. 1999).

The life expectancy of humpback whales is difficult to estimate because whaling removed most 'old' whales from the population (Clapham 2000). Ages of humpback whales were

originally calculated by counting the laminations (light and dark layers) that accumulate in earplugs (waxy accretions that form in the auditory canal) (Chittleborough 1959b, 1965) as one growth layer (GLG). Chittleborough (1959a) also used an alternative method of age determination using the growth of cortical layers in the baleen plates. However this latter method was found to be unreliable (Chittleborough 1959a, Robins 1960, Best 2006, 2011). Earplug readings provided an earplug age estimate of two GLG's accrued per annum for humpback whales (Chittleborough 1959b, Robins 1960). Using this method Chittleborough (1965), reported that the oldest whale he examined off western Australia was 48 years old. A review of the original GLG counts and available age calibration evidence from corpora lutea (a structure that develops in an ovary) concluded that one GLG is accrued annually, rather than two (Best 2006, 2011). Consequently this finding doubles the estimated time to sexual maturity of humpback whales from age 5 to 11 years from that population at that time and suggests the likelihood that the Chittleborough 48 year old whale may have been 96 years of age (Chittleborough 1959b, 1965; Clapham 1992; Gabriele *et al*. 2007a). However, longitudinal identification studies have reported differing data on sexual maturity for some populations. In the Gulf of Maine, Clapham (1992) reported sexual maturity at five years of age based on individually identified whales, while in southeastern Alaska Gabriele *et al*. (2007) reported ages at first calving at an average 11.8 years. The variance in these results remains unresolved (Best 2011).

Sexual maturity is defined by the presence of sperm in the testes of males or the occurrence of ovulation in females (Chittleborough 1954, 1955a, and b). Whaling biologists determined sexual maturity in male and female humpback whales from the histological examination of whaling carcasses. In particular they examined the weight and diameter of the testes in males and compared the increase of testis size with body length and maturity. To determine whether a female humpback whale was sexually mature, whale biologists undertook histological

examination of the ovaries and the ovarian cycle, mammary glands and foetuses (Matthews 1937, Omura 1953, Chittleborough 1954, 1955a, and b, Nishiwaki 1959). Physical maturity of humpback whales is based on their body lengths and is generally defined by the complete epiphysial fusion of a cap at the bone of joints in the vertebrae (Chittleborough 1955b).

During the winter months in both the Northern and Southern Hemisphere humpback whales migrate to tropical and sub-tropical breeding areas where they aggregate in large numbers to mate or give birth (Clapham 2000). Parental care of calves is provided exclusively by females (Clapham 2000) who seek shallow water in which to give birth and possibly to minimize harassment from mature males (Smultea 1994, Craig and Herman 2000). Because female humpbacks are widely dispersed in the breeding areas males cannot monopolize groups of females or defend resource-based territories (Clapham 1996, 2000). Consequently, males compete for single rather than multiple females, which involves intrasexual aggression among males in competitive groups (Darling *et al*. 1983, 2006; Tyack and Whitehead 1983, Baker and Herman 1984b, Clapham *et al*. 1992, 1993; Clapham 2000, Herman *et al*. 2008). Males also organize themselves through communal singing displays (Darling *et al*. 2006), and are involved in escorting or guarding females (Darling and Berube 2001). A male biased sex ratio has been reported in breeding grounds (Herman *et al*. 2011). Humpback whales are considered to be polygamous and promiscuous with females observed with multiple males, and males observed with multiple females (Baker 1985, Clapham and Palsboll 1997, Clapham 2000). However, the mating system of humpback whales is still not fully understood (Herman and Tavolga 1980, Clapham 1996, Cerchio *et al*. 2005, Darling *et al*. 2006).

### *1.3.2 Diet and foraging behaviour*

Humpback whales feed on dense patches of euphausiids (krill) and small schooling fish (Clapham 2000). Known prey organisms include *Euphausia*, *Thysanoessa*, or *Meganyctiphanes* krill (Ingebrigtsen 1929, Matthews 1937, Mackintosh 1942, Nemoto 1959, Slijper 1962, Nowacek *et al*. 2011); *Clupea* herring (Hain *et al*. 1982, Baker *et al*. 1985, Clapham *et al*. 1997, Sharpe and Dill 1997, Overholtz and Link 2007); *Scomber* mackerel (Geraci *et al*. 1989, Mikhalev 1997); *Ammodytes* sand lance (Overholtz and Nicolas 1979; Hain *et al*. 1982; Auster *et al*. 1986; Payne *et al*. 1986, 1990; Friedlaender 2009); *Mallotus* capelin (Matthews 1937, Clapham *et al*. 1997, Witteveen *et al*. 2008); *Sardinops* sardine (Clapham *et al*. 1997, Mikhalev 1997, Schweigert *et al*. 2007); and *Engraulis* anchovy (Kieckhefer 1992, Clapham *et al*. 1997).

Humpback whales are described as ‘gulp feeders’; they engulf a single mouthful of prey at a time (Watkins and Schevill 1979, Hain *et al*. 1982, Clapham 2000). Feeding behaviours include swimming/lunging and bubble netting (Jurasz and Jurasz 1979, Hain *et al*. 1982, Goldbogen *et al*. 2008). Humpback whales either forage alone, in pairs or sometimes in cooperative groups (Whitehead 1983, Baker and Herman 1984a, Perry *et al*. 1990, Straley 1990, Baker *et al*. 1992, Clapham 1993, Clapham 2000). However, major differences have been reported in feeding techniques used by humpback whales in different oceans (Clapham 2000). It has been suggested that certain feeding behaviours are spread through the population by cultural transmission (Weinrich *et al*. 1992) and that feeding behaviours change simultaneously with changes in prey behaviour (Friedlaender *et al*. 2009).

### *1.3.3 Threats and potential anthropogenic impacts*

By the mid-20th century most humpback whale populations were in rapid decline and were in danger of becoming severely depleted by the onslaught of modern whaling. Clapham and Baker (2008) reported that between 1904 and 1983 197,000 humpback whales were taken in the Southern Hemisphere. Extensive illegal and unreported catches of humpback whales by the Soviet whaling occurred between 1947 and 1973, leading to the collapse of regulated shore-based whaling on the east coast of Australia and New Zealand (Clapham and Baker 2008, Clapham *et al.* 2009). In 1963 humpback whales were declared to be protected in the Southern Hemisphere, and by 1986 when a global moratorium on commercial whaling came into force most populations of humpback whales were exhibiting signs of increasing abundance. However the threat remains of unregulated special permit whaling in the Antarctic (Clapham *et al*. 2003). The proposal in 2005 by Japan to take a self-declared quota of 50 humpback whales annually starting in the 2007 season onwards, although not acted upon, is still a potential threat to Antarctic humpback whales (Nishiwaki *et al*. 2007).

Humpback whales are under threat from a range of issues (see recent review in Fleming and Jackson 2011). Major threats to humpback whales in the Northern and Southern Hemisphere include vessel strikes resulting in mortality, injury and strandings (Laist *et al.* 2001, Lammers *et al*. 2003, Gabriele *et al.* 2007b, Van Waerebeek *et al.* 2007, Douglas *et al*. 2008, Glass *et al*. 2009, Marcondes and Engel 2009, Strahan 2009, Braulik *et al*. 2010, Carrillo and Ritter 2010, Silber *et al.* 2010, Pace 2011); entanglement in fishing gear (Johnson *et al*. 2005, Glass *et al*. 2009, Kiszka *et al*. 2009, Neilson 2009, Robbins *et al*. 2009, Strahan 2009, Robbins 2010, Cassoff *et al* 2011, Meyer *et al*. 2011); marine debris, which could be linked to strandings (Williams *et a*l. 2011, Baulch and Perry 2012); contaminants (Geraci *et al*. 1989, Aguilar *et al*. 2002, Elfes *et al*. 2010) and anthropogenic sound (Frankel and Clark 2000,

2002; McCauley *et al*. 2000; Johnson and Tyack 2003; Wright *et al*. 2007; Van Parijs *et al.* 2009).

Seismic surveys for oil and gas exploration worldwide and its potential impact on marine mammals from acoustic noise, have been widely investigated and monitored (McCauley *et al*. 2000, Engel *et al*. 2004, Cerchio *et al*. 2010). Further potential impacts on humpback whale populations include the effects of climate change on the ocean environment and its marine food web (Orr *et al*. 2005, Kurihara 2008, Moore and Huntington 2008, Nicol *et al*. 2008, Wootton *et al*. 2008, Doney *et al*. 2009, Simmonds and Eliott 2009, Alter *et a*l. 2010); whale watching (Corkeron *et al*. 1995, O'Connor *et al*. 2009, Weinrich and Corbelli 2009, Schaffar and Garrigue 2010, Franklin *et al*. 2011); and natural mortality from killer whale attacks on humpback whales, particularly calves (Naessig and Lanyon 2004, Steiger *et al*. 2008).

## 1.4 DISTRIBUTION AND MIGRATORY PATTERNS

### *1.4.1 Asynchronous timing of migrations*

Humpback whales are cosmopolitan and are found in all oceans of the world. They migrate over long distances up to 16,000 km each year between summer feeding areas in temperate or near-polar waters and winter breeding grounds in tropical and near-tropical waters (Baker *et al*. 1990, Rasmussen *et al.* 2007). The Northern and Southern Hemisphere humpback whales are asynchronous in the seasonal timing of their migrations between low-latitude tropical breeding grounds and high-latitude feeding areas (Omura 1953; Dawbin 1956, 1966; Chittleborough 1965; Baker *et al*. 1990; Clapham 2000).

Spatial overlap between Southern and Northern Hemispheres by southern humpback whales occurs in Central America and the Gulf of Guinea, West Africa (Acevedo and Smultea 1995, Van Waerebeek 2003, Stevick *et al.* 2004, Best 2008). Rasmussen *et al.* (2007) suggested that the spatial overlap of Southern Hemisphere whales across the equator into Northern Hemisphere waters may be related to water temperatures for breeding.

### *1.4.2 Ancient lineages and maternally directed fidelity*

There are three major worldwide oceanic divisions of humpback whale populations based on genetic differentiation: North Atlantic, North Pacific, and Southern Hemisphere populations (Baker *et al.* 1993, Baker and Medrano-Gonzalez 2002). Baker *et al*. (1990) reported a marked segregation of mitochondrial DNA haplotypes among subpopulations of humpback whales on different feeding and wintering grounds of the North Pacific and western North Atlantic oceans as well as between the two oceans. They interpreted this segregation to be the consequence of maternally directed fidelity to migratory destinations. Baker *et al*. (1993) suggested that the existing humpback whale lineages are of ancient origin. Photo-identification of individual humpback whales over long periods of time has documented maternally directed fidelity to feeding destinations (Martin *et al*. 1984, Clapham and Mayo 1987, Katona and Beard 1990, Clapham *et al*. 1993, Palsboll *et al*. 1997). There have been few reports of exchange between distant feeding grounds, with neighbouring feeding grounds being more frequent sites for exchange (Katona and Beard 1990, Stevick *et al*. 2006).

### *1.4.3 Northern Hemisphere: feeding, breeding and migration*

In the Northern Hemisphere humpback whale populations are widely dispersed in two major ocean basins, the North Atlantic Ocean and the North Pacific Ocean and there is a single population in the North Indian Ocean (Clapham 2000, Fleming and Jackson 2011).

#### *1.4.3.1 North Atlantic Ocean*

In the North Atlantic ocean the feeding areas are located in the Gulf of Maine (Clapham and Mayo 1987, 1990; Katona and Beard 1990; Weinrich 1991; Clapham 1993; Clapham *et al*. 1993; Palsboll *et al*. 1995, 1997; Smith *et al*. 1999; Stevick *et al*. 2003, 2006; Clark and Clapham 2004; Robbins 2007); the Gulf of St Lawrence, Newfoundland and Labrador in Canada and West Greenland in the western North Atlantic (Whitehead 1983; Katona and Beard 1990; Palsboll *et al*. 1995, 1997; Smith *et al*. 1999; Stevick *et al*. 2003, 2006); and in the eastern North Atlantic in Iceland including the Jan Mayen and Bear Islands and the Barents Sea off northern Norway (Ingebrigtsen 1929; Martin *et al*. 1984; Katona and Beard 1990; Palsboll *et al*. 1995, 1997; Smith *et al*. 1999; Stevick *et al*. 1999b, 2003, 2006).

Humpback whales feeding in the western and eastern Atlantic migrate annually to primary winter breeding grounds in the West Indies (Ingebrigtsen 1929; Balcomb and Nichols 1982; Whitehead and Moore 1982; Martin *et al*. 1984; Mattila and Clapham 1989; Mattila *et al*. 1989, 1994; Palsboll *et al*. 1995, 1997; Stevick *et al*. 1998, 1999a, 2003; Smith *et al*. 1999; Charif *et al*. 2001; Reeves *et al*. 2001).

Stone *et al*. (1987) reported that Bermuda is a mid-ocean habitat and stopover for western North Atlantic humpback whales en route to, and from, the West Indies breeding grounds. They also reported evidence suggesting that feeding occurs in the deep waters off Bermuda during the stopover.

### *1.4.3.2 North Pacific Ocean*

Feeding areas in the North Pacific Ocean range from Russia in the western North Pacific to Alaska in the north-eastern Pacific and California in the eastern Pacific (Clapham 2000, Calambokidis *et al*. 2008, Fleming and Jackson 2011).

The most westerly summer feeding areas in the North Pacific were found in Russian waters in the Gulf of Anadyr, the east side of Kamchatka, the Commander Islands, the Kuril Islands and the western end of the Aleutian Islands (Baker *et al*. 2008, Calambokidis *et al*. 2008). Dense feeding aggregations occur across the Alaskan region with specific feeding locations identified in the eastern Aleutian Islands, the Bering Sea, the western and northern Gulf of Alaska and southeastern Alaska (Baker *et al*. 1985, 1990, 1992, 1994, 1998a, 2008; Perry *et al*. 1990; Calambokidis *et al*. 1996, 2008). The most easterly feeding areas in the North Pacific are along the North American coastline at northern and southern British Columbia off Canada, and northern Washington, Oregon and California off the west coast of the United States (Baker *et al*. 1994, 1998a, 2008; Calambokidis *et al*. 1996, 2000, 2008; Darling *et al*. 1996).

Humpback whales feeding across the North Pacific migrate annually between at least five primary over-wintering breeding regions, Asia, Hawaii, offshore Mexico, mainland Mexico/Central America (Calambokidis *et al.* 2008). The specific breeding grounds in these regions are: Asia including the waters off the northern Philippines and Taiwan, Okinawa and the Ryukyu Islands near Japan and the Ogasawara and Mariana Islands (Nishiwaki 1959; Baker *et al*. 1998a, 2008; Calambokidis *et al*. 2008); the main Hawaiian Islands including Kauai, Oahu, Penguin Bank, Molokai, Maui and the Big Island (Herman and Antinoja 1977; Baker and Herman 1981; Glockner and Venus 1983; Baker *et al*. 1994, 1998b, 2008; Calambokidis *et al*. 2008; Herman *et al.* 2011); and Mexican waters including the mainland

Pacific coast, the southern Baja Peninsula, offshore in the Revillagigedo Archipelago and Central America (Baker *et al*. 1994, 1998b, 2008; Urban *et al*. 1999; Calambokidis *et al*. 2000, 2008; Rasmussen *et al*. 2004, 2012; May-Collado *et al*. 2005; Oviedo and Solis 2008; Rasmussen 2008). The principal breeding ground for the North Pacific humpback whales is the Hawaiian Islands (Calambokidis *et al*. 2008, Herman *et al*. 2011).

In addition, the low proportion of photographic matches between the Bering Sea and the currently known breeding areas strongly suggests the existence of another, as-yet-undiscovered breeding ground for North Pacific humpback whales (Calambokidis *et al*. 2008).

Calambokidis *et al*. (2008) reported that the linkages between feeding areas and breeding grounds in the North Pacific are complex with a high degree of maternally directed fidelity to both feeding areas and breeding grounds. Hawaii and the Revillagigedos are the principal breeding grounds for higher latitude feeding areas of the eastern Aleutians, Bering Sea, Gulf of Alaska, southeastern Alaska, northern and southern British Columbia, and northern Washington (Baker *et al*. 1985, 1990, 1994, 1998a, 2008; Calambokidis *et al*. 2008). Humpback whales feeding in Russian waters in the eastern Pacific migrate annually to Asian breeding grounds (Baker *et al.* 2008, Calambokidis *et al.* 2008), while humpbacks feeding off the Washington Oregon Californian coast primarily migrate to Mexican and Central American breeding grounds (Baker *et al*. 1990, 1994, 1998a, 2008; Calambokidis *et al*. 2000, 2008; Rasmussen *et al*. 2012). Darling *et al.* (1996) reported a humpback whale migrating between British Columbia and Japan.

Interchange between the principal wintering regions across seasons (Asia, Hawaii and Mexico) is relatively low, and interchange between the two feeding groups (one group offshore of California and Oregon and another feeding group offshore of northern

Washington and southern British Columbia) is relatively uncommon (Calambokidis *et al*. 2008).

Calambokidis *et al*. (2008) reported low levels of interchange between western Pacific feeding and breeding areas in Russian and Asian waters and the central and eastern North Pacific, and interchange between the breeding regions of Asia, Hawaii and Mexico were also relatively low. The movements of humpback whales between the two breeding grounds of Japan and Hawaii have been reported (Darling and Cerchio 1993, Salden *et al*. 1999).

#### *1.4.3.3 Northern Indian Ocean*

In the Northern Indian Ocean a single isolated humpback whale population is located in the waters of the Gulf of Oman and the Arabian Sea off Oman on the Arabian Peninsula (Reeves *et al*. 1991, Mikhalev 1997, Minton 2004, Rosenbaum *et al*. 2009, Minton *et al*. 2011).

Mikhalev (1997) reported that examination of individual whales taken from this population during Soviet whaling in the mid-nineteen sixties showed significant differences from Antarctic humpback whales and provided strong evidence that the population was both feeding and breeding in Arabian waters year-round. The isolation of this population was subsequently confirmed by both photo-identification and genetic analysis (Minton 2004, Rosenbaum *et al*. 2009, Minton *et al*. 2011). This small (< 100 individuals, Minton *et al*. 2011) unique non-migratory population is endangered and threatened by anthropogenic impacts (Baldwin *et al*. 2010, Braulik *et al.* 2010, Corkeron *et al*. 2011, Minton *et al.* 2011). Corkeron *et al*. (2011) suggested that spatial models of sparse data could inform conservation planning for mitigating impacts on the endangered Arabian Sea population of humpback whales.

### *1.4.4 Southern Hemisphere: breeding, feeding and migration*

#### *1.4.4.1 Southern Hemisphere Populations*

Kellogg (1929) reported six populations of humpback whales in the Southern Hemisphere; two populations in each of the Southern Atlantic, Indian and Pacific Oceans. Based on recent information of humpback whale populations in the Southern Hemisphere the International Whaling Commission (IWC) has identified seven breeding populations categorised as A to G (IWC 2006, Fig 1.1): A, is Brazil in the southwestern Atlantic; B, is West Africa in the southeastern Atlantic; C, is East Africa in the southwestern Indian Ocean; D, is western Australia in the southeastern Indian Ocean; (E1), is eastern Australia in the southwestern Pacific Ocean; E2 and E3, are in southwestern Oceania; and F, is in central Oceania. Finally, G is in the southeastern Pacific off South America (IWC 2006, Fig 1.1).

The IWC adopted six Management Areas for feeding areas in Antarctica (IWC 2006, Fig 1.1): Area I, below western South America; Area II, below eastern South America; Area III, below Africa; Area IV, below central Indian Ocean and Western Australia; Area V, below eastern Australia and western Pacific and VI, below the central Pacific.

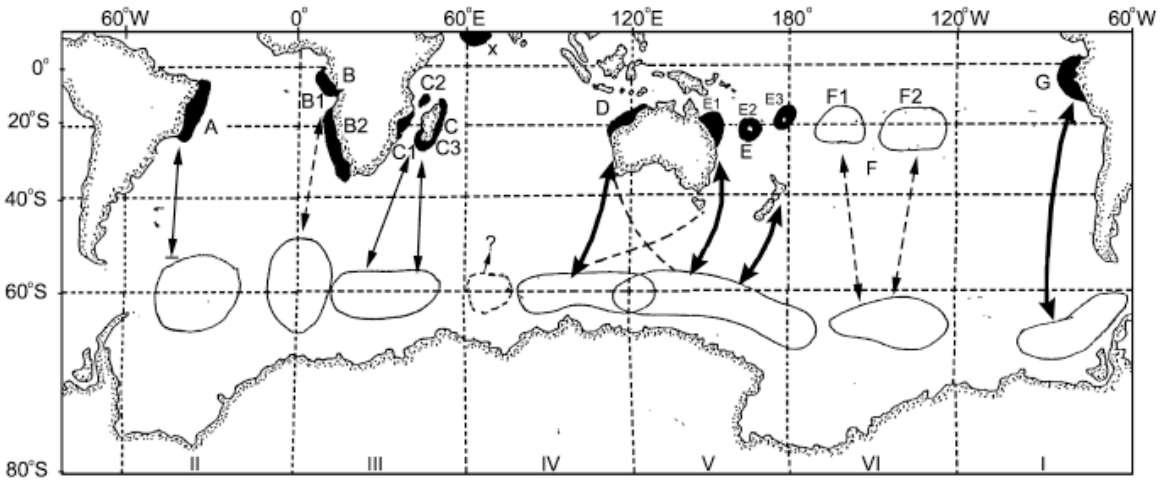



*Figure 1.1.* Southern Hemisphere breeding grounds (A to G) and feeding areas (I to VI). The areas and sub-areas identified reflect approximate, rather than exact boundaries. A dotted line represents a hypothetical connection, thin lines represent a small number of documented connections between areas using Discovery tags, photo-identification, genetics or satellite tracked whales and thick lines represent a large number of documented connections between areas from resights using Discovery tags, photo-identification, genetics or satellite tracked whales (source, IWC 2006).

### *1.4.4.2 South America, southeastern Pacific (Breeding G; feeding Area I)*

The most northerly breeding grounds for Southern Hemisphere humpback whales migrating from the Antarctic feeding areas are located above the equator (see 1.3.1 above, overlap between Northern and Southern Hemisphere humpback whales) in waters off Central America and the northwest South American continent at: Costa Rica (Acevedo and Smultea 1995; Rasmussen *et al*. 2000, 2004, 2007, 2012; May-Collado *et al*. 2005; Acevedo *et al*. 2007, 2008a, 2008b; Florez-Gonzalez *et al*. 2007); Panama (Acevedo *et al*. 2007, 2008a;

Florez-Gonzalez *et al*. 2007; Rasmussen *et al*. 2008, 2012) and Colombia (Florez-Gonzalez 1991, Caballero *et al*. 2001, Olavarria *et al*. 2006a, Florez-Gonzalez *et al*. 2007, Acevedo *et al*. 2008a).

Further south below the equator, breeding aggregations of humpback whales are located in the waters off Ecuador (Felix and Haase 1997, 2001a, 2001b; Scheidat *et al*. 2000; Felix *et al*. 2006a, 2007, 2009a, 2009b; Olavarria *et al*. 2006a; Florez-Gonzalez *et al*. 2007; Castro *et al*. 2008, 2011), Galapagos Islands (Felix *et al*. 2006b), and the northern coast of Peru (Ramirez 1988, Florez-Gonzalez *et al*. 2007).

Humpback whales breeding in Central America and off the northwestern coast of South America migrate annually to feeding areas in the Magellan Strait, Chile and the western Antarctic Peninsula (Caballero *et al*. 2001; Acevedo *et al*. 2006, 2008a, 2008b; Florez-Gonzalez *et al*. 2007). Photo-identification and genetic data suggest that humpback whales breeding in Central America predominantly feed in the Magellan Strait, while humpback whales breeding off the northwestern coast of South America feed off the western Antarctic Peninsula (Olavarria *et al*. 2006a, Acevedo *et al*. 2008b).

#### *1.4.4.3 South America: Southwestern Atlantic Ocean (Breeding A, feeding Area II)*

The primary breeding ground for humpback whales in the southwestern Atlantic is located along the coastline of Brazil ranging from the waters off Natal in northeast Brazil, the waters off Rio de Janeiro in the south, with the main concentrations in the Abrolhos Archipelago (Martins *et al*. 2001; Zerbini *et al*. 2004, 2006; Darling and Sousa-Lima 2005; Rosenbaum *et al*. 2006, 2009; Engel *et al*. 2008; Rossi-Santos *et al*. 2008; Andriolo *et al*. 2010; Cypriano-Souza *et al*. 2010; Wedekin *et al*. 2010a, 2010b) (Fig 1.1).

Humpback whales breeding off the Brazilian coast migrate annually to feeding areas located in offshore waters of the South Sandwich Islands, the western Antarctic Peninsula and possibly South Georgia (Zerbini *et al*. 2006, Engel *et al*. 2008, Engel and Martin 2009) (Fig 1.1).

#### *1.4.4.4 West Africa: Southeastern Atlantic Ocean (Breeding B; Feeding Area II and III)*

Humpback whale breeding grounds in the waters off West Africa are located in the Gulf of Guinea (breeding stock B1, IWC 2006) in the waters of the Bight of Benin, Togo, the Sao Tome and Principe Archipelago and Pagalu to the north (Aguilar 1985; Van Waerebeek 2003; Rosenbaum and Mate 2006; Picanco *et al.* 2009), and further south in the waters off Gabon, Congo and Angola (Walsh *et al*. 2000; Rosenbaum *et al.* 2004, 2009; Darling and Sousa-Lima 2005; Pomilla and Rosebaum 2006; Rosenbaum and Collins 2006; Rosenbaum and Mate 2006; Weir 2007; Cerchio *et al*. 2010). Recent genetic studies indicate that humpback whales migrating off Namibia and west South Africa are from a separate breeding sub-population (breeding stock B2, IWC 2006), the location of which has yet to be identified (Barendse *et al*. 2006, 2011; Rosenbaum and Mate 2006; Rosenbaum *et al.* 2009). Macleod and Bennet (2007) reported humpback whales in the waters of St Helena Island in the southeastern Atlantic.

Feeding areas for humpback whales breeding on the western coast of Africa have been identified south of the Walvis Ridge off Namibia and the waters of Saldanha Bay southwest Africa (Best *et al.* 1995; Barendse *et al*. 2006, 2011). It has also been suggested that West African humpback whales migrate to the areas in waters off Bouvet Island, southwest of Africa (Rosenbaum and Mate 2006, Engel and Martin 2009).

#### *1.4.4.5 East Africa, southwestern Indian Ocean (Breeding C; feeding Area III)*

There are three separate breeding aggregations of humpback whales in waters off East Africa: Seychelles Tanzania Mozambique (C1, IWC 2006), (Reeves *et al*. 1991, Best *et al*. 1998, Hermans and Pistorious 2008, Rosenbaum *et al*. 2009, Findlay *et al*. 2011); Comoros Islands Mayotte Island and islands and reef of the Mozambique Channel (C2, IWC 2006), (Best *et al*. 1998; Ersts *et al*. 2006, 2011; Kiska *et al.* 2007; Rosenbaum *et al*. 2009; Findlay *et al*. 2011) and the coastal waters of Madagascar (C3, IWC 2006), (Wray and Martin 1983; Rosenbaum *et al*. 2009; Best *et al*. 1998; Ersts *et al*. 2003, 2006, 2011; Pomilla and Rosenbaum 2006; Murray *et al*. 2009). Humpback whales have also been observed in the migratory corridor off Cape Vidal, northern Natal (Findlay and Best 2006).

Best *et al*. (1998) suggested that humpback whales migrating from East Africa to Antarctic feeding grounds travel along three proposed routes: one southeast along the eastern coastline of southern Africa; a second south from the Mozambique Channel and a third southwards from southern Madagascar. The summer feeding distribution of east African humpback whales is unknown. The putative feeding areas may be in Antarctic waters of Area III between $5^0$ E and $60^0$ E (IWC 2006, Tynan 1998, Fig. 1.1).

#### *1.4.4.6 Western Australia, southeastern Indian Ocean (Breeding D; feeding Area IV and V)*

The most northerly aggregation of humpback whales off the western Australian coast is at Camden Sound, in the Kimberley Region ($15^0$S to $18^0$S), which has also been identified as a major calving area (Bannister and Hedley 2001, Jenner *et al*. 2001). During the southern migration, resting areas have been reported at Exmouth Gulf ($21^0$S) and Shark Bay ($25^0$S) (Bannister, 1994, Bannister and Hedley 2001, Jenner *et al*. 2001).

Chittleborough (1959a, 1965) reported whaling catches in the migratory corridor off Point Cloates ($22^0$S), Carnarvon ($25^0$S) and in the waters off Albany ($35^0$S). The migratory corridor also includes the Dampier Archipelago ($20^0$S) and the Perth Basin ($33^0$S) (Jenner and Jenner 1994, Jenner *et al*. 2001).

The summer feeding areas for western Australian humpback whales are in Antarctic waters above $56^0$S and between $80^0$E and $110^0$E (Area IV, IWC 2006, Fig 1.1) (Rayner 1940; Chittleborough 1959a, 1965; Gill and Burton 1995; Matsuoka *et al*. 2006; Franklin *et al*. 2008). Discovery Mark data and recent satellite tag data suggest some mixing of western Australian and eastern Australian humpback whales during summer feeding in Area IV (Chittleborough 1965, Gales *et al*. 2009).

#### *1.4.4.7 South Pacific Islands (Oceania) (Breeding E2, E3 and F1, F2; feeding Area V, VI and I)*

Four breeding populations have been identified in tropical waters in the South Pacific Ocean; two are in the western Pacific designated E2 and E3 and two in the central Pacific F1 and F2 (IWC 2006, Fig.1.1).

Breeding locations for E2 are in the waters off New Caledonia (18-23°S, 163-169°E) and Vanuatu ($17^0$S, $168^0$E) (Garrigue and Gill 1994; Garrigue *et al.* 2004, 2010; Baker *et al*. 2006; South Pacific Whale Research Consortium 2009). Breeding locations for E3 are in the waters off Fiji (18°S, 178°E) (Paton and Clapham 2002, South Pacific Whale Research Consortium 2009); Samoa and American Samoa (13°S, 173-170°W) (Baker *et al*. 2006, Noad *et al*. 2006, Robbins and Mattila 2006, South Pacific Whale Research Consortium 2009, Carretta *et al*. 2010) and Tonga (15-23°S, 173-177°W) (Abernethy *et al*. 1992, Baker *et al*. 2006, Olavarria *et al*. 2007, South Pacific Whale Research Consortium 2009).

In the central South Pacific breeding area F1 is located in the waters of the Cook Islands (8-23°S, 156-167°W) (Hauser *et al*. 2000, Baker *et al*. 2006, Hauser and Clapham 2006, South Pacific Whale Research Consortium 2009; Hauser *et al*. 2010) and F2 is located in the waters of French Polynesia (8-27°S, 134-155°W) (Poole 2002, 2006; Gannier 2004; Baker *et al*. 2006; Carretta *et al*. 2010; South Pacific Whale Research Consortium 2009). Hauser and Clapham (2006) report that although the observations of humpback whales in the Cook Islands have the primary characteristics of a breeding area the low density of whales and the absence of inter-annual resightings suggest that it may not be a central breeding location but rather a migratory corridor. This is also supported by satellite tagging from the area (Hauser *et al.* 2010).

Discovery Marks, photo-identification data and genetic data have established low levels of interchange among breeding locations consistent with E2, E3, F1 and F2 being breeding sub-populations (Chittleborough 1959b; Dawbin 1964; Constantine *et al*. 2007; Olavarria *et al*. 2007; Garrigue *et al*. 2000, 2011a; Franklin *et al*. in press-b).

Humpback whales migrating from the western Pacific (E2 and E3) to Antarctic feeding areas travel through New Zealand waters and disperse widely to feeding areas in Antarctic Area V (Dawbin and Falla 1949; Dawbin 1956, 1966; Steel *et al*. 2008; Gales *et al*. 2009; Franklin *et. al*. in press-a, b). Hauser *et al*. (2010) using a satellite-monitored track reported a single humpback whale travelling from the Cook Islands (F1) to eastern Area VI off Antarctica. Steel *et al*. (2008) reported a genotype match between Tonga (E2) and Antarctic Area VI. Movements of a few humpback whales have been reported between American Samoa (E2) and French Polynesia (F2) and feeding Area I near the Antarctic Peninsula (Robbins *et al*. 2008, Albertson-Gibb *et al*. 2009).

## 1.5 EASTERN AUSTRALIAN HUMPBACK WHALES

### *1.5.1 Population structure, migration and migratory interchange*

The International Whaling Commission (1WC), consider eastern Australian humpback whales to be a relatively discrete breeding stock termed E1, which forms part of the IWC's Antarctic Area V management area ($130^0$ E-$170^0$ W) (IWC 2006, Olavarria *et al*. 2006*b*). Eastern Australian humpback whales migrate annually between semi-tropical and tropical overwintering and breeding grounds along the northeast coast of Queensland Australia and high latitude feeding areas in Antarctic Area V (Chittleborough 1965, Dawbin 1966, Franklin *et al*. 2012).

Discovery Marks, photo-identification, genetic and acoustic data have revealed low levels of interchange between eastern Australia, western Australia and western Oceania populations consistent with eastern Australia being a separate breeding population (Chittleborough 1965; Dawbin 1966; Garrigue *et al*. 2000, 2011*b*; Noad *et al*. 2000; Olavarria *et al*. 2006*b*; Anderson *et al*. 2010; Franklin *et al*. in press-*b*).

### *1.5.2 Breeding grounds and northern coastal migratory cycle*

The inter-reef lagoon of the Great Barrier Reef, between $16^0$S and $23^0$S is considered to be the primary overwintering and breeding ground of eastern Australian humpback whales (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999, Smith *et al*. 2012). There are no recent published data on the aggregations of humpback whales in the eastern Australian breeding grounds.

Based on resighting intervals of humpback whales at Byron Bay ($28^0$ 37'S) and Ballina ($28^0$ 52'S) in New South Wales and Hervey Bay ($25^0$ 00'S) in Queensland, it has been calculated that the average residency time of eastern Australian humpback whales in the breeding

grounds is 4 weeks and that the travel time from Byron Bay to the southern end of the putative breeding ground ($21^0$S) and the return journey to Ballina is 5 weeks. On average eastern Australian humpback whales spend a total of 9 weeks on the northern migratory cycle (Burns *et al*. in press).

During the peak of the northward migration in June and July (Paterson 1991), humpback whales returning from the Antarctic summer feeding areas approach the southeastern coastline of Australia at various latitudes and are deflected to the northeast until they reach Cape Byron (Dawbin and Falla 1949, Dawbin 1966, Paton *et al*. 2011). After passing the most easterly point of Australia at Byron Bay ($28^0$S) the migratory stream moves up along the coastline past Point Lookout ($27^0$S) and north to the east of Fraser Island and Hervey Bay ($25^0$S, Fig. 1.6.1 below) (Paterson 1991, Noad *et al*. 2008). On the northward migration humpback whales do not enter Hervey Bay (Paterson 1991, Corkeron *et al*. 1994). The migration stream passes Breaksea Spit to the northeast of Hervey Bay ($24^0$S) and then inclines to the northwest dispersing widely within the inter-reef lagoon of the Great Barrier Reef (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999, Smith *et al*. 2012).

The southward migration from the breeding grounds commences in late July and continues until late October (Dawbin 1966, Paterson 1991). The main southward migratory corridor is to the east of Fraser Island and Hervey Bay (Fig. 1.6.1) (Paterson 1991) and the migratory stream continues south past Point Lookout ($27^0$S), Byron Bay ($28^0$S) and Eden ($37^0$S) (Paterson 1991, Gales *et al*. 2009). Gales *et al*. (2009) using satellite-monitored tracks deployed off Eden reported that some eastern Australian humpbacks migrated eastwards towards New Zealand, and some migrated due south past the east coast of Australia and Tasmania, while a single humpback whale moved through Bass Strait southwest towards Antarctic Area IV.

### *1.5.3 Antarctic feeding areas*

Eastern Australian humpback whales predominantly feed in Antarctic Area V (Dawbin and Falla 1949, Dawbin 1966, Bryden 1985, Gales *et al*. 2009, Anderson *et al*. 2010, Franklin *et al*. 2012), however there is some evidence that the feeding range of some individuals extends westward into Area IV (Chittleborough, 1965, Gales *et al*. 2009).

### *1.5.4 Trends in abundance of eastern Australian humpback whales*

Recent modeling suggests that the eastern Australian humpback whale population prior to the last period of commercial whaling was estimated to be 22, 093 (95% PPI, 20,062-26,673) (Jackson *et al*. 2009). Commercial coastal and Antarctic pelagic whaling together with illegal Soviet whaling from the mid-1940s to the early 1970s devastated the eastern Australian humpback whale population (Clapham *et al*. 2009). In 1963 when the IWC declared complete protection for southern ocean humpback whales it was estimated there were possibly fewer than 200 survivors of the eastern Australian humpback whale population (Paterson *et al*. 1994, Jackson *et al*. 2009). In the thirty years from 1962 to 1992 the eastern Australian humpback whale population was estimated to have only increased to 1,900 (95% CI 1,650-2,150, Paterson *et al*. 1994). During the 18 years of this study the eastern Australian humpback whale population is estimated to have increased to 13,098 whales at an average rate of over 10% per annum (Noad et al. 2004, 2011; Jackson et al. 2009). The estimates of yearly abundance of the eastern Australian humpback whale population from 1991 to 2009 are presented in Figure 1.5.4.1.

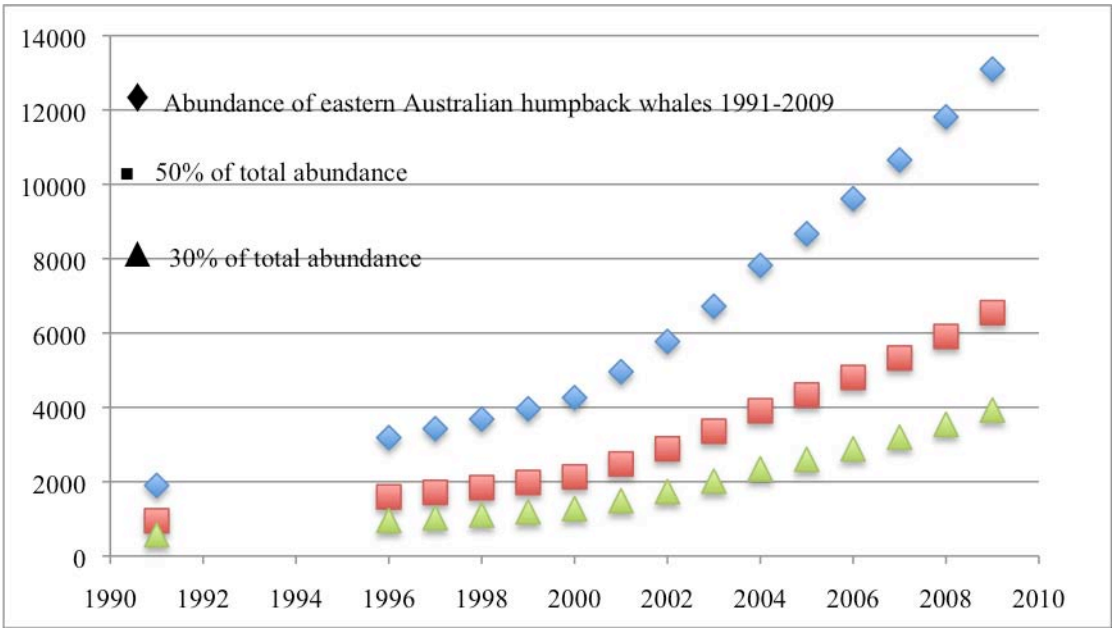



*Figure 1.5.4.1.* Estimates of yearly abundance of eastern Australian humpback whales (Data provided by Dr M. Noad, University of Queensland: the 1991 estimate is from Paterson *et al.* 1994; the 1996 estimate is from Bryden *et al.* 1996; the 2000 estimate is from an unpublished report by Brown *et al.* 2000 which was partly reported in Brown *et al.* 2003; the 2004 estimate is an updated but unpublished estimate of the estimate reported in Noad *et al.* 2011; The other years are interpolated, while those post 2004 are based on the relative abundance surveys and the 2004 data published in Noad *et al.* 2004). Chaloupka *et al.* 1999 suggested that from 30% to 50% of eastern Australian humpback whales enter Hervey Bay during the southern migration.

## 1.6 HERVEY BAY, QUEENSLAND AUSTRALIA

Hervey Bay is located at $25^0$S, $153^0$E on the eastern coast of Queensland (Fig.1.6.1), $2^0$ south of the southern end of the putative overwintering and breeding grounds for eastern Australian humpback whales (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999).

Paterson (1991) reported that the pattern of the southern migration differed from the northern migration. On the northern migration humpback whales bypass Hervey Bay (Fig. 1.6.1, migratory pathway A), whereas on the southern migration large numbers of humpback whales make a diversion from the primary migratory pathway and pass inside Breaksea Spit to enter Hervey Bay (Fig.1.6.1, migratory pathway B) (Paterson 1991). Aerial surveys undertaken in 1988 to 1990 confirmed that southbound humpback whales enter Hervey Bay from the north and aggregate in shallow waters close to the western shore of Fraser Island in the eastern part of the Bay (Fig. 1.6.1,B and C) (Corkeron 1994). On departure from Hervey Bay humpback whales need to travel westward to clear Ferguson Spit, which runs west of Rooney Point, before turning northwards to clear Breaksea Spit (Fig. 1.6.1, D), prior to turning east and joining the main southern migratory pathway (Fig. 1.6.1, A).

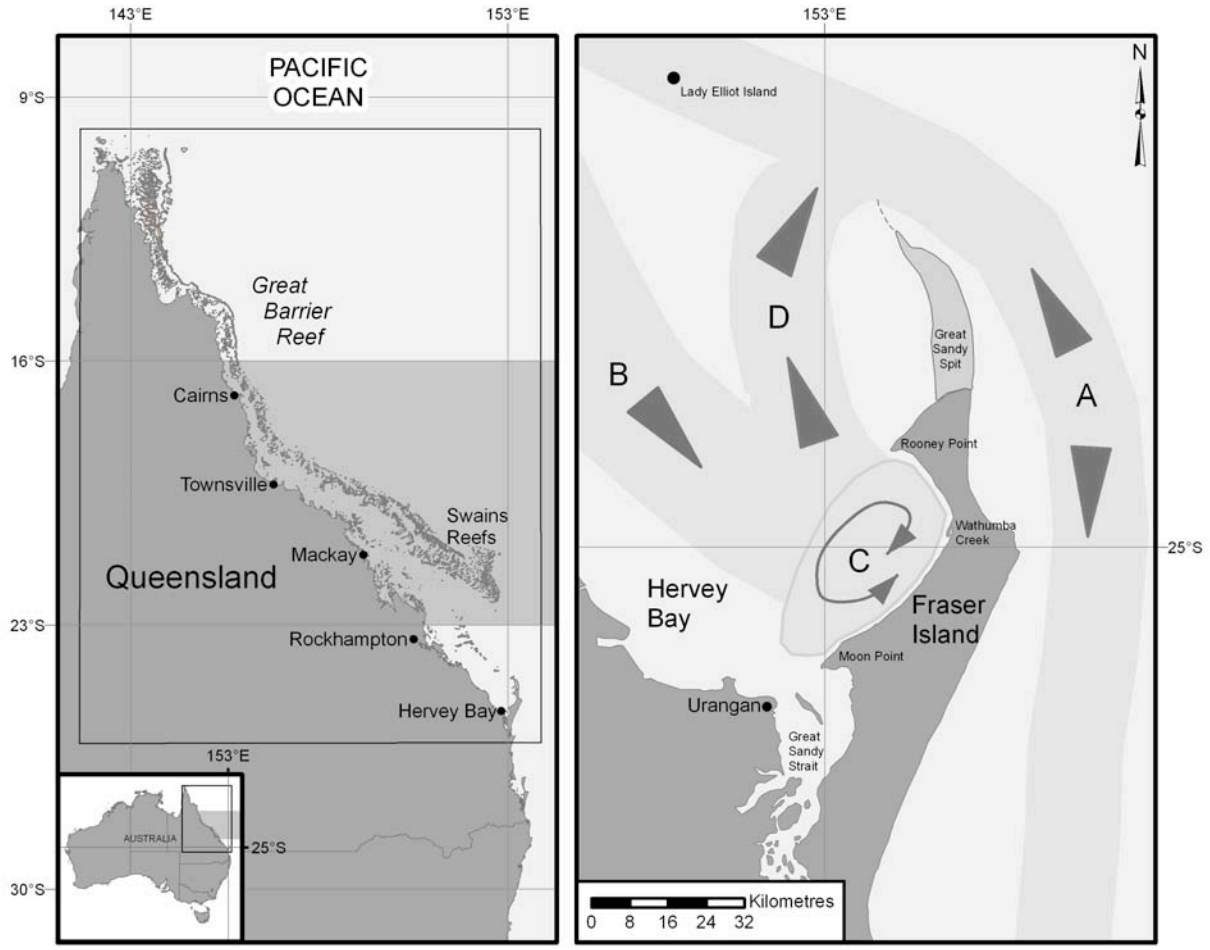



*Figure 1.6.1* The location of Hervey Bay on the eastern coast of Australia and its geographic relationship to the putative overwintering and breeding grounds within the inter-reef lagoon of the Great Barrier Reef is shown in the left side map. The migratory pathways into and out of Hervey Bay (B and D); the area where the humpback whales aggregate (C) and the main north south migratory pathway (A) are shown in the right side map.

Hervey Bay is formed by Fraser Island, the largest sand island in the world (126 km long) and the Australian mainland to the west. It is a wide shallow bay approximately 4,000 $km^2$ in area and is generally less than 18 m deep, with a sand and mud bottom (Vang 2002). Fraser Island

lies along a northeasterly axis and its northern end bridges the continental shelf. The most southerly islands of the Great Barrier Reef are directly north of Hervey Bay at a distance of between 111 and 222 km (Fig. 1.6.1).

Early research during the late 1980s and early 1990s involving aerial surveys and boat-based photo-identification reported that humpback whales visited and resided in Hervey Bay for short periods of time (Corkeron 1994). It was also estimated that large numbers of humpback whales, representing between 30 to 50% of the eastern Australian population, visited Hervey Bay annually (Chaloupka *et al*. 1999). This research established Hervey Bay as a stopover for eastern Australian humpback whales. Specifically the research investigated pod sizes, temporal variation in classes of humpback whales, residency and pod behaviour (Corkeron *et al*. 1994, 1995). Corkeron *et al*. (1994) reported short residency times that were similar to the Northern Hemisphere breeding grounds in the West Indies and suggested that the non-random clustering of humpback whales aggregating in Hervey Bay might be related to social factors. However, there were no data indicating that Hervey Bay was of importance to any particular class of humpback whale (Corkeron *et al.* 1994).

## 1.7 FOCUS OF THESIS AND RESEARCH OBJECTIVES

Why do humpback whales make a diversion from the main migratory pathway? Paterson (1991, p. 337) suggested that; “The geographic relationship of Breaksea Spit and Fraser Island to the mainland may explain in part why humpback whales enter Hervey Bay.” It is clear from earlier studies in Hervey Bay that to answer the fundamental question of what is the function of Hervey Bay in the migration of humpback whales, further data were required.

In order to fully understand the function of Hervey Bay in the migration of eastern Australian humpback whales, the thesis will address several underlying and related questions: what classes of humpback whales are using the bay?; is Hervey Bay important to any particular class of humpback whale?; are there any changes in pod sizes and composition over years and within season?; what behaviours are occurring in Hervey Bay over years and within season and are these behaviours different from other overwintering and breeding grounds and if so, why?; what can the observed behaviours tell us about the function of Hervey Bay in the migration?; is there temporal segregation of the reproductive and maturational classes of humpback whales entering Hervey Bay, and if so, how does this compare to the temporal segregation in the migration reported by Dawbin (1966, 1997)?; what can observed behaviour and the temporal segregation of classes of humpback whales in Hervey Bay tell us about the social organisation of humpbacks whales?; is the trend in abundance of the eastern Australian humpback whales population likely to have density/dependent affects for humpback whales visiting Hervey Bay?

The aim of this research was to investigate the ecological and social significance of Hervey Bay, Queensland for eastern Australian humpback whales.

The specific research objectives were:

- To investigate the seasonal changes in humpback whale pod characteristics within and between seasons;
- To investigate the seasonal social behaviour of humpback whales during the southern migratory stopover in Hervey Bay, in terms of pod associations, competitive behaviour and non-agonistic social behaviour within and between seasons;

- To investigate and analyse the temporal segregation and behaviour of reproductive and maturational classes of known individual humpback whales in Hervey Bay, within and between seasons, and to consider the implications for social organisation.

## 1.8 THESIS FORMAT

This thesis presents chapters on the main research theme, which is the ecological and social significance of Hervey Bay for the eastern Australian humpback whales. Chapter 1 provides a general introduction to the biology and ecology of humpback whales. Chapter 2 describes the general methodology including: the background to The Oceania Project's Hervey Bay humpback whale study; the study site and survey timing; vessel-based surveys; observation, photo-identification and other data; and photographic data analysis. Chapter 3 is based on a published paper (Franklin *et al*. 2011), which investigates the pod characteristics of different classes of humpback whales entering Hervey Bay throughout the winter season. Chapter 4 is a manuscript in preparation and investigates the seasonal social behaviour of different classes of humpback whales, and considers the influence of the different classes of whales on the occurrence of observed behaviours. Chapter 5 is a manuscript in preparation: the chapter examines the context of Hervey Bay in terms of the migration of eastern Australian humpback whales between their putative breeding ground in the Great Barrier Reef and their summer feeding areas in the Antarctic. The chapter also examines the migratory movement, timing and residency of the different maturational and reproductive classes of whales and the behaviour of known-age individuals. The findings are compared with the pioneering work of Dr. William Dawbin on the temporal segregation of humpback whales during the period of commercial whaling in the 20th century. There is some overlap (and therefore unavoidable

repetition) in methodology between Chapters 2, 3, 4 and 5 because they are formatted as papers for publication or submission. Chapter 6 provides a synthesis and general conclusion of the thesis and examines conservation issues for humpback whales in Hervey Bay.

# *Chapter 2*

# Study Background and Methodology

## 2.1 THE OCEANIA PROJECT'S HERVEY BAY HUMPBACK WHALE STUDY

The Oceania Project (TOP) was established by Trish and Wally Franklin in 1988 as a not–for-profit research and education organisation, with a primary focus on humpback whale research in Hervey Bay, southeast Queensland. In 1989, a six-week vessel-based expedition was completed as a pilot study to assess the feasibility of conducting a long-term study of humpback whales in Hervey Bay.

Earlier research on humpback whales in Hervey Bay by Dr Peter Corkeron for the Queensland National Parks and Wildlife Service (QNPWS), reported in Corkeron (1993) and Corkeron *et al*. (1994), concluded that there were insufficient data available to determine the importance of Hervey Bay for any class of humpback whales. To obtain the data required to address the issue of the importance of Hervey Bay for eastern Australian humpback whales, Corkeron (1993) recommended a dedicated long-term systematic vessel-based photo-identification survey be undertaken. This provided the rationale for the study design and the focus for TOP's Hervey Bay humpback whale research study, and the focus of this thesis on the social behaviour and social organisation of humpback whales in Hervey Bay.

A QNPWS research permit was approved in early 1991, and fieldwork protocols for the study were trialed and reviewed with the assistance of Dr. Tim Stevens of QNPWS in Hervey Bay during August to October 1991. Research undertaken in Hervey Bay between 1992 and 2009 was conducted under research permits issued by the QNPWS (permit numbers MP2006/020 and WISP03749806).

## 2.2 STUDY SITE AND SURVEY TIMING

Hervey Bay, formed by Fraser Island and the Australian mainland, is located at $25^0$S, $153^0$E on the eastern coast of Queensland (Fig. 2.1). It is a wide, shallow bay approximately 4,000 km$^2$ in area and is generally less than 18 m deep, with a sand and mud bottom (Vang 2002). Fraser Island is 126 km long; it lies along a northeasterly axis and its northern end bridges the continental shelf. The most southerly islands of the Great Barrier Reef are directly north of Hervey Bay at a distance of between 111 and 222 km (Fig. 2.1).

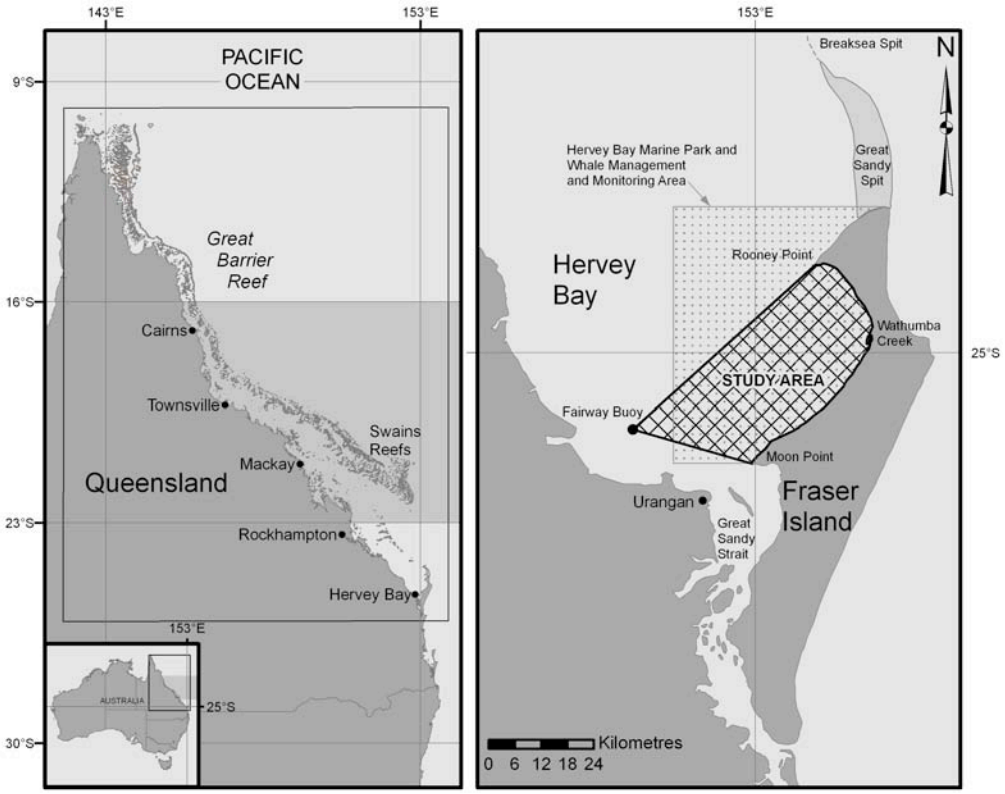



*Figure 2.1.* The location of Hervey Bay on the eastern coast of Australia and its geographic relationship to the reefs and inter-reef lagoon of the Great Barrier Reef is shown in the left side map. The primary overwintering and breeding ground for eastern Australian humpback whales is believed to be off the Queensland coast within the Great Barrier Reef inter-reef lagoon between $16^0$S and $23^0$S (shaded) (Simmons and Marsh 1986, Paterson 1991,

Chaloupka and Osmond 1999). The study area and the Hervey Bay Marine Park boundaries are shown on the eastern side of Hervey Bay.

Paterson (1991) reported that the annual southern migration from the Great Barrier Reef began in late July, with humpback whales moving into and out of Hervey Bay from early August to mid-October. Additional information from the Queensland Environment Protection Agency (QEPA) and the whale-watching industry confirmed the presence of humpback whales in the bay from the first week of August to mid-October between 1987 and 1991. Accordingly, a 10 week survey commencing on the first Sunday after 5 August each season was chosen to provide a representative sample of the seasonal occurrence of humpback whales in Hervey Bay.

## 2.3 VESSEL-BASED SURVEYS

Vessel-based surveys for this study were conducted for 9 weeks in 1992 and for 10 weeks each year between 1993 and 2009, commencing on the first Sunday after the 5$^{th}$ of August until mid-October. The study area (Fig. 2.1) is approximately 27.8 km from Urangan Boat Harbour, Hervey Bay. Fieldwork was planned for six days each week, leaving Urangan harbour at 0800 each Sunday and returning at 1500 the following Friday. Planned daily operations were from 0930 to 1700 on Sunday, 0700 to 1700 Monday to Thursday, and from 0700 to 1330 on Friday, to allow for return travel to Urangan harbour.

Four different motorized vessels were utilised as dedicated research platforms from 1992 to 2009: two were mono-hulls and two were catamarans, ranging in length from 11 to 27 m. When searching for humpback whale pods the normal range of operational speed of the four research vessels was 12.9-18.5 km h. When searching for pods GPS locations (waypoints in

degrees of latitude and longitude) were recorded every hour on the hour. Upon commencement of observations of a pod the rate of travel of the research vessel was adjusted to match the speed of the pod.

## 2.4 OBSERVATIONS, PHOTO-IDENTIFICATION AND OTHER DATA

Observations and photo-identification began on the first sighted pod or singleton, with no *a priori* selection of any particular pod class. If no pod or singleton was in sight, either a random direction of travel was commenced until a pod or singleton was sighted or, if information about the location of pods or singletons was available from one of the local commercial whale-watching vessels, travel was commenced towards that location. If a pod or singleton was sighted en route it was selected for observation.

Photography of the ventral fluke patterns, shape and size of dorsal fins and lateral body markings were obtained to allow identification of individual humpback whales (Katona *et al*. 1979, Katona and Whitehead 1981). Photographs were taken with Canon EOS cameras, using a 100-300mm lens. A marker shot of Fraser Island was taken prior to commencement of photography on a pod and after completion of photography on a pod. In addition if a photograph of a dorsal fin was followed immediately by a fluke photograph of the same individual whale a marker shot (of the ship's railings) was taken to verify that the preceding series of photographs were of the same individual whale.

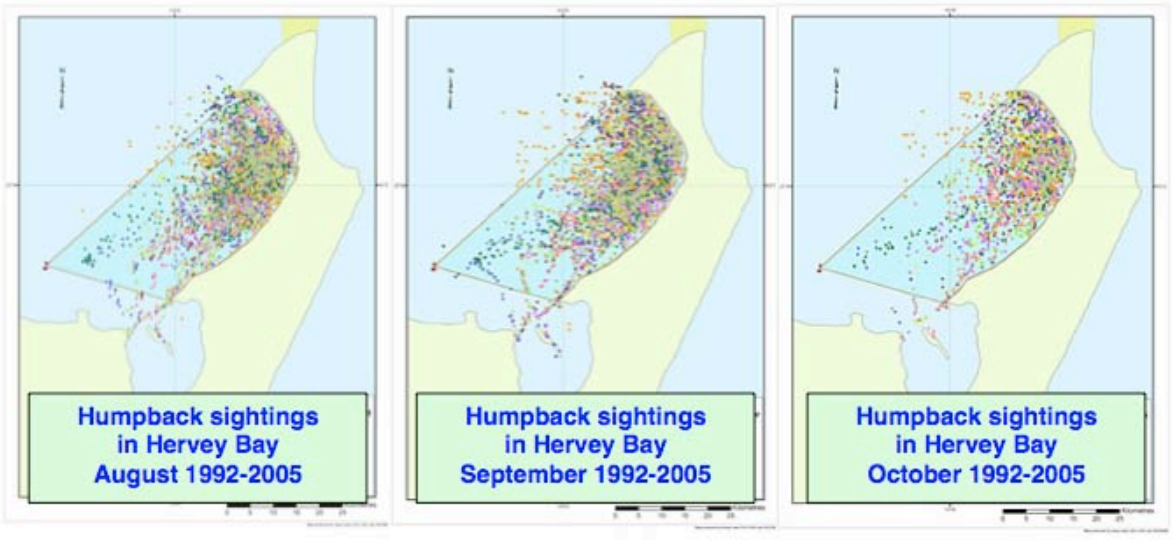



*Figure 2.2* GPS locations of sightings of humpback whales observed in Hervey Bay during the months of August, September and October over the years 1992-2005.

Data collected during the observation of each pod included: date, time, depth and GPS location at commencement of observation, every fifteen minutes during observation and at the completion of the observation. As well, the following data were recorded: pod identification code; the observed number of individuals in the pod; pod composition; associations and disassociations of pods and surface behaviours (continuous sampling; Altmann, 1974). Information on sex-identification was obtained where possible. Sex-identification was determined by the observation of the genital area and the presence of a hemispherical lobe posterior to the genital slit in the case of females and its absence in the case of males (True 1904, Glockner 1983). Furthermore, sex can also be inferred from social roles: an adult individual accompanying a calf consistently and providing nurturing behaviours towards the calf can be inferred to be female (Tyack and Whitehead 1983). Similarly, escorts and singers have been found to be male (Glockner and Venus 1983, Tyack and Whitehead 1983, Baker and Herman 1984*a*, Clapham 2000). With few exceptions, Nuclear Animals in competitive groups have been found to be female (Darling *et al.* 1983; Tyack and Whitehead 1983; Baker

and Herman 1984*b*; Clapham *et al.* 1992, 1993; Clapham 2000; Darling *et al.* 2006). Chu and Nieukirk (1988) reported that individual humpback whales with distinct vertical and horizontal dorsal fin scars, resulting from competitive activity could be inferred as males. These marks were only used in conjunction with the resighting histories and the observed social roles to infer an individual as a male.

Members of the research team constantly scanned $360^0$ for any pods approaching the pod under observation. All pod and observation data were recorded daily in field notes and entered into a FileMaker Pro database each evening.

In addition to pod and observation data, daily weather and environmental readings were recorded. These included wind speed and direction, sea state (Beaufort scale), cloud cover and precipitation. Also daily readings of sea temperature, salinity and turbidity were recorded and systematic water samples were obtained for chlorophyll a analysis within the Hervey Bay humpback whale habitat. As well, sloughed-skin samples were opportunistically collected for genetic analyses.

The principal investigators were supported each season by Research Assistants who were predominantly undergraduate students or graduates participating in environmental or marine science degrees at Southern Cross University and other Australian and overseas Universities. Research Assistants rostered and supervised Interns, who volunteered on a weekly basis, to assist with fieldwork aboard the expedition. Interns were rostered on morning and afternoon shifts for photo-identification note taking, GPS readings, weather and environmental readings, water sampling, sloughed-skin collection and daily data entry.

## 2.5 PHOTOGRAPHIC MATCHING SYSTEM AND DATA ANALYSIS

After completion of fieldwork, photography for each pod was examined, and photographs were organised into ventral flukes, dorsal fins and lateral body markings for each individual humpback whale in the pod utilising Adobe Photoshop CS software. Photographs that provided useful information of individuals in each pod were archived as high-resolution JPEG files at a standard ratio of 1536 pixels by 1024 pixels at 300 dpi. The selected photographs were analysed in conjunction with the field notes on observations of pod composition, behaviours observed and sex-identification information.

The best ventral fluke photographs of individual humpback whales were assessed for photographic quality and individual information. Annual fluke catalogues for the years 1992 to 2009 were compiled and analysed for intra- and inter-season resights of individual humpback whales using a propriety matching system based on categorisation of flukes utilising an array of coded discrete characteristics (ACDC), applied to the file name of each fluke photograph (Table 2.1 and 2.2, Figure 2.3). The ACDC categories were based on individually unique and stable patterns of black and white pigmentation on the underside of the tail flukes (Katona *et al*. 1979, Katona and Whitehead 1981). The ACDC characteristics selected for the system (Table 2.1) were derived from a visual analysis of 28,000 fluke photographs taken between 1992 and 2003. The system allowed each fluke to be allocated to contiguous stratified categories using the ACDC codes in the image filename for visual display and organisation to facilitate photographic analyses and matching (Figure 2.3). A standard protocol was utilised for the allocation of ACDC codes to the filename of each fluke image (Table 2.1). When matching a fluke against the fluke catalogue it was pairwise matched with other photographs within its ACDC colour and pattern category and then if not matched it was then subsequently compared with photographs within adjacent categories. As

the majority of flukes were predominantly all white (63.5%, Table 2.2) the shape and colouration of the trailing edge and notch were important characteristics in the matching process (Carlson *et al.* 1990, Mizroch *et al.* 1990, Blackmer *et al*. 2000, Friday *et al.* 2000). Because pigmentation patterns and marks of individual flukes may change over years (Carlson *et al.* 1990), utilising a consistent protocol in the assignment of ACDC characteristics minimised mismatch errors. If for example a resighting of a particular individual showed a change in marks, the ACDC filename reflects the change in that year. Photographic analysis outcomes together with original field data were incorporated into a single FileMaker Pro relational database.

The ACDC characteristic codes selected for the system and protocol used to assign ACDC codes are reported in Table 2.1. Examples of how ACDC categories display in photo-identification analysis software are presented in Figure 2.3.

*Table 2.1* Array of Coded Discrete Characteristics (ACDC) applied to ventral fluke image filenames for photo-id matching of intra and inter-season resightings of individual humpback whales and the protocol used for the ACDC code assignment and order in filename.

| Code | Description | Protocol used for code assignment [(a)] |
|---|---|---|
| (A) Primary Characteristics: | | Step I |
| BB | Black Border | View and examine the ventral fluke photo from posterior to anterior across the horizontal plane for primary characteristics. |
| BC | Black Centre | |
| BK | Black | Step II |
| TE | Trailing edge | Compare to examples (Fig 2.2) and assigned primary code or codes. If BB & BC both present BB precedes BC. If BB, BC or BK not present, TE, will be the sole primary code. Separate each four digits of code by a hyphen. |
| NT | Notch | |
| (B) Secondary Characteristics: | | Step III |
| BS | Black Stem | View and examine the ventral fluke photo from posterior to anterior across the horizontal plane for secondary characteristics. |
| DM | Damaged | |
| RK | Rake Marks | |
| CR | Curled | Step IV |
| WP | White Patch | Compare to examples (Fig 2.2) and assign secondary codes from posterior to anterior for characteristics present. Separate each four digits of code by a hyphen. |
| BP | Black Patch | |
| (C) Tertiary Characteristics: | | Step V |
| SM | Scratch Marks | View and examine the ventral fluke photo posterior to anterior across the horizontal plane for any tertiary characteristics present. |
| DT | Dots | |
| RG | Rings | Step VI |
| | | Compare to examples (Fig 2.2) and assign tertiary codes posterior to anterior for characteristics present. If SM, DT and/or RG occur on in the same horizontal plane SM precedes DT and, DT precedes RG in the code array. Separate each four digits of code by a hyphen. |

[(a)] The examples (Figure 2.3 below) illustrate the stratification of categories from the applied ACDC codes in each fluke photograph filename.

BBBC-NTSM-2007-3225

BBBC-NTSM-DTRG-2008-8533

BBNT-BSSM-DT-2004-1887

BBRK-NTBS-SM-2007-2621

BCNT-SMDT-RG-2005-3285:86

BCNT-SMDT-RG-2007-2094

BKNT-SMRG-2007-0839

BKWP-NTSM-RG-2006-0130

TEBB-NTBS-SMDT-RG-2001

TEBB-NTBS-SMDT-RG-2003-3838

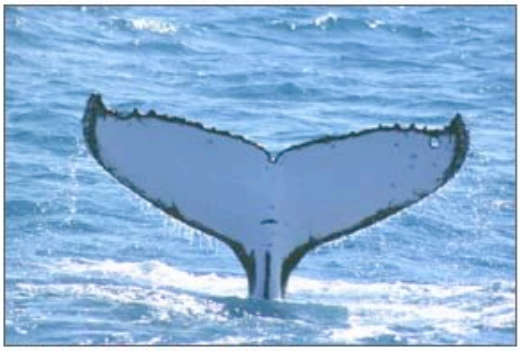
TECR-NTBS-SMDT-2001-1013:14

TECR-NTBS-SMDT-RG-2005-5077:78

TEDM-NTBS-SM-2004-4103

TEDM-NTBS-SMDT-2007-0789:0808

TEHL-NTBS-DTRG-2003-0890



TEHL-NTBS-SMRG-2002-0146

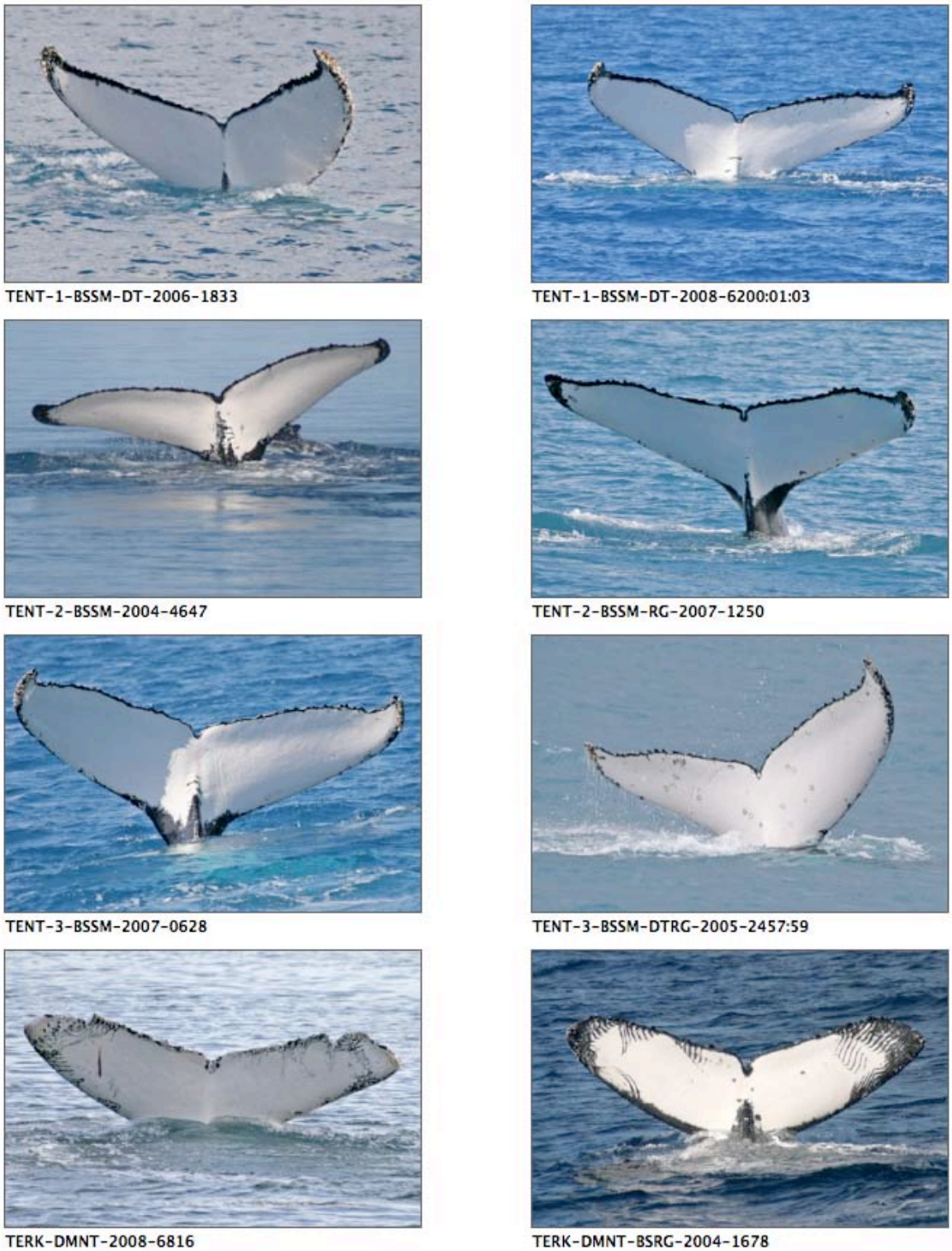



Figure 2.3 *A selection of 24 fluke photographs illustrating how the ACDC code in the filename facilitates visual display to facilitate photo-identification matching. Each filename is*

*composed of the assigned ACDC codes, year photograph was taken and photo-id archive number of the fluke photograph.*

The Hervey Bay fluke catalogue for the period 1992 to 2009 was fully reconciled within and between seasons using the ACDC fluke matching system and consisted of 2,821 individual humpback whales. The number and percentage of flukes in each of the primary ACDC categories is reported in Table 2.2.

Life histories of individual humpback whales based on resightings over two or more years were compiled from observations recorded in the annual fluke catalogues. A total of 578 life histories were obtained with resightings of individually identified whales ranging over a period of eighteen years. A summary of fieldwork, observations and data in Hervey Bay from 1992 to 2009 is presented in Table 2.3.

*Table 2.2* Number and % of flukes by primary ACDC categories in 1992-2009 fluke catalogue.

| Primary ACDC categories [(1)] | Number of Flukes | % |
|---|---|---|
| BBBC/BBDM/BBNT/BBRK (Black Borders plus) | 51 | 1.8 |
| BCBP/BCDM/BCCR/BCNT/BCRK (Black Centres plus) | 214 | 7.6 |
| BKDM/BKNT/BKRK/BKWP (Black plus) | 86 | 3.0 |
| TEBB (Trailing Edge, Black Border) | 311 | 11.0 |
| TEBP/TECR (Trailing Edge, Black Patch or Curled) | 9 | 0.3 |
| TEDM (Trailing Edge, Damaged) | 93 | 3.3 |
| TEHL (Trailing Edge, Holes) | 52 | 1.8 |
| TENT-1 (Trailing Edge (Thick), Notch) | 372 | 13.2 |
| TENT-2 (Trailing Edge (Medium), Notch) | 722 | 25.6 |
| TENT-3 (Trailing Edge (Fine), Notch) | 696 | 24.7 |
| TERK (Trailing Edge, Raked) | 215 | 7.6 |
| Total Flukes 1992-2009 | 2821 | 100.00 |

[(1)] The primary ACDC category is made-up of the first four digits of code in the filename, except for the TENT categories (See Table 2.1 above). The TENT category is further categorised based on the thickness of black pigmentation along the trailing edge of the fluke as 1 (Thick, but less than BB), 2 (Medium), 3 (Fine). All TENT flukes are predominantly white pigmentation.

*Table 2.3.* Summary of fieldwork, observations and data: Hervey Bay from 1992 to 2009.

| | Effort and observations | | | | | Data | | |
|---|---|---|---|---|---|---|---|---|
| | Fieldwork | | | Observations | | Yearly Catalogues | | Cumulative |
| Year | First day | Last day | Field days | Pods (*n*) | Whales (*n*) | Flukes (*n*) | Resighting histories | Resighting histories |
| 1992 | 10th Aug | 9th Oct | 42 | 189 | 387 | 4 | 4 | 4 |
| 1993 | 6th Aug | 15th Oct | 53 | 229 | 442 | 5 | 3 | 7 |
| 1994 | 7th Aug | 14th Oct | 50 | 163 | 380 | 47 | 36 | 43 |
| 1995 | 6th Aug | 13th Oct | 51 | 172 | 374 | 47 | 27 | 70 |
| 1996 | 4th Aug | 11th Oct | 48 | 185 | 410 | 70 | 26 | 96 |
| 1997 | 1st Aug | 17th Oct | 64 | 300 | 693 | 140 | 52 | 148 |
| 1998 | 9th Aug | 16th Oct | 58 | 410 | 934 | 190 | 56 | 204 |
| 1999 | 28th Jul | 15th Oct | 63 | 399 | 929 | 210 | 43 | 247 |
| 2000 | 6th Aug | 13th Oct | 58 | 380 | 815 | 206 | 50 | 297 |
| 2001 | 12th Aug | 19th Oct | 57 | 432 | 954 | 234 | 43 | 340 |
| 2002 | 11th Aug | 17th Oct | 59 | 409 | 968 | 268 | 56 | 396 |
| 2003 | 10th Aug | 17th Oct | 56 | 390 | 928 | 270 | 42 | 438 |
| 2004 | 5th Aug | 15th Oct | 60 | 419 | 952 | 303 | 49 | 487 |
| 2005 | 30th Jul | 14th Oct | 61 | 448 | 1,050 | 376 | 43 | 530 |
| 2006 | 3rd Aug | 13th Oct | 58 | 420 | 984 | 341 | 23 | 553 |
| 2007 | 30th Jul | 11th Oct | 60 | 399 | 945 | 297 | 14 | 567 |
| 2008 | 7th Aug | 17th Oct | 61 | 508 | 1,283 | 407 | 11 | 578 |
| 2009 | 6th Aug | 16th Oct | 55 | 396 | 901 | 317 | 0 | 578 |
| | | Totals | 1,014 | 6,248 | 14,329 | 3,732 | 578 | |

As noted in Chapter 1, the primary data chapters for this thesis (Chapters 3, 4 and 5) are based on a published paper and two manuscripts formatted as papers for submission, that provide

further relevant details of the methods and analyses; hence there is some unavoidable repetition in the relevant Method section of each of those Chapters.

# *Chapter 3*

# Seasonal changes in pod characteristics of eastern Australian humpback whales *(Megaptera novaeangliae)*, Hervey Bay 1992-2005

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Declaration of Authorship:

| | |
|---|---|
| Conception of the study: | TF (70%), WF (30%) |
| Survey Design: | TF (70%), WF (30%) |
| Data collection: | TF (80%), WF (20%) |
| Data analysis: | TF (80%), WF (20%) |
| Statistical analysis: | TF (10%), WF (10%), LB (80%) |
| Interpretation of data: | TF (60%), WF (10%), PH (10%) PC (10%), LB (10%) |
| Writing of manuscript: | TF (70%), WF (20%), PH, PC, LB, PB (10%) |

## 3.1 ABSTRACT

This study investigated the characteristics and composition of 4,506 humpback whale pods observed in Hervey Bay between 1992 and 2005. These data were used to analyse and model the variability of pod size and composition, and to assess the importance of Hervey Bay for particular classes of humpback whales. Pods ranged in size from one to nine individuals. Pairs were the most frequent pod type (1,344, 29.8%), followed by mother-calf alone (1,249, 27.7%), trios (759, 16.8%), singletons (717, 15.9%), and 4+ whales (437, 9.7%). Of the 4,506 pods, calves were present in 40%, and 10.8% of all pods had one or more escorts present. Of the 1,804 pods observed with calves present, 1,251 (69.4%) were mothers alone with their calves. The size and composition of pods in the study area varied significantly as the season progressed. Pods with calves present were rarely recorded early in the season but dominated later in the season. A significant increase over years in larger groups may be related to social and behavioural changes as the population expands. The data indicate that Hervey Bay is important to immature males and females early in the season, to mature males and females in mid-season, and to mother-calf pairs (either alone or with escorts) in mid-to-late season.

## 3.2 INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) are found in all oceans of the world and maintain an annual migratory cycle from low-latitude winter breeding grounds to high-latitude summer feeding areas in both the Northern and Southern Hemispheres (Chittleborough 1965, Dawbin 1966, Baker *et al.* 1986, Clapham 2000). Winter assemblages of humpback whales occur in tropical and subtropical waters either around islands or along continental coastlines (Dawbin 1956). Relatively shallow and sheltered warm-water areas appear to be a preferred habitat for calving females (Dawbin 1966, Whitehead and Moore 1982, Smultea 1994, Clapham 2000, Craig and Herman 2000, Ersts and Rosenbaum 2003).

Eastern Australian humpback whales commence the southern migration from the breeding grounds to their Antarctic feeding areas in July each year and return at some point by June the following year (Dawbin 1966). Chittleborough (1965) suggested that there is no particular latitude along the eastern coast of Australia where migration ceases and breeding activities commence.

One of many places that are used by humpback whales during the winter is Hervey Bay in Queensland; this is slightly west of the main northward migratory stream and 2◦ south of the Great Barrier Reef lagoon. Humpback whales do not enter Hervey Bay on their northward migration that peaks during June and July. The migration stream passes Breaksea Spit to the northeast of Hervey Bay and then inclines to the northwest, with whales dispersing widely between the outer Great Barrier Reef and the Australian coast (Paterson 1991).

Previous studies suggested that the large inter-reef lagoon of the Great Barrier Reef, between 16◦S and 23◦S, represents the primary overwintering and breeding grounds of eastern Australian humpback whales (Simmons and Marsh 1986, Paterson 1991, Chaloupka and

Osmond 1999). There are no recent published data on aggregations of humpback whales north of Hervey Bay.

On the southward migration, large numbers of humpback whales make a slight diversion from the southern migratory pathway and pass inside Breaksea Spit to enter Hervey Bay (Paterson 1991). It has been suggested that the proportion of eastern Australian (E1 breeding ground) humpbacks entering Hervey Bay is 30%–50% (Chaloupka *et al.* 1999). Humpback whales move into Hervey Bay from late July and during August, September, and October. They enter and leave from the north and aggregate in shallow water close to the western shore of Fraser Island in the eastern part of the bay (Corkeron *et al.* 1994). Aerial surveys have shown that pods are not randomly distributed but tend to aggregate in clusters (Corkeron 1993). Mother and calf pods are the final cohort to migrate southwards (Dawbin 1966, 1997) and enter Hervey Bay during September and October (Corkeron 1995, Corkeron and Brown 1995). On leaving the area, humpback whales initially travel north, rounding Breaksea Spit to the east before rejoining the southward migratory stream (Corkeron 1993, Corkeron *et al.* 1994).

Calves are frequently observed in Hervey Bay, singers are heard, and competitive groups are observed in the bay (Corkeron 1993, Corkeron *et al.* 1994); the latter involve intrasexual competition among males for access to females (Clapham 2000). Previous studies of humpback whales in Hervey Bay in the late 1980s and early 1990s examined migratory movement, distribution, pod size, residency, relative abundance (Corkeron 1993, Corkeron *et al.* 1994), behavioural response to whale watching vessels (Corkeron 1995, Corkeron and Brown 1995), seasonal abundance trends, and survival probabilities (Chaloupka *et al.* 1999). Corkeron *et al.* (1994) suggested that the nonrandom clustering of humpback whales aggregating in Hervey Bay might be related to social factors. However, there were no data indicating that Hervey Bay was of importance to any particular class of humpback whale (Corkeron *et al.* 1994).

This study investigates the sizes and composition (classes of whales) of 4,506 humpback whale pods observed in Hervey Bay between 1992 and 2005. The primary objective of the study was to investigate and analyse pod size and composition over years and within season, and to use these data to assess the importance of Hervey Bay for particular classes of humpback whales.

## 3.3 METHODS

### *3.3.1 Definitions*

***Pod***: Refers to either a lone whale (singleton) [1] or two or more humpback whales swimming side-by-side within one–two body lengths of each other, generally moving in the same direction and coordinating their speed of travel (Whitehead 1983, Clapham 1993, Corkeron *et al.* 1994). Although in some species, for example, *Orcinus orca*, the term pod is used to describe stable groups, our use of the term "pod" does not imply stable groups.

Adult—For the purpose of this study, the term "adult" is used in the results and modeling, to describe the number of whales in a pod that were not calves. The term "adult" is therefore used for convenience to identify all non-calves but does not imply sexual maturity. A proportion of the whales here classified as adults are likely to be immature whales and they are not identified separately as such in this paper.

***Calf:*** An individual whale was considered to be a calf if it appeared to be less than half the length of a particular adult with whom it maintained a constant and close relationship. In most observations, no other whale was seen coming between a mother and calf (Tyack and Whitehead 1983). The adult in the dyad was assumed to be the mother.

[1] Although a single whale is not a pod, the term singleton is used for convenience for the purpose of these analyses

***Escort***: Is defined as a whale accompanying a mother and her calf (Herman and Antinoja 1977). Escorts have been generally found to be male and may be mature males waiting for a postpartum estrous mating opportunity ((Herman and Antinoja 1977, Glockner and Venus 1983, Tyack and Whitehead 1983, Baker and Herman 1984, Clapham 2000).

### *3.3.2 Surveys*

Vessel surveys for this study were conducted for nine weeks in 1992 and for ten weeks each year between 1993 and 2005, commencing on the first Sunday after 5 August until mid-October. The study area (Fig. 2.1) is approximately 27.8 km from Urangan Boat Harbour, Hervey Bay. Fieldwork was planned for 6 d each week, leaving Urangan harbour at 0800 each Sunday and returning at 1500 the following Friday. Planned daily operations were from 0930 to 1700 on Sunday, 0700 to 1700 Monday to Thursday, and from 0700 to 1330 on Friday.

Four different motorised vessels were utilised as dedicated research platforms between 1992 and 2005: two were mono-hulls and two were catamarans, ranging in length from 11 to 27 m. When searching for humpback whale pods, the normal range of operational speed of the four research vessels was 12.9–18.5 km/h. Upon commencement of observations, the rate of travel of the research vessel was adjusted to match the speed of the pod.

Pods were chosen for observation on a “first pod available” basis with no a priori selection of any particular pod class. On arrival in the study area, or prior to departing an overnight anchorage within the study area, the nearest pod in sight was selected. If no pod was in sight, either a random direction of travel was commenced until a pod was sighted or, if information about the location of pods was available from one of the local commercial whale-watching vessels, travel was commenced toward that location. If a pod was sighted en-route, it was selected for observation.

The pod was used as the basic observational unit in analysis for the 4,506 pods observed. The hours spent weekly on survey and observing whales, the weekly total numbers of pods and whales observed, and the mean hourly rates of observation of pods and whales over weeks were documented prior to analysis of the size and composition of pods.

## 3.4 STATISTICAL ANALYSIS

To examine the variation in pod size and composition, the whole sample frequencies and percentages of pod sizes (all whales), and pod sizes categorised by no calves present, versus calves present are reported. The proportions of pods for the classes, calves and escorts in terms of the number of calves and the number of escorts present are reported. For the variation over years and within season, the proportion of pods with a calf present and the proportion of all whales in the pod size categories (1, 2, 3, 4+ whales) are reported.

For further analysis, the frequencies by week (1–10) of the pod size categories 1, 2, 3, 4+ adults of pods in which a calf was present or not present, and the frequencies by week (1–10) of the pod size category 1, 2, 3, 4+ of all whales in pods with calves present are reported.

A multinomial logistic regression model was developed to estimate variation in the proportion of pods of 1, 2, 3+ adults over years, and over weeks within year of pods in which a calf was present or not present.

## 3.5 RESULTS

### *3.5.1 Effort and observations*

A total of 139 six-day survey periods (Sunday–Friday) were conducted in the Hervey Bay study area between 1992 and 2005 (Fig. 2.1). Data were obtained on 770 of the planned 834

survey days. Total survey time was 6,160 h and observations of humpback whale pods were conducted for a total of 2,760 h.

Observations were made and data collected on a total of 10,179 humpback whales in 4,506 pods during the 139 6-day survey periods. Six-day survey and observation hours, and numbers of pods and whales observed in each survey period, are plotted in Figure 3.1A and B. Figure 3.1C shows the hourly rates of pods and whales observed. A Loess curve (Cleveland 1979) was added to Figure 3.1C to show the growth of mean observation rates over time.

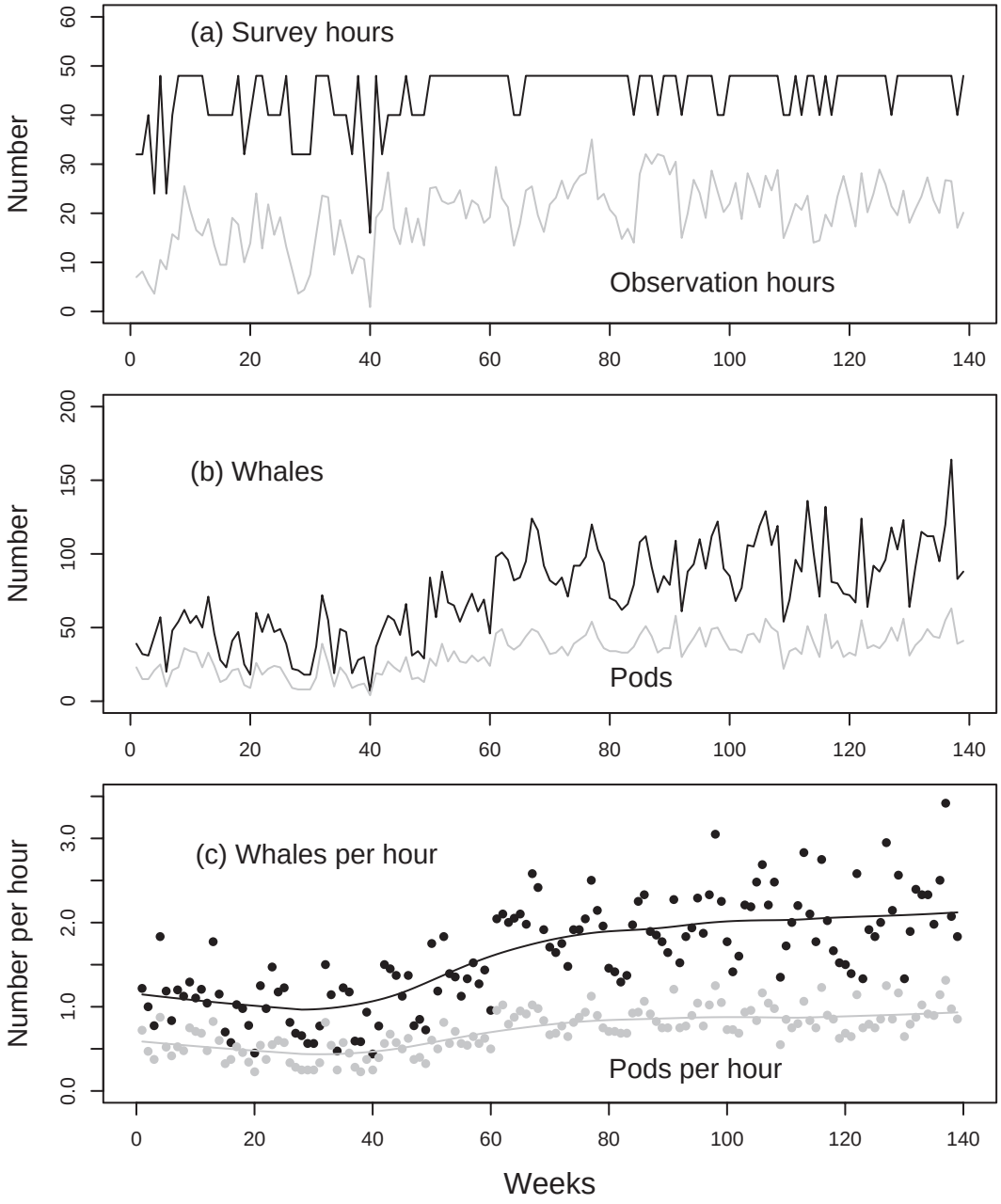


*Figure 3.1*. (A) Weekly survey and observation hours 1992–2005, (B) weekly observations of humpback whale pods and whales 1992–2005, (C) humpback whales and pods observed per hour in survey periods 1992–2005 with Loess growth curves.

### *3.5.2 Pod sizes in Hervey Bay 1992-2005*

The frequencies and percentages of pod sizes for the whole sample are summarised in Table 3.1, and divided into two categories by "no calves present, or calves present" in Table 3.2.

*Table 3.1*. Number of whales in pods *(N)* in Hervey Bay, between 1992-2005.

| Number of whales in pods | All whales (calves included) | |
|---|---|---|
| | N | % |
| 1 | 717 | 15.9 |
| 2 | 2,593 | 57.5 |
| 3 | 759 | 16.8 |
| 4 | 281 | 6.2 |
| 5 | 96 | 2.1 |
| 6 | 38 | 0.8 |
| 7 | 12 | 0.3 |
| 8 | 7 | 0.2 |
| 9 | 3 | 0.1 |
| Total | 4,506 | 100.0 |

Pods ranged in size from 1 to 9 individual whales (mean = 2.26, SD = 0.10). Pods with two whales present were the most frequently observed pod size (57.5%) followed by trios (16.8%), and singletons (15.9%). Only 9.7% of pods were composed of four or more whales (Table 3.1).

*Table 3.2*. Number of whales in pods *(N)* by no calves present and calves present

| Number of whales in pods | Pods with no calves present | | Pods with calves present | |
|---|---|---|---|---|
| | N | % | N | % |
| 1 | 717 | 26.5 | 0 | 0 |
| 2 | 1,344 | 49.7 | 1,249 | 69.2 |
| 3 | 393 | 14.5 | 366 | 20.3 |
| 4+ | 248 | 9.2 | 189 | 10.5 |
| Total | 2,702 | 100.0 | 1,804 | 100.0 |

Of the 4,506 pods, 2,702 (59.96%) had no calves present and 1,804 (40.04%) had calves present (Table 3.2). Of the 2,593 pods with two whales in the whole sample (Table 3.1), 1,344 (51.8%, Table 3.2) were made up of two adults, and 1,249 (48.2%, Table 3.2) were composed of mothers alone with their calves. In pods with no calves present, 23.7% had three or more whales and in pods with calves present, 30.8% of pods had three or more whales present.

### *3.5.3 Observations of Pods with Calves and Escorts Present in Hervey Bay 1992–2005*

The number of pods observed with calves present, and the number of pods with escorts present by number and percentage for the whole sample are summarised in Table 3.3. Of the 4,506 pods, 1,804 (40%) had one or more calves present; 38.2% had one calf present, 1.6% two, and 0.2% included three calves. One or more escorts were recorded in 10.8% of the 4,506 pods.

*Table 3.3.* Pods with calves/escorts present (by number & percentage).

| Number of calves/ Escorts present | Calves (Number of pods) | | Escorts (Number of pods) | |
|---|---|---|---|---|
| | N | % | N | % |
| None present | 2,702 | 60.0 | 4,019 | 89.2 |
| 1 | 1,721 | 38.2 | 371 | 8.2 |
| 2 | 75 | 1.6 | 71 | 1.6 |
| 3 | 8 | 0.2 | 37 | 0.8 |
| 4 | | | 4 | 0.1 |
| 5 | | | 3 | 0.1 |
| 6 | | | 1 | 0.0 |
| Total | 4,506 | 100.0 | 4,506 | 100.0 |

### *3.5.4 Trends in Pod Size and Composition in Hervey Bay 1992–2005*

The proportion of pods with calves present and the number of whales in pods over years and within season are summarised in Figure 3.2A, B, C, and D.

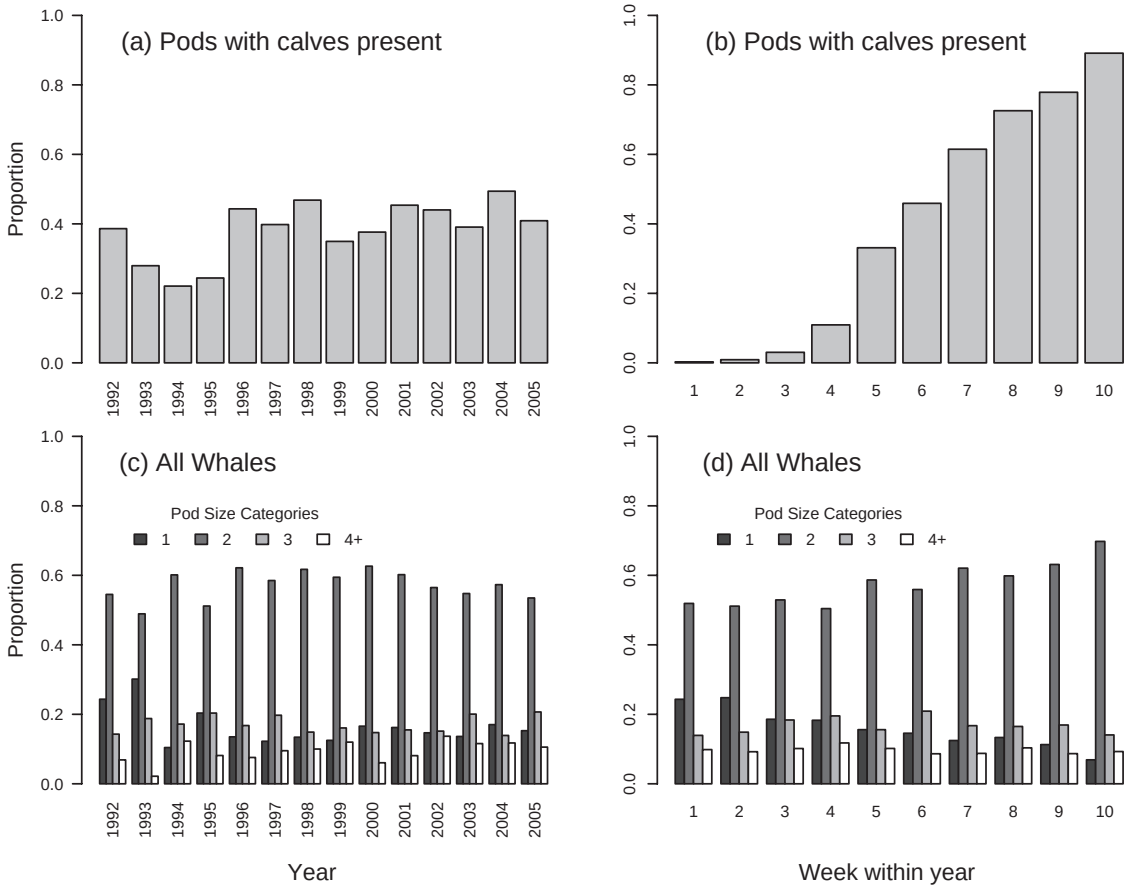


*Figure 3.2*. Observed proportions: (A) pods with calves present by year, (B) pods with calves present by week within year, (C) all whales in pod (calves included): pod size by year, (D) all whales in pod (calves included): pod size by week within year.

While the variation over years (Fig. 3.2A and C) does not have an obvious pattern except for the decline in the proportion of pods with calves present between 1992 and 1993, the variation over weeks within year was more systematic (Fig. 3.2B and D). The proportion of pods with calves present increased strongly from week 4 to the end of the season (late August–

September, to mid-October; Fig. 3.2B).

For all whales (Fig. 3.2C and D), pods with two whales consisted of either two adults, or a mother alone with her calf (Table 3.2). For all whales, the number of pods with two whales present—expressed as a proportion of all pods—increased with time during the season, while the proportion representing singleton pods decreased. The proportion of all pods represented by larger pods (3 and 4+ whales) increased from week 1 to about week 6 (early August to mid-September) and decreased thereafter (Fig. 3.2D).

### *3.5.5 The Effect of the Presence or Absence of Calves on Seasonal Variation in Pod Size and Composition*

Singletons as a proportion of all pods were highest in the first four weeks when pods with calves were rarely seen; however, in the same period there were still more pairs than singletons (Fig. 3.2D). The proportion of pods with a calf present increased in the second half of the season, along with a rapid increase in the proportion of mothers alone with their calves (Fig. 3.2B and D).

To analyse and compare the size and composition of pods with calves present and pods with no calves present, we adopted the approach used by Mobley and Herman (1985) of counting and analysing the number of adults in pods. Table 3.4 summarises the pod data by week within year, categorised by the number of adults in pods with no calves present, all whales in pods with calves present, and the number of adults in pods with calves present.

*Table 3.4.* Number of pods by week within year for size categories (1, 2, 3, 4+), for: (a) Number of adults (in pods with no calves present); (b) All whales (in pods with calves present) and (c) Number of adults (in pods with calves present). Relevant percentages are reported below columns.

| | (a) Number of adults in pods with no calves present | | | | | (b) All whales in pods with calves present | | | | (c) Number of adults in pods with calves present[1] | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Week \ Size | 1 | 2 | 3 | 4+ | Total | 2 | 3 | 4+ | Total | 1 | 2 | 3 | 4+ | Total |
| 1 | 89 | 190 | 50 | 36 | 365 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 |
| 2 | 110 | 223 | 66 | 41 | 440 | 4 | 0 | 0 | 4 | 4 | 0 | 0 | 0 | 4 |
| 3 | 86 | 239 | 80 | 42 | 447 | 6 | 5 | 5 | 16 | 6 | 5 | 4 | 1 | 16 |
| 4 | 87 | 209 | 77 | 51 | 424 | 31 | 16 | 5 | 52 | 31 | 16 | 3 | 2 | 52 |
| 5 | 72 | 169 | 40 | 28 | 309 | 102 | 32 | 19 | 153 | 102 | 33 | 11 | 7 | 153 |
| 6 | 64 | 117 | 42 | 15 | 238 | 129 | 50 | 23 | 202 | 129 | 55 | 9 | 9 | 202 |
| 7 | 64 | 102 | 15 | 17 | 198 | 217[2] | 71 | 28 | 316 | 219[2] | 81 | 13 | 3 | 316 |
| 8 | 67 | 53 | 10 | 8 | 138 | 248 | 73 | 44 | 365 | 248 | 84 | 22 | 11 | 365 |
| 9 | 52 | 31 | 11 | 8 | 102 | 260 | 67 | 32 | 359 | 260 | 84 | 7 | 8 | 359 |
| 10 | 26 | 11 | 2 | 2 | 41 | 252 | 51 | 33 | 336 | 252 | 63 | 13 | 8 | 336 |
| Total | 717 | 1,344 | 393 | 248 | 2,702 | 1,249 | 366 | 189 | 1,804 | 1,251 | 422 | 82 | 49 | 1,804 |
| % of Total | 26.5 | 49.7 | 14.5 | 9.2 | 100 | | | | | 69.4 | 23.4 | 4.5 | 2.7 | 100 |

[1] For the number of adults (Table 3.4c), if one adult is present it was a mother alone with her calf, 2 adults can either be 2 mothers together, or a mother with an escort. Similarly, if 3 adults are present, they can be a combination of up to 3 mothers (2 mothers with 1 escort, or 1 mother with 2 escorts), while 4+ can be a combination of up to 3 mothers and escorts.

[2] There were two observations of a mother with two calves present in this week in different years, which accounts for the differences in this row between 'All whales, in pods with calves present' and 'Number of adults, in pods with calves present'.

Of the 1,804 pods observed with calves present (Table 3.4c), 1,251 (69.4%) included one adult, i.e. mothers alone with their calves, 23.4% had two adults, and 7.2% had three or more adults. Where no calves were present (Table 3.4a, 2,702 pods), pairs were the dominant pod type (49.7%); singletons (26.5%) and 23.7% had 3 or more adults.

Of singleton pods (Table 3.4a), 51.9% occurred in the first four weeks of the season when pods with a calf present were rarely seen. Similarly, 64.1% of adult pairs and 69.1% of 3 and 4+ pods with no calves present occurred in the first four weeks of the season. In contrast, during the last four weeks of the season, when the majority of pods had calves present, the occurrence of singleton pods was 29.1%, adult pairs 14.7%, and 3 and 4+ adults, 11.4% (Table 3.4a).

### *3.5.6 Statistical Model*

A statistical model was designed to examine the number of adults in pods over years, and over weeks within season, and to compare the number of adults in pods in which a calf was present or not present. The pod sizes were summarised to the categories 1, 2, 3+ adults for this analysis. These categories were chosen to simplify the model, and to ensure that there were reasonable numbers in the cells of the design while capturing the main features of the data.

An ordered multinomial logistic regression model (Hosmer and Lemeshow 2000) was fitted to the data using MLwiN V2.02 software (Rasbash *et al.* 2005) to assess the joint effects of year, week within year, and presence of a calf on the probabilities of occurrence of 1, 2, 3+ adults. It was necessary to aggregate the first three weeks within years in order to fit the presence of the calf by week within year interaction effect because so few calves were

observed early in the seasons. A linear effect for year and a quadratic effect for week within year were employed to smooth and describe the systematic pattern in the data.

Table 3.5 summarises the parameter estimates, their standard errors and P-values from an ordered multinomial logistic regression model for the proportions of size categories 1, 2, 3+ adults as a function of year (linear), week within year (quadratic), absence or presence of calf, and the interaction of week within year by presence of calf.

*Table 3.5*. Ordered multinomial logistic regression model for the proportions of size categories 1,2,3+ adults (calves excluded from count): fixed effects parameter estimates, their standard errors and p-values.

| [1] $\gamma_{3j} = \pi_{3j}$ ; $\gamma_{2j} = \pi_{3j} + \pi_{2j}$ ; $\gamma_{1j} = 1$. | Logit ($\gamma_{2j}$) | | | Logit ($\gamma_{3j}$) | | |
|---|---|---|---|---|---|---|
| **Parameter** | **Estimate** | **SE** | [3]**p** | **Estimate** | **SE** | [3]**p** |
| [2] Intercept | 0.942 | 0.105 | <0.0001 | -1.601 | 0.129 | <0.0001 |
| Year | 0.007 | 0.009 | 0.436 | 0.044 | 0.012 | <0.0002 |
| Week | -0.231 | 0.024 | <0.0001 | -0.138 | 0.032 | <0.0001 |
| Week x Week | -0.048 | 0.012 | <0.0001 | -0.020 | 0.015 | 0.182 |
| Calf | -1.646 | 0.110 | <0.0001 | -1.136 | 0.155 | <0.0001 |
| Week x Calf | 0.161 | 0.056 | 0.004 | -0.069 | 0.078 | 0.376 |
| Week x Week x Calf | 0.038 | 0.020 | 0.058 | 0.046 | 0.029 | 0.112 |

[1] Model: $response_{ij}$ = ordered multinomial ($pod_j$, $\pi_{ij}$), where $\pi_{ij}$ = probability of i (1,2,3+) adults (calves excluded from count), and reference category = 1 adult.

[2] Year referred to 1992, Week centred at Week 6, Calf referred to 'calf not present'

[3] Two-tailed p-values based on z = Estimate/SE.

The estimates reported in Table 3.5 were based on a parameterisation using the size category of one adult as the reference category. The column labeled Logit (2j) compares (on the natural

logarithm scale) the probability of encountering two or more adults relative to a single adult, and the column labeled Logit (3j) compares the probability of encountering three or more adults relative to a single adult.

The P-values in Table 3.5 indicate that there were significant effects for variation in relative pod size probabilities by year (linear), week within year (quadratic), presence of calf in a pod, and the interaction of week within year by presence of calf.

The model parameter estimates reported in Table 3.5 were used to calculate the estimated probabilities of the three response categories, 1, 2, 3+ adults by year, week within year, and absence or presence of calf. The estimated probabilities of 1, 2, or 3+ adults are plotted by year in Figure 3.3A, by week for pods with no calf present in Figure 3.3B, and by week for pods with calves present in Figure 3.3C.

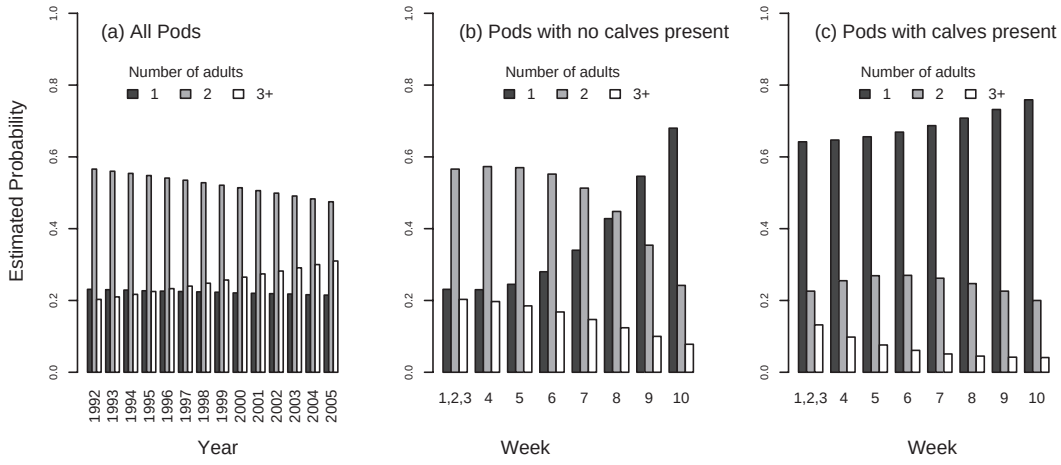


*Figure 3.3*. Estimated probabilities of relative proportions of 1, 2, or 3+ adults in pods: (A) by year, (B) by week within year for pods with no calves present, and (C) by week within year for pods with calves present. (Note: In Fig. 3.3C the single adult category represents mothers alone with their calves and the 2 and 3+ categories are adults accompanying a calf or calves).

The effects estimated by the model are more readily interpreted from the size category probabilities in Figure 3.3A, B, and C than from the Logit scale estimates in Table 3.5.

The proportion of 3+ adults increased significantly over years relative to the proportion of one adult and of either one or two adults. The increase in the proportion of 3+ adults over years (increased from 23% to 31%) corresponded with a greater relative decrease in the proportion of two adults (decreased from 57% to 47%) than in the proportion of one adult (decreased from 23% to 21%) (Fig. 3.3A).

To the extent that the relative size probabilities changed over weeks, those changes differed significantly between pods where a calf was present and pods where a calf was not present (Table 3.5). A comparison of Figure 3.3B with Figure 3.3C shows that there was much greater variation over weeks in the number of adults where a calf was not present than the number of adults where calves were present.

For pods where a calf was not present (Fig. 3.3B), the proportion of singleton pods increased rapidly from about week 4 (late August) (increased from 23% to 68%) with an accompanying decrease in the proportions of larger pods (pods with two adults decreased from 57% to 24% and pods with 3+ adults decreased from 20% to 8%). Where a calf was present (Fig. 3.3C), the proportion of pods that included only the mother increased (from 64% to 76%) while the proportions of larger pods decreased over weeks (pods with two adults went from 23% to 20% via a peak of 27% in mid-September, and pods with 3+ adults decreased from 13% to 4%).

The proportion of pods where calves were present increased sharply from about week 4 (late August), so that by week 10 (mid-October) about 90% of all pods included calves (Fig. 3.3B). Consequently, the rapid increase in the proportion of singleton pods over weeks (Fig. 3.3B)

occurred in the context of an ever-decreasing proportion of the total number of pods that did not include a mother and calf (Table 3.4a).

## 3.6 DISCUSSION

### *3.6.1 Increase of Larger Pods in Hervey Bay over Years*

In the Southern Hemisphere, at least seven populations of humpback whales are recognised (IWC 2006). Eastern Australian humpback whales are considered by the International Whaling Commission (IWC) to be a relatively discrete breeding stock termed E1, and form part of the IWC's Antarctic Area V management area (130◦E– 170◦W) (IWC 2006, Olavarrıa *et al.* 2006). Recent modelling suggests that, prior to the last period of commercial and illegal whaling (Clapham and Zerbini 2006, Clapham *et al.* 2009), the eastern Australian and Oceania humpback whale population may have ranged from 40,595 to 44,476 (95% CI 36,642–66,129, Jackson *et al.* 2006). In 1963, when the IWC declared complete protection for Southern Ocean humpback whales, it was estimated that there may have been fewer than 100 survivors in the eastern Australian population (Paterson *et al.* 1994). During the 30 yr from 1962 to 1992, the eastern Australian humpback whale population was estimated to have only increased to 1,900 whales (95% CI 1,650–2,150, Paterson *et al.* 1994). During the 14 yr of this study, 1992–2005, the eastern Australian humpback whale population is estimated to have increased to 7,024 (95% CI 5,163–9,685; Paton *et al.* 2012).

Accordingly, the numbers of humpback whales available to enter Hervey Bay during the study period increased by a factor of approximately 3.7. The increase in the population of eastern Australian humpback whales in Hervey Bay may be one of the factors contributing to the significant increase (Table 3.5) over years of larger groups (pods with 3+ adults, Fig.

3.3A) compared to pods of one or two adults. Hence, as the population increased, larger groups became more common.

The increase in the number of pods observed over the study period (Fig. 3.1C) is consistent with the growth in the population, which is likely to have generated a skewed distribution in the population toward younger whales. Humpback whale males and females may reach sexual and social maturity as early as 5 yr (Chittleborough 1965, Clapham 1992), although a recent study suggests it could be 10 or more years in some populations (Gabriele *et al.* 2007). Consequently, male and female humpback whales in the early stages of sexual and social development may also have contributed to the significant growth in pods with 3+ adults (Fig. 3.3A) over years in Hervey Bay.

Dawbin (1956, 1966) suggested that humpback whales require some period in suitable semitropical coastal waters for normal breeding behaviour, and that maximum aggregations can be expected to occur toward the northern part of the migration closest to the breeding grounds. Hervey Bay is near the putative breeding ground of eastern Australian humpback whales located in the Great Barrier Reef lagoon (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999). They do not migrate directly through Hervey Bay, but divert from the main migratory pathway to move into and out of the bay from the north. Humpback whales in Hervey Bay aggregate in non-random clusters on the eastern side of the Bay (Corkeron *et al.* 1994). Therefore, due to the density and movements around the bay by humpback whales, there is an increased likelihood of interactions (aggregation and disaggregation) among pods, which may also contribute to the formation of larger groups or to the probability of encountering recently aggregated pods.

There were significant changes in the pod characteristics of humpback whales utilising Hervey Bay from the beginning to the end of the study, notably the increase in larger groups. Given that this population is known to have increased in size from about 1,900 to 7,000

whales (Paterson *et al.* 1994; Paton *et al.* 2012) during the period 1992–2005, these changes may be indicative of social and behavioural changes that occur as a population expands. If so, it may be useful to review similar long-term data from other areas hosting recovering populations (notably Hawaii and the West Indies), to search for similar changes in pod characteristics and social behaviour as populations expand over extended study periods. Studies from Hawaii have reported that the range of humpback whales has expanded as the population increased (Mobley *et al.* 1999, Johnston *et al.* 2007), and that whales regularly move between islands separated by $4^0$ of longitude (Cerchio *et al.* 1998).

### *3.6.2 Seasonal Change in Pod Characteristics Early to Mid-Season*

Dawbin (1966, 1997) reported that females in early pregnancy and resting non- lactating females were among the first to commence the southern migration and that they preceded lactating females by about a month. Furthermore, they were either accompanied or closely succeeded by immature males and females. Mature males and females follow immature males and females but also precede lactating females with calves and escorts. The timing and presence of the sexual and maturational classes as described by Dawbin (1966, 1997) is likely to contribute to the higher proportion and number of pairs in Hervey Bay during August.

In the early part of the season, when calves were rarely present, the highest proportion and numbers of pods were pairs (Fig. 3.3B, Table 3.4a). Recent genetic studies of humpback whales in breeding grounds off the coast of South Africa and Brazil reported that most pairs consist of male–female dyads (Pomilla and Rosenbaum 2006, Cypriano-Souza *et al.* 2010). Brown and Corkeron (1995) also reported that male–female associations represented the greatest proportion of pairs observed during the southern migration along the eastern coast of Australia.

Compared to pairs, there were relatively fewer singletons in the early part of the season (Fig. 3.3B). The proportion and number of singletons were higher during the first two weeks of August, compared to the last two weeks of August and the first week of September (Fig. 3.2D, Table 3.4a). Clapham (1994) showed that, in the southern Gulf of Maine, immature male and female humpback whales spent relatively more time alone in their early years, with solitary time diminishing as they approached sexual and social maturity. Specifically, he found that males were alone in 55.8% of observations at the age of one, but in only 26.8% of sightings by the age of six. The comparable figures for lone females were 49.9% at age 1 yr to 20.5% at 6 yr. Male and female humpback whales in the early stages of maturity are likely to contribute to the proportion of singletons observed in August.

### *3.6.3 Presence of Calves Affect Pod Composition after Mid-Season*

Modeling of the systematic variability of observed pod size and composition within season in Hervey Bay revealed the significant influence of pods with calves present on pod size and composition in mid-to-late season (Fig. 3.3C, Table 3.4c).

Adult pairs and mothers alone with their calves were the most frequent pod size and type observed in Hervey Bay, with mothers alone with their calves accounting for just under half of such pods (Table 3.1, 3.2). However, the composition of pods with two whales present changed significantly over the season (Fig. 3.3B and C) as the mothers with calves moved into the bay from mid-season onwards and dominated the latter half of the season (Fig. 3.2B), coinciding with a rapid decrease of adult pairs (Fig. 3.3B). Mothers were alone with their calf in 69.4% of observations of pods with calves present, (Table 3.4c), and the proportion of lone mother-calf pods in Hervey Bay was greater than has been reported for other regions (Hawaii:

Mobley and Herman 1985, Herman and Antinoja 1977; West Indies: Mattila and Clapham 1989, Mattila *et al.* 1994).

Mobley and Herman (1985) found that when they excluded calves from the count, the overall distributions of pod sizes were very similar. In contrast in Hervey Bay, there were significant differences in pod sizes in pods with and without a calf, when the calf was excluded from the count (Fig. 3.3B and C). One of the major differences between the Hervey Bay and Hawaiian studies was that the modal size for pods having a calf present was three, mother-calf and escort (Herman and Antinoja 1977, Herman *et al.* 1980, Glockner and Venus 1983). By contrast, in Hervey Bay in pods with calves present the modal size was two, because of the significantly higher proportion of mothers alone with their calf (Table 3.4c).

When mothers were not alone with their calves, they were either accompanied by an escort or escorts, or were mixing with other females with calves (Table 3.3, 3.4c). It has been reported that mother and calf pods rarely associate with other mother-calf pods in winter breeding grounds (Herman and Antinoja 1977, Baker and Herman 1984, Mobley and Herman 1985). In contrast in Hervey Bay, although the proportion of pods with more than one calf present is low, interaction between mother-calf pods does occur. Possibly by mid-to-late season in Hervey Bay, when the calves are more mature and mother-calf bonds are well established, mothers may be more comfortable mixing with other mother-calf pods (see below).

### *3.6.4 Hervey Bay as a Habitat for Mothers with Calves*

Forty percent of all pods observed in Hervey Bay had one or more calves present (Table 3), and there were more mother-calf pods observed in Hervey Bay compared to earlier reports in other regions (Hawaii: Herman and Antinoja 1977, Mobley and Herman 1985, West Indies: Mattila and Clapham 1989, Mattila *et al.* 1994).

Hervey Bay is slightly off the migratory pathway and south of the putative breeding ground

and may provide mothers and calves with a suitable and convenient location for maternal care in the early stages of the southern migration. Mothers of humpback calves exclusively provide maternal care in the form of food, protection, and preparation for their calves' first migration to high-latitude feeding areas (Clapham 2000). It has been suggested that females with calves prefer shallower waters close to shore to minimise predation by sharks and/or to avoid harassment by males (Whitehead and Moore 1982, Glockner and Venus 1983, Mattila and Clapham 1989, Smultea 1994), or as a function of social organisation (Ersts and Rosenbaum 2003).

It has also been suggested that escorts may serve a protective function, and that it may be advantageous for mothers with calves to travel with an escort during migration (Herman and Antinoja 1977, Brown and Corkeron 1995). A recent study reported that females with a calf may tolerate a single escort as a "bodyguard" strategy to avoid harassment by other males (Cartwright and Sullivan 2009). However, the low proportion of escorts observed in Hervey Bay may provide a further advantage to mothers in that they have the opportunity of spending most of their time alone with their calves without having to take into account the presence of male escorts, or of being harassed by male escorts.

The first calves observed in Hervey Bay occurred in late August. Therefore, calves accompanied by mothers may be between a few weeks to 2 months of age (Chittleborough 1953, 1958). Consequently, Hervey Bay does not appear to be a calving ground, but rather a suitable stopover for mothers to engage in maternal activity with older calves during the early stages of their southern migration.

## 3.7 CONCLUSIONS

Hervey Bay is south of the putative breeding grounds and is a habitat utilised by eastern Australian humpback whales during the early stages of the southern migration. These data on pod characteristics of humpback whales in Hervey Bay indicate that the shallow, sheltered waters of the eastern bay provide an important habitat for mothers and calves, as a temporary stopover during their initial southern migration to Antarctic feeding areas. In addition, Hervey Bay provides a suitable and important habitat for other classes of humpback whales primarily during the early part of the migratory season, specifically immature males and females in early August and mature males and females in late August. The significant seasonal changes in pod characteristics of humpback whales in Hervey Bay appear to be related to the different sexual and maturational classes of humpback whales using the bay.

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# *Chapter 4*

# Seasonal changes in social behaviour of eastern Australian humpback whales *(Megaptera novaeangliae)* during the southern migratory stopover in Hervey Bay, Queensland, 1992-2005

## 4.1 ABSTRACT

This study investigated the social behaviour of humpback whales in 3,949 pods observed in Hervey Bay (Queensland, Australia) between 1992 and 2005. The 3,949 pods consisted of 3,484 pods that did not change size while under observation and 465 newly associated pods that ranged in size from 2 to 14 whales. The rate of formation of newly associated pods was significantly higher in the first four weeks of the season compared with later in the season. Of the 3,949 pods competitive behaviour was observed in 216 (5.5%) pods, non-agonistic social behaviour was observed in 432 (10.9%) pods, both competitive behaviour and non-agonistic social behaviour were observed in 33 pods (0.8%), while other behaviour was observed in 3,268 (82.8%) pods. Non-agonistic social behaviour was observed more frequently earlier in the season and rarely occurred in pods with calves present. In contrast, competitive groups were observed more frequently later in the season when mother-calf pods predominated. The frequency of competitive groups increased significantly towards the end of the season as pod size and composition changed. Competitive groups and non-agonistic social behaviour were more frequently observed in both larger and newly associated pods. Seasonal changes in social behaviour appear to be associated with the timing of different maturational and reproductive classes using Hervey Bay as a stopover during their southern migration with an increasing proportion of mothers and calves later in the season.

Key words: humpback whales, *Megaptera novaeangliae*, Hervey Bay, Australia, social behaviour, competitive groups, non-agonistic social behaviour

## 4.2 INTRODUCTION

Hervey Bay (Queensland $25^0$S, $153^0$E) is located south of the putative breeding ground of eastern Australia humpback whales and is neither a calving ground nor a terminal destination (Franklin *et al*. 2011). Previous studies suggested that the large inter-reef lagoon of the Great Barrier Reef, between $16^0$S and $23^0$S, represents the primary overwintering and breeding ground of eastern Australian humpback whales (Simmons and Marsh 1986, Paterson *et al*. 1981, Chaloupka and Osmond 1999). Humpback whales on their northern migration do not enter Hervey Bay, but on their southward migration, large numbers of humpback whales make a slight diversion from the southern migratory pathway and pass inside Breaksea Spit to enter Hervey Bay (Paterson 1991). Between 30% and 50% of eastern Australian humpback whales enter Hervey Bay during the southern migration (Chaloupka *et al*. 1999). They aggregate in shallow waters close to the western shore of Fraser Island in the eastern part of the bay, and enter and leave Hervey Bay from the north (Corkeron *et al*. 1994, Franklin *et al*. 2011). As an accessible stopover early in the southern migration from their winter breeding grounds to their Antarctic feeding areas, Hervey Bay offers a unique opportunity to study the social behaviour of humpback whales during their migration, in contrast to the social groupings and dynamics reported from traditional breeding grounds and feeding areas in other studies.

Franklin *et al.* (2011) studied pod characteristics of humpback whales in Hervey Bay between 1992 and 2005, and reported that there was a significant increase over these years in the numbers of pods of 3+ whales and this was related to population growth and density. Adult pairs were the most frequent pod type, followed by mothers alone with their calves (Franklin *et al*. 2011). They found that the size and composition of pods in Hervey Bay varied significantly as the season progressed (Franklin *et al*. 2011). Pods with calves present were rarely recorded during the first four weeks of the season but dominated for the last six weeks

of the season (Franklin *et al*. 2011). The pod data were consistent with the timing of reproductive and maturational classes reported by Dawbin (1966, 1997) suggesting that the predominant age/sex structure of whales in Hervey Bay during the first two weeks of the season were immature males and females, followed by mature males and females during mid season, and mothers with calves (either alone or with escorts) during September through to mid-October (Dawbin 1966, 1997; Franklin *et al*. 2011). Franklin *et al*. (2011) reported significant differences in pod size and composition compared to the Hawaiian and West Indies breeding grounds (Herman and Antinoja 1977, Herman *et al.* 1980, Mobley and Herman 1985, Mattila *et al*. 1989, 1994), and suggested this may be related to Hervey Bay being a migratory stopover early in the southern migration.

Social organisation and behaviour of humpback whales has been well documented in the Northern Hemisphere in both the feeding areas and breeding grounds (Clapham 1993, 2000; Craig *et al.* 2002; Darling *et al*. 2006; Herman *et al*. 2011). Studies have investigated group size and examined the factors influencing the formation and dynamics of groups. There is general agreement that beyond the mother-calf association, which lasts for 11 to 12 months (Chittleborough 1958, Clapham 2000), the social organisation of humpback whales is characterised by small unstable groups, involving brief associations lasting for periods of a few hours or less, with some associations lasting over several days or (rarely) over longer periods (Herman and Antinoja 1977, Tyack and Whitehead 1983, Baker and Herman 1984*a*, Mobley and Herman 1985, Mattila *et al*. 1994, Clapham 2000).

Humpback whales of both sexes and all maturational classes from calves to adults, engage in a range of surface behaviours and activities observed frequently in both high and low latitudes (see review in Clapham 2000). There are certain group classes observed at breeding grounds that appear to be related to mating. These include competitive groups (Tyack and Whitehead, 1983; Baker and Herman, 1984*b*; Clapham *et al*. 1992; Spitz *et al*. 2002; Herman *et al*. 2008;

Pack *et al*. 2009), mother-calf escort groups (Clapham 2000, Craig *et al*. 2002), and male-female dyads (Pack *et al*. 2012). Large fast-moving groups of humpback whales involved in high levels of aggressive behaviour were first described by Tyack and Whitehead (1983) and Baker and Herman (1984*a*), who suggested that the groups consisted of mature males competing for access to a single female. This hypothesis that competitive groups contained a single female and competing males was later largely confirmed using molecular techniques (Clapham *et al*. 1992). Individual humpback whales in the company of mother-calf pairs on the breeding grounds were also proved to be male and supported the evidence that a proportion of females may become pregnant while lactating (Chittleborough 1958, 1965; Clapham 2000, Craig *et al*. 2002). A recent study of the body lengths of male-female dyads showed that many were mature-sized and that mature-sized females preferred associating with large mature-sized males (Pack *et al*. 2012). However, mating has never been observed in this species (Clapham 2000, Pack *et al*. 2002, Herman *et al*. 2008) and the mating system is still not fully understood (Herman and Tavolga 1980, Clapham 1996, Cerchio *et al*. 2005, Darling *et al*. 2006). Helweg and Herman (1994) reported that humpback whales in breeding grounds may spend up to 90% of their time underwater. Because it is often difficult to study humpback whales underwater for extended periods (Herman *et al*. 2008) researchers often rely on surface observations to describe social behaviour and organisation. Consequently the study of humpback whale surface behaviours is important in understanding individual and group social behaviour and social organisation.

Competitive behaviours have predominantly been reported occurring within competitive groups, which typically consist of a single female (with or without a calf) and two or more male escorts competing for access to her (Tyack and Whitehead 1983, Baker and Herman 1984*b*, Clapham *et al*. 1992). Competitive groups primarily occur at winter breeding grounds and may involve a series of aggressive and sometimes escalating agonistic behaviours (Baker

and Herman 1984*b*). The roles of both male and female humpback whales within competitive groups, the sex composition of groups, and the role of escorts, in terms of their maturational status, stamina and experience, have been investigated and described in the breeding grounds of the Northern Hemisphere (Darling *et al.* 1983; Tyack and Whitehead 1983; Baker and Herman 1984*b*; Clapham *et al.* 1992; Clapham 2000; Pack *et al.* 2002, 2009; Spitz *et al.* 2002) and in the Southern Hemisphere (Brown and Corkeron 1995). Reports of agonistic behaviour outside of competitive groups are rare (Tyack and Whitehead 1983, Clapham *et al.* 1992, Clapham 1996, Darling and Berube 2001).

Humpback whale surface behaviours that have no obvious competitive component have been reported in several studies; the behaviours include, pectoral fin slapping, rolling over ventral side up, head-rising, spy-hopping, pectoral fin extensions, fluke extensions and breaching. It has been suggested that these behaviours may be associated with courtship and mating in humpback whales (Dawbin 1956, Tyack 1981, Tyack and Whitehead 1983, Herman and Antinoja 1977). Tyack and Whitehead (1983 p.137) reported that "In Hawaii some groups of more than three adults appeared to lack the Nuclear Animal, Principal Escort structure...and... whales in these groups seemed to tolerate the approach of any other member of the group. Surfacings were much more relaxed in these groups, unlike the lunging surfacings seen in more active groups. Furthermore, the very rapid rate of travel which characterizes large active groups did not occur." Herman and Antinoja (1977) reported slow-moving milling groups involved in spatially undirected activity occurring within a small area. Herman *et al.* (2008) described underwater behaviours by female humpback whales that may be acting in a non-agonistic solicitous manner towards males.

Non-agonistic male-male interactions have been reported during the winter migrations and at breeding grounds. Clapham *et al.* (1992) speculated that the existence of apparently mutually non-agonistic male-male coalitions in the Northern Hemisphere breeding grounds may be an

indicator that these humpback males cooperate in their effort to secure access to a female. Darling *et al*. (2006) reported in a recent study of singers that in Hawaii singer/joiner male-male dyads occurred and that overall 80% of male-male relations were considered non-agonistic in nature. They suggested that singer/joiner relations may provide mutual assistance in mating when joining competitive groups. They also speculated that non-agonistic social behaviour might be more prevalent in humpback whale social organisation than had been previously reported.

The social behaviour of eastern Australian humpback whales has been studied during the northern and southern seasonal migration from and to the Antarctic feeding areas. Brown and Corkeron (1995) reported that during migration group formation and behaviour were influenced by social factors and that most male-male interactions were characterised by non-agonistic and occasionally cooperative interactions. Valsecchi *et al*. (2002) studied the social structure of migrating humpback whales off eastern Australia and reported that with the exception of the mother-calf relationship, there was an absence of kin-relatedness within small groups.

Corkeron *et al.* (1994) suggested that the non-random distribution of pods of humpback whales aggregating in Hervey Bay might be related to social factors, but there were no data indicating that the bay was of importance to any particular class of humpback whale. The seasonal social behaviour of humpback whales in Hervey Bay has not been previously described and no study to date has systematically investigated non-agonistic social behaviour in pods within season and over years.

This study summarises behavioural observations of humpback whales in 3,949 pods recorded during the fourteen-year period 1992 to 2005. The primary objective was to investigate the seasonal social behaviour of humpback whales in Hervey Bay. Specifically, the study investigated the occurrence of pod associations, competitive groups and non-agonistic social

behaviour pods within and among seasons. These data were used to investigate and analyse competitive behaviour and non-agonistic social behaviour and to discuss whether the timing of occurrence of different maturational classes influences the seasonal social behaviour of humpback whales in Hervey Bay.

## 4.3 METHODS

### *4.3.1 Study area and timing of surveys*

Hervey Bay is located at $25^0$S, $153^0$E on the eastern coast of Queensland and is formed by Fraser Island and the Australian mainland, (Fig. 2.1 above). It is a wide shallow bay with a sand and mud bottom, approximately 4,000 $km^2$ in area, and is generally less than 18 m deep, (Vang 2002). Fraser Island is 126 km long; it lies along a northeasterly axis and its northern end bridges the continental shelf. Directly north of Hervey Bay, at a distance of between 111 and 222 km, are the most southerly islands of the Great Barrier Reef (Fig. 2.1 above).

The southern migration from the Great Barrier Reef begins in late July, with humpback whales moving into and out of Hervey Bay from early August to mid-October (Paterson 1991, Corkeron *et al.* 1994, Franklin *et al.* 2011). Accordingly, a 10-week survey commencing on the first Sunday after the $5^{th}$ of August each season was chosen to provide a representative sample of the seasonal flow of humpback whales in Hervey Bay.

### *4.3.2 Definitions*

***Singleton:*** a lone humpback whale.

***Pod:*** two or more humpback whales swimming side by side within one to two body lengths of each other, generally moving in the same direction and coordinating their speed of travel (Whitehead 1983, Clapham 1993, Corkeron *et al.* 1994). Although in some species for example *Orcinus orca*, the term pod is used to describe stable groups, our use of the term 'pod' does not imply stability.

***Initial pod:*** this is a group of whales (or a singleton) as first encountered, prior to any change in pod size. If the initial singleton or pod joins, or is joined by, one or more singleton or pod it is referred to as a ***newly associated pod***:

***Calf:*** an individual whale was considered to be a calf if it appeared to be less than half the length of a particular adult with which it maintained a constant and close relationship. In most observations, no other whale was seen coming between a mother and her calf (Tyack and Whitehead 1983). The adult in the dyad was assumed to be the mother. Yearlings were distinguished from calves visually by an experienced observer to be unambiguously small relative to adults but too large to be calves of the year (Clapham *et al.* 1999, Craig *et al.* 2003).

***Escort***: is defined as a whale accompanying a mother with calf. The term 'escort', was first used by Herman and Antinoja (1977). Escorts have been found to be male and may be mature males waiting for a post-partum estrous mating opportunity (Glockner and Venus 1983, Tyack and Whitehead 1983, Baker and Herman 1984*a*, Clapham 2000).

***Competitive Group:*** a group of three or more whales exhibiting competitive behaviour, and which usually consists of a single female and a variable number of males (Clapham *et al.* 1992, 1993; Clapham 2000). Roles within the competitive group are defined as follows: a Nuclear Animal refers to a whale that is centrally located within the group, and is usually passive. A Principal Escort is a whale that is spatially closest to the Nuclear whale in the

group, and appears to fend off approaches to the Nuclear whale by other participants (Tyack and Whitehead 1983). A Challenger is any whale observed to make such an approach. The interaction between the Principal Escort and any challenger may involve a series of escalating aggressive behaviours increasing in intensity (Baker and Herman 1984*b*). A Secondary Escort is any participant in the group that is neither the Nuclear Animal nor the Principal Escort and is not observed in a Challenger role. A competitive group may contain a female with or without a calf. Behaviours observed in competitive groups may include high-speed chasing, strong loud exhalations, head lunging, inflated head lunging, blocking, linear bubble streaming and side tail thrashes (Darling *et al.* 1983, Tyack and Whitehead 1983, Baker and Herman 1984*b*, Clapham 2000, Darling *et al.* 2006).

***Non-Agonistic Social Behaviour:*** this occurs in pods consisting of at least two whales (excluding a mother alone with her calf). The surface behaviours concerned involve spatially undirected activity occurring within a small area (Herman and Antinoja 1977), and calm interactions where no high-energy actions, aggression or competitive behaviours are observed (Darling *et al*. 2006). The behaviours include: pectoral fin slapping, pectoral fin extensions, head rising, spy-hops and fluke-extensions, rolling over ventral side up, milling, all involving slow coordinated movements (Herman and Antinoja 1977, Tyack 1981, Tyack and Whitehead 1983).

***Other Behaviour:*** occurs in pods that are neither competitive groups nor non-agonistic social behaviour pods and include surface travelling, resting or surface activity, for example breaching, lobtailing or singing and in the case of mother-calf pods maternal activities, either alone or with an escort.

***Sex-identification***: sex can be determined by the observation of the genital area and the presence of a hemispherical lobe posterior to the genital slit in the case of females and its absence in the case of males (True 1904, Glockner 1983). Furthermore, sex can also be

inferred from social roles: an individual accompanying a calf consistently and providing nurturing behaviors towards the calf can be inferred to be female (Tyack and Whitehead 1983). Similarly, escorts and singers have been found to be male (Glockner and Venus 1983, Tyack and Whitehead 1983, Baker and Herman 1984*a*, Clapham 2000). Chu and Nieukirk (1988) reported that individual humpback whales with distinct vertical and horizontal dorsal fin scars, resulting from competitive activity could be inferred as males. These marks were only used in conjunction with the resighting histories and the observed social roles to infer an individual as a male. With few exceptions, Nuclear Animals in competitive groups have been found to be female (Darling *et al.* 1983; Tyack and Whitehead 1983; Baker and Herman 1984*b*; Clapham *et al.* 1992, 1993; Clapham 2000; Darling *et al.* 2006).

### *4.3.3 Fieldwork surveys*

Vessel surveys for this study were conducted for nine weeks in 1992 and for ten weeks each year between 1993 and 2005. The study area (Fig. 4.1) is approximately 27.8 km from Urangan Boat Harbour, Hervey Bay. Fieldwork was planned for 6 d each week, leaving Urangan harbor at 0800 each Sunday and returning at 1500 the following Friday. Planned daily operations were from 0930 to 1700 on Sunday, 0700 to 1700 Monday to Thursday, and from 0700 to 1330 on Friday.

Four different motorised vessels were utilised as dedicated research platforms: two were mono-hulls and two were catamarans, ranging in length from 11 to 27 m. When searching for humpback whales the normal range of operational speed of the four research vessels was 12.9-18.5 km/h (7-10 kts). During commencement of observations, the rate of travel of the research vessel was adjusted to match the speed of the pod or singleton. Observations were conducted from the upper deck or flying bridge of each vessel, which provided a clear vantage point for 5 or more nautical miles.

### *4.3.4 Observations, photo-identification and data analysis*

Observations and photo-identification began on the first sighted pod or singleton, with no *a priori* selection of any particular pod class. If no pod or singleton was in sight, either a random direction of travel was commenced until a pod or singleton was sighted or, if information about the location of pods or singletons was available from one of the local commercial whale-watching vessels, travel was commenced towards that location. If a pod or singleton was sighted en route it was selected for observation.

Photography of the ventral fluke patterns, shape and size of dorsal fins and lateral body markings were obtained to allow identification of individual humpback whales (Katona *et al*. 1979, Katona and Whitehead 1981). Data collected during the observation of each pod included: date, time and GPS location at commencement every 15m during the observation and at completion of the observation. In addition the following information was recorded for each pod; a pod identification code, the observed number of individuals in the pod, pod composition, and surface behaviours (continuous sampling; Altmann, 1974). Information on sex-identification was obtained where possible in accordance with the definitions above. The duration of observation was maintained until the composition and size of each pod was determined and the surface behaviours occurring were recorded.

Upon commencement of observation of the initial pod a member of the observation team continually scanned for and reported on other pods within a radius of a kilometre. If one or more of those pods were tracking towards the initial pod, or if the initial pod was tracking towards them then the duration of observation was extended to observe and record associations as they occurred. The details of each associating pod, including time, GPS location, size, composition and surface behaviours, were recorded. Each newly associated pod was designated as either a consecutive association (e.g. a mother-calf pod attracts one escort at time 1, then another at time 2, then another at time 3, and so forth making five associations

in an observation period) or as a simultaneous association (e.g. three singletons approaching each other and associating simultaneously). Disassociations were also recorded, however, as the focus of this study was pod associations, competitive groups and non-agonistic social behaviour pods the rate of changes in membership of pods were not analysed.

All data were recorded daily in field notes and entered into a FileMaker Pro database each evening. Photography for each pod was analysed in conjunction with the field notes on observations of pod composition, behaviours observed and sex-identification information. Ventral fluke photographs of individual humpback whales were assessed for photographic quality using an established photo-identification quality protocol (Calambokidis *et al*. 2001). Annual fluke catalogues for the years 1992 to 2005 were compiled and analysed for intra- and inter-season resights of individual humpback whales using a propriety matching system based on categorisation of flukes utilising an array of coded discrete characteristics (ACDC), applied to the file name of each fluke photograph (see Chapter 2 for further details). The ACDC categories were based on individually unique and stable patterns of black and white pigmentation on the underside of the tail flukes (Katona *et al*. 1979, Katona and Whitehead 1981). The system allowed each fluke to be allocated to contiguous stratified categories for visual display and organisation during photographic analyses. When matching a fluke against the fluke catalogue it was compared with other photographs within its colour and pattern category and then if not matched it was then subsequently compared with photographs within adjacent categories. Photographic analysis outcomes together with original field data were incorporated into a single FileMaker Pro relational database.

For the purposes of analysis in this study, pods were categorised into pods that did not associate while under observation and pods that did associate while under observation forming newly associated pods. All logged information on surface behaviours and composition for each pod was reviewed and each pod in the data set was then further

categorised, on the basis of surface behaviours occurring, as a competitive group, non-agonistic social behaviour pod or other behaviour pod in accordance with the definitions described above.

### *4.3.5 Statistical analysis*

The pod or singleton was used as the basic observational unit in analyses. The pods used in the analyses were the initial pods that did not change size while under observation, and the newly associated pods that did change size while under observation. The size of the newly associated pods by number of pods associating and size of the initial pod were reported. The duration of observations of competitive groups, non-agonistic social behaviour pods and other behaviour pods were reported.

The frequencies of competitive groups, non-agonistic social behaviour pods and other behaviour pods, split by pods with no calves present and pods with calves present, by newly associated pods and pods that did not associate while under observation, and by number of adults in pods (1, 2, and 3+) were reported.

As the focus of this study was competitive behaviour and non-agonistic social behaviour the analysis was undertaken on the subset of pods that met the definition (see above) of a competitive group (i.e. pods that included at least three whales of which at least 2 were non-mothers); and pods that met the definition (see above) of a non-agonistic social behaviour pod (i.e. pods that included at least two whales, excluding a mother alone with her calf).

The data on competitive groups, non-agonistic social behaviour pods and newly associated pods, by week within season (1-10), together with the sub-set of pods used in statistical analysis and modelling were reported. Finally sex-identified males and females in competitive groups and non-agonistic social behaviour pods were reported. However, as sex could not be unambiguously identified for all individuals, the data were not used in analysis.

Variation in the proportion of newly associated pods by year, by week within year (1-10), by calf present or not present, and by pod size were assessed using chi-square analyses.

The variation in the proportion of competitive groups and non-agonistic social behaviour pods (independent analyses) by year, by week within year, by pods that did not associate while under observation and newly associated pods, and by pods with no calves present and pods with calves present were examined.

Chi-square analyses were used to document the univariate associations between the occurrence of competitive groups and newly associated pods, year, week within year, number of whales (excluding calves) and presence of a calf in the pod prior to fitting a binary logistic regression model to assess the joint effects of the above factors on the probability of occurrence of competitive groups.

Similarly, chi-square analyses were used to document the univariate associations between the occurrence of non-agonistic social behaviour pods and newly associated pods, year, week within year, number of whales (excluding calves) and presence of calf in the pod prior to fitting a binary logistic regression model to assess the joint effects of the above factors on the probability of occurrence of non-agonistic social behaviour pods.

## 4.4 RESULTS

### *4.4.1 Effort and observations*

A total of 139 6-day survey periods (Sunday to Friday) were conducted in the Hervey Bay study area (Fig. 4.1) between 1992 and 2005. Data were obtained on 770 of the planned 834 survey days. Total survey time was 6,160 hr and observations of humpback whale pods were conducted for a total of 2,760 hr.

Observations were made and data collected on 4,506 pods. The hours spent weekly on survey and observing whales, the weekly total numbers of pods and individual whales observed, and the mean hourly rates of observation of pods and individuals over weeks are reported in Franklin *et al*. (2011).

### *4.4.2 Data set*

Of the 4,506 pods, 3,484 (77.3%) were pods that did not associate while under observation and the other 1,022 (22.7%) were pods that did associate while under observation and were involved in associations of from 2 to 5 pods, forming 465 newly associated pods (Table 1). The data set of 3,949 pods used for analysis in this study is made up of the 3,484 (88.2%) pods that did not associate and the 465 (11.8%) newly associated pods.

### *4.4.3 Newly associated pods*

Newly associated pods, formed by the consecutive or simultaneous association of up to 5 pods during the period of observation, with calves present versus those without calves present are reported in Table 4.1.

*Table 4.1.* Size (excluding calves[1]) of newly associated pods (2, 3, 4, 5+); by number of pods associating (2, 3, 4, 5), size (excluding calves[1]) of initial pod under observation (1, 2, 3, 4+), split by pods with no calves present and pods with calves present (by number of pods with sub-totals and percentage).

| Number of pods associating | Size of initial pod (excluding calves[1]) | Size (excluding calves[1]) of newly associated pods: Pods with no calves present | | | | | | Pods with calves present | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | 2 | 3 | 4 | 5+ | Sub-total | % | 2 | 3 | 4 | 5+ | Sub-total | % | Total | % |
| 2 | 1 | 17 | 19 | 8 | 1 | 45 | 15.25 | 39 | 13 | 1 | 2 | 55 | 32.35 | 100 | |
| | 2 | na | 41 | 60 | 23 | 124 | 42.03 | na | 27 | 19 | 3 | 49 | 28.82 | 173 | |
| | 3 | na | na | 14 | 30 | 44 | 14.92 | na | na | 6 | 9 | 15 | 8.82 | 59 | |
| | 4+ | na | na | na | 28 | 28 | 9.49 | na | na | na | 8 | 8 | 4.71 | 36 | |
| | Sub-total | 17 | 60 | 82 | 82 | 241 | | 39 | 40 | 26 | 22 | 127 | | 368 | 79.14 |
| 3 | 1 | na | 2 | 3 | 6 | 11 | 3.73 | na | 6 | 6 | 6 | 18 | 10.59 | 29 | |
| | 2 | na | na | 6 | 23 | 29 | 9.83 | na | na | 5 | 8 | 13 | 7.65 | 42 | |
| | 3 | na | na | na | 6 | 6 | 2.03 | na | na | na | 2 | 2 | 1.18 | 8 | |
| | 4+ | na | na | na | 3 | 3 | 1.02 | na | na | na | 3 | 3 | 1.76 | 6 | |
| | Sub-total | na | 2 | 9 | 38 | 49 | | na | 6 | 11 | 19 | 36 | | 85 | 18.28 |
| 4 | 1 | na | na | na | 1 | 1 | 0.34 | na | na | 2 | 1 | 3 | 1.76 | 4 | |
| | 2 | na | na | na | 3 | 3 | 1.02 | na | na | na | 1 | 1 | 0.59 | 4 | |
| | 3 | na | na | na | 1 | 1 | 0.34 | na | na | na | 0 | 0 | 0.00 | 1 | |
| | 4+ | na | na | na | 0 | 0 | 0.00 | na | na | na | 1 | 1 | 0.59 | 1 | |
| | Sub-total | na | na | na | 5 | 5 | | na | na | 2 | 3 | 5 | | 10 | 2.15 |
| 5 | 1 | na | na | na | 0 | 0 | 0.00 | na | na | na | 1 | 1 | 0.59 | 1 | |
| | 2 | na | na | na | 0 | 0 | 0.00 | na | na | na | 0 | 0 | 0.00 | 0 | |
| | 3 | na | na | na | 0 | 0 | 0.00 | na | na | na | 1 | 1 | 0.59 | 1 | |
| | 4+ | na | na | na | 0 | 0 | 0.00 | na | na | na | 0 | 0 | 0.00 | 0 | |
| | Sub-total | na | na | na | 0 | 0 | | na | na | na | 2 | 2 | | 2 | 0.43 |
| | Total | 17 | 62 | 91 | 125 | 295 | 100 | 39 | 46 | 39 | 46 | 170 | 100 | 465 | 100 |
| | % | 5.76 | 21.02 | 30.85 | 42.37 | 100 | | 22.94 | 27.06 | 22.94 | 27.06 | 100 | | | |
| | % | | | | | 63.44 | | | | | | 36.56 | | 100 | |

[1]Pod sizes in Table 1 report the number of adults in the pod excluding calves. Calves are excluded from the count to facilitate comparisons between pods with no-calf present and pods with calf present (This is consistent with the method adopted in Franklin *et al.* 2011, derived from Mobley and Herman 1984).

Of the 465 newly associated pods, 368 (79.1%) consisted of two pods (or singletons) associating, 85 (18.3%) of three pods associating, 10 (2.2 %) of four pods associating and 2 (0.4%) of five pods associating. Of the 465 newly associated pods, 295 (63.4%) had no calf present, and 170 pods (36.6%) had a calf or calves present.

Of the 465 newly associated pods, 341 (73.3%) were consecutive associations and 124 (26.7%) were simultaneous associations. There were 171 (36.8%) of the 465 newly associated pods in which disassociations were recorded.

### *4.4.4* Competitive groups, non-agonistic social behaviour and other behaviour

The frequencies and the duration of observations of competitive groups, non-agonistic social behaviour pods and pods displaying other behaviours are reported in Table 4.2.

*Table 4.2*. Competitive groups, non-agonistic social behaviour and other behaviour in pods (*n*) (by number and percentage) and duration of observations (by hours with minimum, maximum, median and mean with standard deviation).

| Behaviour observed | Number of pods | | Duration of observations (hr) | | | | |
|---|---|---|---|---|---|---|---|
| | *n* | % | Min | Max | Median | Mean | SD |
| Both competitive groups and non-agonistic social behaviour[1] | 33 | 00.8 | 0.12 | 2.67 | 0.85 | 0.91 | 0.46 |
| Only competitive groups | 216 | 05.5 | 0.07 | 2.50 | 0.73 | 0.91 | 0.49 |
| Only non-agonistic social behaviour | 432 | 10.9 | 0.05 | 5.07 | 0.73 | 0.85 | 0.55 |
| Only other behaviour[2] | 3268 | 82.8 | 0.02 | 3.72 | 0.43 | 0.56 | 0.46 |
| Total | 3949 | 100 | 0.02 | 5.07 | 0.50 | 0.61 | 0.49 |

[1] In 24 of the 33 pods (72.7%) non-agonistic social behaviour preceded competitive group behaviour; in 6 pods (18.2%) non-agonistic social behaviour and competitive group behaviour were observed simultaneously, while in 3 pods (9.1%) competitive group behaviour preceded non-agonistic social behaviour.

[2] There were a few cases (28 pods, 0.71% of 3949 pods) in other behaviour of pods displaying agonistic behaviour, involving avoidance or repulsion, which did not meet the definitions of a competitive group and these are reported separately in the text.

The frequencies and proportions of competitive groups, non-agonistic social behaviour pods and pods displaying other behaviours are reported in Table 4.3 for: all pods, pods with no calves present, pods with calves present, and by newly associated pods and pods that did not associate.

*Table 4.3*. Competitive groups (CG), non-agonistic social behaviour (NASB) and other behaviour (OB) in all pods, pods with no calves present and pods with calves present, split by newly associated pods (NAP) and pods that did not associate with other pods (PDNA) (*n*) (by numbers and percentage).

| Behaviour observed | All Pods | | | | | | Pods with no calves present | | | | | | Pods with calves present | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | NAP | | PDNA | | Total | | NAP | | PDNA | | Total | | NAP | | PDNA | | Total | |
| | *n* | % | *n* | % | *n* | % | *n* | % | *n* | % | *n* | % | *n* | % | *n* | % | *n* | % |
| Both CG & NASB | 20 | 4.3 | 13 | 0.4 | 33 | 0.8 | 15 | 5.1 | 11 | 0.6 | 26 | 1.2 | 5 | 2.9 | 2 | 0.1 | 7 | 0.4 |
| CG Only | 120 | 25.8 | 96 | 2.7 | 216 | 5.5 | 74 | 25.1 | 62 | 3.2 | 136 | 6.1 | 46 | 27.1 | 34 | 2.2 | 80 | 4.6 |
| NASB Only | 119 | 25.6 | 313 | 9.0 | 432 | 10.9 | 100 | 33.9 | 295 | 15.3 | 395 | 17.7 | 19 | 11.2 | 18 | 1.2 | 37 | 2.1 |
| OB Only | 206 | 44.3 | 3062 | 87.9 | 3268 | 82.8 | 106 | 35.9 | 1565 | 80.9 | 1671 | 75.0 | 100 | 58.8 | 1497 | 96.5 | 1597 | 92.8 |
| Total | 465 | 100 | 3484 | 100 | 3949 | 100.0 | 295 | 100 | 1933 | 100 | 2228 | 100 | 170 | 100 | 1551 | 100 | 1721 | 100 |
| % | 11.8 | | 88.2 | | 100 | | 13.2 | | 86.8 | | 100 | | 9.9 | | 90.1 | | 100 | |
| % | | | | | 100 | | | | | | 56.4 | | | | | | 43.6 | |

The duration of observation of pods that did not associate while under observation ranged from 0.02 h to 3.72 hr (median = 0.45 h, mean = 0.56 h, SD = 0.48 h, *n* = 3,484). The duration of observation of newly associated pods ranged from 0.02 h to 5.07 hr (median = 0.83 h, mean = 0.97 h, SD = 0.58 h, *n* = 465).

Competitive groups, non-agonistic social behaviour pods and pods that displayed both competitive and non-agonistic social behaviour, were observed with greater frequency in newly associated pods than in pods that did not associate while under observation (25.8% to 2.7%, 25.6% to 9.0% and 4.3% to 0.4% respectively). In contrast, pods displaying other behaviour occurred with greater frequency in pods that did not associate while under observation (87.9%, 3,062 of 3,484) than in newly associated pods (44.3%, 206 of 465).

Of the data set of 3,949 pods, 1,721 pods (43.6%) had calves present while 2,228 pods (56.4%) had no calves present. Competitive groups, non-agonistic social behaviour pods and pods that displayed both competitive and non-agonistic social behaviour were observed with greater frequency in pods with no calves present than in pods with calves present (6.1% to 4.6%, 17.7% to 2.1% and 1.2% to 0.4% respectively). Conversely, in pods displaying other behaviour 92.8% (1,597 of 1,721) were pods with calves present and 75.0% (1,671 of 2,228) were pods with no calves present.

The frequencies and proportions of competitive groups, non-agonistic social behaviour pods and pods displaying other behaviour by size of pod (excluding calves), for all pods, pods with no calves present and pods with calves present, by newly associated pods and pods that did not associate while under observation are reported in Table 4.4.

*Table 4.4*. Competitive groups (CG), non-agonistic social behavior (NASB) and other behavior (OB) by number of adults (excluding calves[1)] in pod (1, 2, 3+), in all pods, pods with no calves present and pods with calves present, split by newly associated pods (NAP) and pods that did not associate while under observation (PDNA) (*n*) (by number and percentage).

| Behavior observed | Number of adults (excluding calves[1]) | All pods | | | | | | Pods with no calves present | | | | | | Pods with calves present | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | NAP | | PDNA | | Total | | NAP | | PDNA | | Total | | NAP | | PDNA | | Total | |
| | | n | % | n | % | n | % | n | % | n | % | n | % | n | % | n | % | n | % |
| Both CG & NASB | 1 | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na |
| | 2 | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na |
| | 3+ | 20 | 4.3 | 13 | 0.4 | 33 | 0.8 | 15 | 5.1 | 11 | 0.6 | 26 | 1.2 | 5 | 2.9 | 2 | 0.1 | 7 | 0.4 |
| CG Only | 1 | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na |
| | 2 | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na |
| | 3+ | 120 | 25.8 | 96 | 2.8 | 216 | 5.5 | 74 | 25.1 | 62 | 3.2 | 136 | 6.1 | 46 | 27.1 | 34 | 2.2 | 80 | 4.6 |
| NASB Only | 1 | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na | na |
| | 2 | 13 | 2.8 | 163 | 4.7 | 176 | 4.5 | 7 | 2.4 | 151 | 7.8 | 158 | 7.1 | 6 | 3.5 | 12 | 0.8 | 18 | 1.0 |
| | 3+ | 106 | 22.8 | 150 | 4.3 | 256 | 6.5 | 93 | 31.5 | 144 | 7.4 | 237 | 10.6 | 13 | 7.6 | 6 | 0.4 | 19 | 1.1 |
| OB Only | 1 | na | na | 1576 | 45.2 | 1576 | 39.9 | na | na | 469 | 24.3 | 469 | 21.1 | na | na | 1107 | 71.4 | 1107 | 64.3 |
| | 2 | 43 | 9.2 | 1170 | 33.6 | 1213 | 30.7 | 10 | 3.4 | 842 | 43.6 | 852 | 38.2 | 33 | 19.4 | 328 | 21.1 | 361 | 21.0 |
| | 3+ | 163 | 35.1 | 316 | 9.1 | 479 | 12.1 | 96 | 32.5 | 254 | 13.1 | 350 | 15.7 | 67 | 39.4 | 62 | 4.0 | 129 | 7.5 |
| | Total | 465 | 100 | 3484 | 100 | 3949 | 100 | 295 | 100 | 1933 | 100 | 2228 | 100 | 170 | 100 | 1551 | 100 | 1721 | 100 |
| | % | 11.8 | | 88.2 | | 100 | | 13.2 | | 86.8 | | 100 | | 9.9 | | 90.1 | | 100 | |
| | % | | | | | 100 | | | | | | 56.42 | | | | | | 43.6 | |

[1]Pod sizes in Table 4 report the number of whales in the pod excluding calves. Calves are excluded from the count to facilitate comparison of the number of adults between pods with no-calf present and pods with calf present (This is consistent with the method adopted in Franklin *et al.* 2011, derived from Mobley and Herman 1984).

Competitive groups, non-agonistic social behaviour pods, pods which displayed both competitive and non-agonistic social behaviour, and pods displaying other behaviour occurred with greater frequency in newly associated pods of 3+ adults, compared with pods that did not associate with other pods of the same size (25.8% to 2.8%, 22.8% to 4.3%, 4.3% to 0.4% and 35.1% to 9.1% respectively). In contrast, in pods of two adults, non-agonistic social behaviour and other behaviour occurred less frequently in newly associated pods than in pods that did not associate with other pods (2.8% to 4.7% and 9.2% to 33.6% respectively).

Of the 3,949 pods, 1,010 (25.6%) had two adults present, and consisted of 158 pairs involved in non-agonistic social behaviour, and 852 were pairs that displayed other behaviour. Pods of one adult consisted of singletons (24.3%, 469 of 1,933) and mothers alone with their calf (64.3%, 1,107 of 1,721) and these pods displayed other behaviour.

### *4.4.5 Avoidance and repulsion behaviour*

There were instances in the 'other behaviour' category (Table 4.2) of agonistic behaviour that did not meet the definitions of a competitive group. In 28 pods (0.71% of 3,949 pods), a mother repulsed or avoided the advances of an escort (Pack *et al*. 2002). All except one of these pods were trios, consisting of mother-calf and escort; the other pod was a mother in the company of two small calves repulsing an aggressive approach by an escort. Between 1992 and 2005 there were only two sightings of a mother with two calves in Hervey Bay (Franklin *et al*. 2011). Of the 28 pods, 22 (78.6 %) involved avoidance by the mother of the escort and 6 pods (21.4%) involved active repulsion of the escort by the mother.

### *4.4.6 Competitive groups and non-agonistic social behaviour pods within season*

The number of all observed pods, newly associated pods; competitive groups and non-agonistic social behaviour pods are reported by week within season in Table 4.5.

*Table 4.5*. Number of pods, week within year by pods (*n*), newly associated pods (NAP), the subset of pods used in analysis of competitive groups (Subset a), competitive groups (CG), the subset of pods used in analysis of non-agonistic social behaviour (Subset b), non-agonistic social behaviour pods (NASB)

| Week | Pods (*n*) | NAP | Subset (a) [1] | % | CG | Subset (b) [2] | % | NASB |
|---|---|---|---|---|---|---|---|---|
| 1 | 315 | 43 | 105 | 11.2 | 14 | 256 | 11.2 | 83 |
| 2 | 380 | 57 | 136 | 14.5 | 19 | 305 | 13.3 | 84 |
| 3 | 391 | 56 | 139 | 14.8 | 33 | 322 | 14.1 | 81 |
| 4 | 403 | 68 | 160 | 17.0 | 33 | 319 | 13.9 | 87 |
| 5 | 416 | 41 | 99 | 10.5 | 23 | 275 | 12.0 | 51 |
| 6 | 391 | 40 | 89 | 9.5 | 33 | 220 | 9.6 | 25 |
| 7 | 450 | 49 | 74 | 7.9 | 30 | 203 | 8.9 | 21 |
| 8 | 444 | 46 | 64 | 6.8 | 32 | 169 | 7.4 | 15 |
| 9 | 411 | 40 | 49 | 5.2 | 21 | 130 | 5.7 | 13 |
| 10 | 348 | 25 | 25 | 2.7 | 11 | 88 | 3.8 | 5 |
| Total | 3,949 | 465[3] | 940 | 100 | 249 | 2,287 | 100 | 465[3] |
| % | 100 | 11.78 | 23.80 | | 6.31 | 57.91 | | 11.78 |

[1] Subset (a): pods that included at least 3 whales of which at least 2 were non-mothers (see CG definition above). This subset was used in the analysis of competitive groups.

[2] Subset (b): pods that included at least 2 whales (excluding a mother alone with her calf) (see NASB definition above). This subset was used in the analysis of non-agonistic social behaviour.

[3] That the totals in newly associated pods (NAP) and non-agonistic social behaviour (NASB) are the same is a coincidence and these are discrete results. Note: the pods exhibiting CG and NASB behaviours may or may not be newly associated pods (NAP). This is dealt with in the analyses.

The lowest proportion of competitive groups occurred in the first two weeks of the season (33 of 249 pods, 13.3%) when calves were rarely seen (5 of 810 pods, 0.62%; Franklin *et al*. 2011), and during the last two weeks (32 of 249 pods, 12.9%) when the majority of pods had calves present (695 of 838 pods, 82.9%; Franklin *et al.* 2011). In contrast, the highest proportion of non-agonistic social behaviour pods (335 pods, 72.0%) occurred during the first four weeks when calves were rarely seen (73 of 1,749 pods, 4.2%; Franklin *et al*. 2011), and the lowest proportion of non-agonistic social behaviour pods (54 pods, 11.6%) occurred during the last four weeks when the majority of pods had calves present (1,376 of 1,855 pods, 74.2%; Franklin *et al*. 2011).

### *4.4.7* Sex-identified males and females in competitive groups and non-agonistic social behaviour pods

Sex could not be unambiguously identified for all individuals. The frequency and proportion of individuals whose sex could be identified (see Sex-identification in Definitions 4.3.2 and 4.3.4 above) in competitive groups and non-agonistic social behaviour pods by method of sex-identification are reported in Table 4.6.

*Table 4.6.* Sex-identified males and females in competitive groups and non-agonistic social behavior pods by method of sex-identification, number of males *(n)*, number females (*n*) with percentages and totals

| | Competitive groups (*n* = 249) | | | | Non-agonistic social behavior pods (*n* = 285) | | | |
|---|---|---|---|---|---|---|---|---|
| Method of sex-identification | Males (*n*) | % | Females (*n*) | % | Males (*n*) | % | Females (*n*) | % |
| Photography of genital area | 16 | 1.8 | 29 | 10.8 | 65 | 20.8 | 95 | 37.2 |
| Field observation of genital area | 4 | 0.4 | 6 | 2.2 | 15 | 4.8 | 30 | 11.8 |
| Individual resighting histories | 113 | 12.6 | 73 | 27.2 | 56 | 17.9 | 82 | 32.2 |
| Females (mother with calf) | 0 | 0.0 | 43 | 16.1 | 0 | 0.0 | 33 | 12.9 |
| Inferred nuclear females | 0 | 0.0 | 117 | 43.7 | 0 | 0.0 | 15 | 5.9 |
| Inferred males (escort, singer) | 767 | 85.2 | 0 | 0.0 | 177 | 56.5 | 0 | 0.0 |
| Totals | 900 | 100 | 268 | 100 | 313 | 100 | 255 | 100 |

If we assume that all behavioural roles are sex-specific, including the nuclear 'females' in a competitive group, the sex of all individuals in all 249 competitive groups (Table 4.5) was either determined or inferred, with a ratio of 900 males to 268 females (3.36:1) (Table 4.6).

Of the 465 non-agonistic social behaviour pods (Table 4.5) there were 285 pods (61.3%) in which some individuals were sex-identified and 180 pods (38.7%) in which no individuals were sex-identified. In the 285 pods in which the sex of some individuals was identified, there was a ratio of 313 to 255 (1.23:1) sex-identified males to females (Table 4.6). Of the 180 pods, in which no individuals were sex-identified, 87 (48.3%) were pairs and 93 (51.7%) were pods of 3+ whales.

Of these 285 pods in which some individuals were sex-identified, there were 22 (7.7%) pods of pairs and 4 (1.4%) pods of 3+ whales in which all individuals were sex-identified. Of the 22 pairs, 18 (81.8%) consisted of a male and female, 2 (9.1%) consisted of 2 males, and 2 (9.1%) consisted of 2 females. Of the 4 pods of 3+ whales, 2 (50%) consisted of 1 male and 2 females, 1 (25%) consisted of 2 males and 1 female and 1 (25%) consisted of 1 male and 3 females.

### *4.4.8 Statistical analysis and modelling*

#### *4.4.8.1 Newly associated pods*

The proportion of newly associated pods in Hervey Bay varied from 5.0% to 14.4% over the years, and from 16.9% to 7.2% over the weeks within year (Figure 4.1A, 4.1B respectively). Although there was no systematic pattern to the variation over years, the proportion of newly associated pods over weeks within year was significantly greater in the first 4 weeks of the season than the last six weeks of the season (15.0%, 9.8%; Fisher's exact test, $P < 0.001$). This result is consistent with the significant differences in pod characteristics early in the season compared to later in the season reported in Franklin *et al*. (2011).

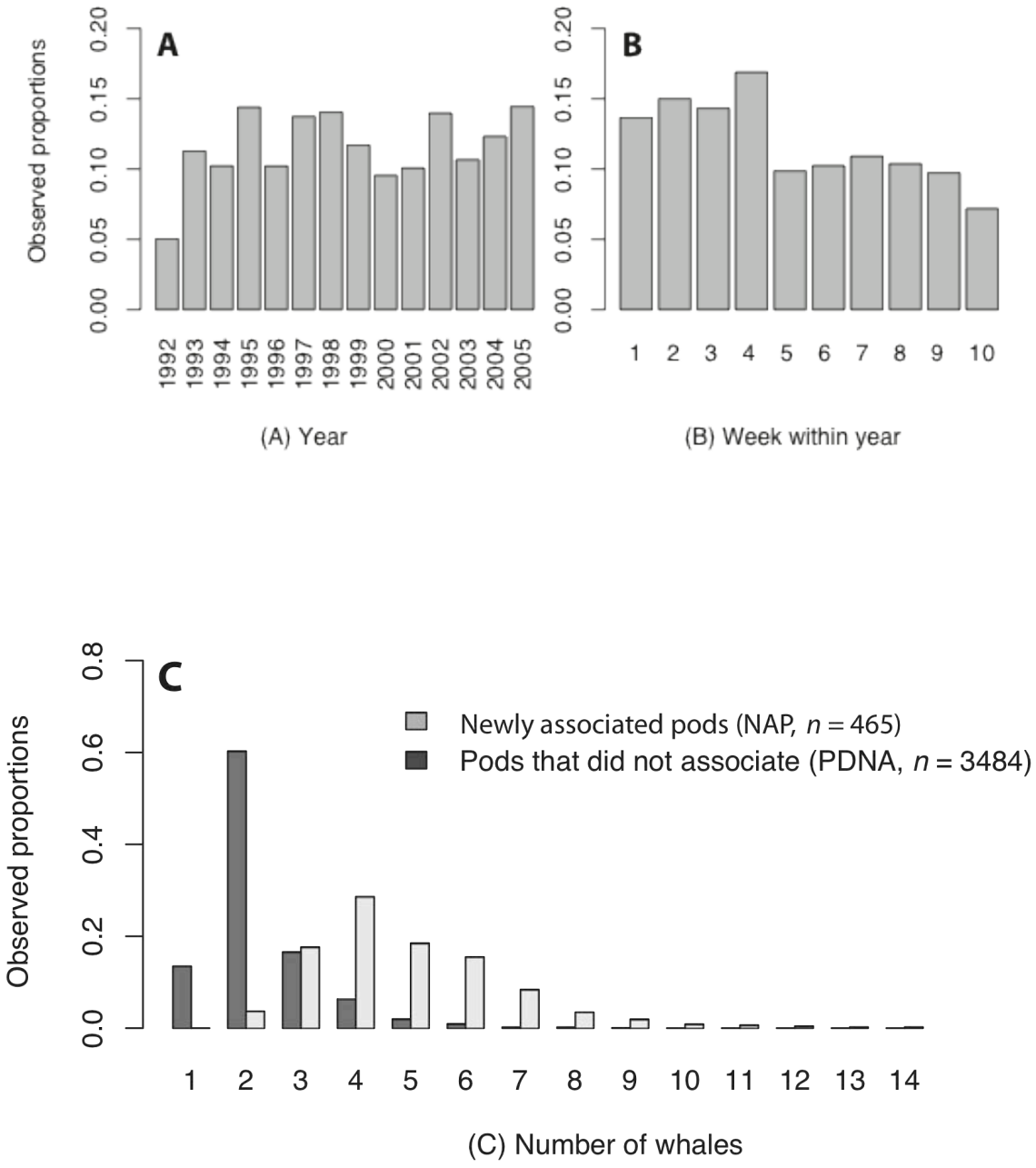


*Figure 4.1.* Observed proportions: (A) newly associated pods by year, (B) newly associated pods by week within year, (C) pods by number of whales in pods for newly associated pods (NAP) and pods that did not associate while under observation (PDNA).

Newly associated pods on average, as expected, were significantly larger than pods that did not associate with other whales while under observation (Mann-Whitney test, $P < 0.001$). Newly associated pods ranged in size from 2 to 14 whales (mode = 4, median = 5, mean = 4.9, SD = 1.85, n = 465) while pods that did not associate with other whales while under observation, ranged from 1 to 9 whales (mode = 2, median = 2, mean = 2.3, SD = 0.98, = 3,484) (Fig. 4.1C, Table 4.3).

The proportion of pods with calves present increased rapidly from week 4 to the end of the season (3.6% to 92.8%, Franklin *et al*. 2011). Pods that included a calf were less likely to associate than pods that did not include a calf (9.9%: 13.2%, $\chi^2 = 10.57$, df=1, $P < 0.001$), and when pods that included a calf did associate, they were much more likely to join with pods that also included a calf than with pods that did not include a calf (70.4%: 29.6%; $\chi^2 = 16.33$, df=1, $P < 0.001$).

#### *4.4.8.2 Competitive groups*

As competitive groups and newly associated pods were closely related (see below), the following analyses were conducted on the data set in Table 4.5, which included the data on newly associated pods and pods that did not associate while under observation. Of the 3,949 pods in the data set, 940 (23.8%, Subset (a), Table 4.5) were pods that included at least 3 whales, of which at least 2 were non-mothers; it is this subset that was analysed. Competitive behaviour was observed in 249 (26.5%) of these 940 pods.

The factors; newly associated pod, year, presence of calf, number of whales in pod (excluding calves), and week within year were each assessed for effects on the probability of observing competitive groups. Competitive groups were:

1. Observed in a greater proportion of newly associated pods (140/376 = 37.2%) than in pods that did not associate while under observation (109/564 = 19.3%) ($\chi^2$ = 37.15, df = 1, $P < 0.001$);
2. Not significantly variable over years ($\chi^2$ = 13.55, df = 13, $P$ = 0.406);
3. Significantly more frequent in pods with calves present (87/191 = 45.5%) than in pods with no calf or calves present (162/749 = 21.6%), ($\chi^2$ = 44.72, df = 1, $P < 0.001$);
4. Observed to significantly increase in frequency with the number of whales in the pod (excluding calves) (70/425 = 16.5%, 72/270 = 26.7% and 107/245 = 43.7% for 3, 4 and 5+ whales respectively, $\chi^2$ = 59.07, df = 2, $P < 0.001$);
5. Observed to significantly increase in frequency over weeks within year (from ~12% to ~45%), $\chi^2$ = 65.66, df = 9, $P < 0.001$).

However, these univariate effects were not independent. Consequently, a binary logistic regression model was fitted to assess the joint effects of newly associated pods (yes, no), presence of calf (present, not present), number of whales (excluding calves) (3, 4, 5+) and week within year (1, 2, …, 10) on the probability of observing competitive groups.

Together the four main effects accounted for a significant proportion of variation in the rate of observation of competitive groups ($\chi^2$ = 137.23, df = 13, $P < 0.001$). However, the marginal Wald tests showed the calf effect to be non-significant in the context of the other effects (Wald = 2.993, df = 1, $P$ = 0.084). The non-significance of the calf effect was largely due to the strength of the association between the increasing proportion of calf pods and week within season.

An attempt to fit interaction effects required considerable collapsing of categories and failed to produce useful results. Consequently, the selected model included only the 3 main effects

for newly associated pods, number of whales (excluding calves) and week within year ($\chi^2$ = 134.26, df = 12, $P < 0.001$, Cox and Snell RSQ = 0.133, Nagelkerke RSQ = 0.194).

While not reported here the individual parameter estimates were used to calculate the estimated probabilities of observing competitive groups by the explanatory factor levels.

The mean probabilities of observing competitive groups by newly associated pods (yes, no), number of whales (excluding calves) (3, 4, 5+) and for week within year are plotted in Figure 4.2.

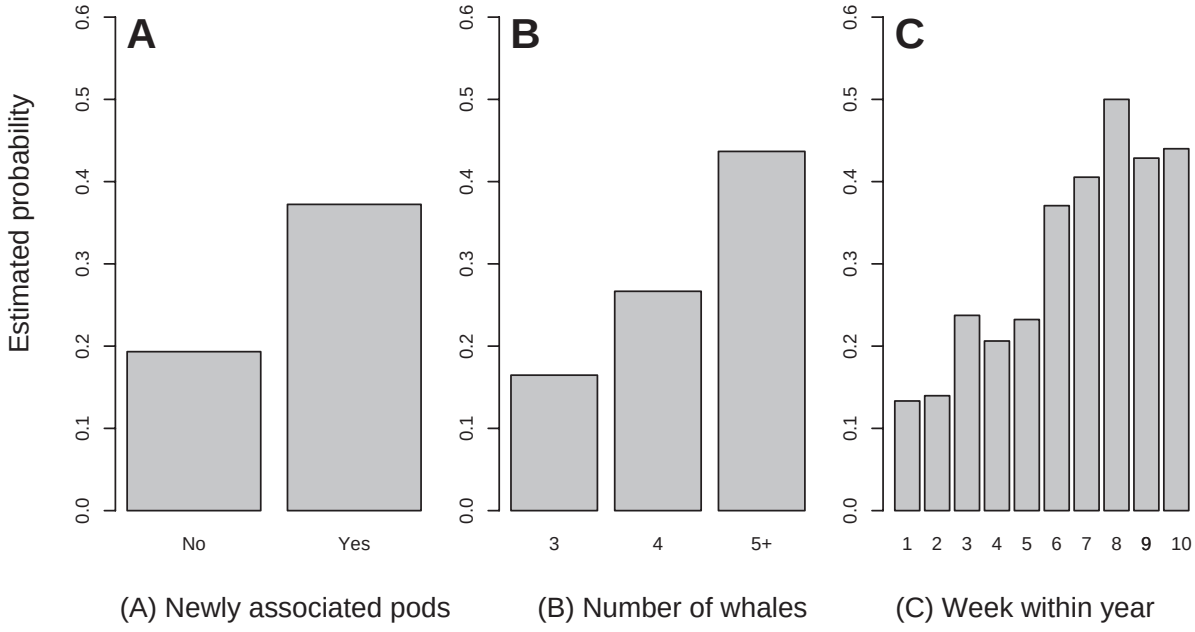


*Figure 4.2.* Estimated probabilities of observing competitive groups: (A) by newly associated pods (No, Yes); (B) by number of whales (excluding calves); and (C) by week within year.

That the effects of increasing pod size and newly associated pods are jointly significant indicates that the rate of competitive groups is greater in newly associated pods than in pods

that did not associate with other whales, and is not simply a function of the increase in pod size following the formation of a newly associated pod. As shown in Figure 4.2B, larger pods were more likely to be competitive, with a larger increase in the frequency of competitive groups between 4 and 5+ whales than between 3 and 4 whales. However, as shown in Figure 4.2A, if those pods have just associated, there is an approximately 17% increase in the frequency of competitive groups compared to (*i.e.*, over and above) pods of the same sizes that did not associate with other whales while under observation.

The calf effect was likely non-significant in the context of the other effects because the presence of calf and week within year were very strongly associated ($\chi^2 = 349.76$, df = 9, $P < 0.001$).

#### *4.4.8.3 Non-agonistic social behaviour pods*

As non-agonistic social behaviour and newly associated pods were closely related (see below), the following analyses were conducted on the data set in Table 4.5, which included the data on newly associated pods and pods that did not associate with other whales while under observation. Of the 3,949 pods in the data set, 2,287 (57.9%, Subset (b), Table 4.5) included at least 2 whales (excluding a mother alone with her calf), and it was this subset that was analysed.

Non-agonistic social behaviour was observed in 465 (20.3%) of the 2,287 pods. The following factors were each assessed for effects on the probability of observing non-agonistic social behaviour: newly associated pod, year, presence of calf, number of whales in pod (excluding calves), and week within year. Non-agonistic social behaviour was:

1. Observed with greater frequency in newly associated pods (139/435 = 32.0%) than in pods that did not associate with other whales (326/1,852 = 17.6%), ($\chi^2$ = 44.79, df = 1, $P$ < 0.001);
2. Significantly variable over years ($\chi^2$ = 44.79, df = 13, $P$ < 0.001);
3. Observed significantly more often in pods with no calf present (421/1,759 = 23.9%) than in pods with a calf or calves present (44/528 = 8.3%) ($\chi^2$ = 61.02, df = 1, $P$ < 0.001);
4. Observed to significantly increase in frequency with the number of whales in the pod (excluding calves) (176/1,319 = 13.3%, 125/446 = 28.0%, 76/276 = 27.5%, 88/246 = 35.8% in pods with 2, 3, 4 and 5+ whales respectively, $\chi^2$ = 101.12, df = 3, $P$ < 0.001);
5. Significantly variable by week within year ($\chi^2$ = 104.88, df = 9, $P$ < 0.001).

However, these univariate effects were not independent. Consequently, a binary logistic regression model was fitted to assess the joint effects of newly associated pods (yes, no), presence of calf (present, not present), year, week within year and number of whales (excluding calves) (2, 3, 4, 5+) on the probability of observing non-agonistic social behaviour.

The five main effects were fitted as a block, which accounted for a significant proportion of variation ($\chi^2$ = 321.41, df = 27, $P$ < 0.001). Adding the two-way interaction effects individually to the model showed that only the newly associated pods by number of whales in the pod interaction effect was significant.

The selected model included the five main effects and the newly associated pods by number of whales (excluding calves) interaction effect ($\chi^2$ = 334.59, df = 30, $P$ < 0.001, Cox and Snell RSQ = 0.136, Nagelkerke RSQ = 0.214, marginal Wald tests for all effects with $P \leq 0.002$).

The parameter estimates and their standard errors are not reported here, although the parameter estimates were used to calculate the estimated probabilities of observing non-agonistic social behaviour by the factors in the model.

The estimated probability of observing non-agonistic social behaviour by year, week within year and by number of whales (excluding calves), in newly associated pods (No, Yes) are plotted in Figure 4.3.

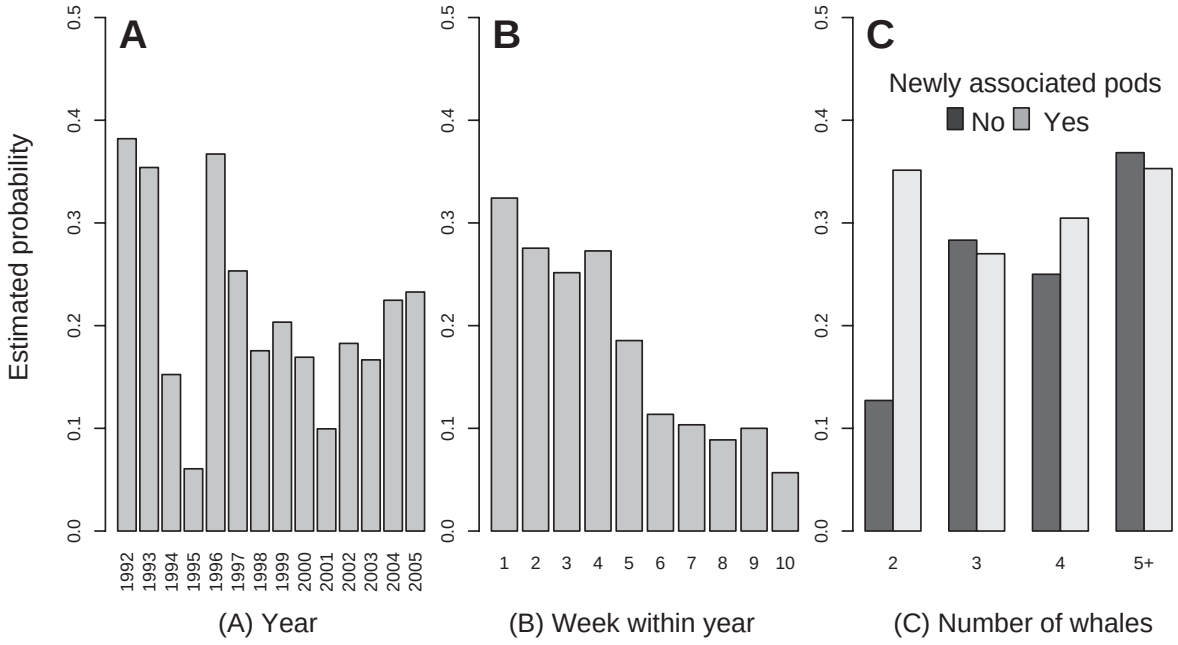


*Figure 4.3*. Estimated probabilities of observing non-agonistic social behaviour: (A) by year; (B) by week within year; (C) by number of whales (excluding calves), in newly associated pods (No, Yes).

The variation over years in the probability of observing non-agonistic social behaviour (Fig. 4.3A) includes a rapid decline over the period 1992 to 1995 followed by a sudden increase in 1996. This is followed by a decline to 2001 and an increase after that to 2005.

The probability of observing non-agonistic social behaviour declined from the beginning of the season, and rapidly after about week 5 (Fig. 4.3B). Although the effect of the presence of a calf in a pod is not shown in Figure 4.3A, 4.3B or 4.3C, there was a significant main effect in the model with the rate of occurrence of non-agonistic social behaviour being significantly lower in pods that included calves (8.3% with calves, 23.9% without calves). That both the presence of calf and week within year effects were significant in the model indicates that the calf effect is not simply due to the rapidly increasing proportion of pods that included calves later in the season (3.6% to 92.8%, Franklin *et al*. 2011): *i.e*., the calf effect is over and above the decline in the rate of non-agonistic social behaviour shown in Figure 4.3B.

The probability of observing non-agonistic social behaviour increased with the number of whales (excluding calves) in the pod, and was higher for pods of 2 whales (excluding calves) that were newly associated, than for pods of 2 whales that did not associate with other whales while under observation (Fig. 4.3C). This difference largely accounts for the pod size effect. Thus, the effect of newly associated pods is largely confined to the difference between newly associated pods of 2 (2 singletons associating) rather than newly associated pods of larger size.

## 4.5. DISCUSSION

### *4.5.1 Seasonal variation in newly associated pods*

While there was no systematic pattern in the frequency of newly associated pods over years, the rate of formation of newly associated pods within season was significantly higher during the first four weeks of the season compared to the last six weeks of the season (Fig. 4.1A and B). Furthermore, in pods, which met the definition of non-agonistic social behaviour (Subset (b), Table 4.5) non-agonistic social behaviour was observed more frequently early in the

season when calves were rarely present. In contrast, in pods, which met the definition of competitive group behaviour (Subset (a), Table 4.5) competitive groups were observed more frequently later in the season when mother-calf pods predominated. These results, together with the significant differences in pod characteristics and composition within season reported in Franklin *et al*. (2011), suggest that there are biological differences in the classes of humpback whales present in Hervey Bay in the first four weeks of the season compared to the last six weeks of the season.

Dawbin (1966, 1997) reported that the first sexual and maturational classes to commence the southern migration were newly pregnant females with resting non-lactating females, closely succeeded by immature males and females, preceding mature males and females. The highest proportion and numbers of pods in Hervey Bay during the first four weeks of the season were pairs (Franklin *et al.* 2011). Genetic studies of humpback whales in breeding grounds off the coast of South Africa and Brazil reported that most pairs consist of male-female dyads (Pomilla and Rosenbaum 2006, Cypriano-Souza *et al.* 2010). Herman *et al.* (2011) reported that the majority of dyads in the Hawaiian wintering grounds were composed of male-female pairs. Brown and Corkeron (1995) also reported that male-female associations represented the greatest proportion of pairs observed during the southern migration along the east coast of Australia and reported only two female-female pairs out of a sample size of twenty-seven pairs. Pack *et al*. (2012) investigated body size-assortative pairing of humpback whales in the Hawaiian breeding grounds and reported that male-female pairs predominated, followed by male-male pairs with four female-female pairs out of 258 pairs sampled. In the Gulf of Maine feeding ground (Clapham 1993) reported male-female pairs predominated and that 5.4% of pair pods (372 of 6,829) were female-female pairs. In this study 81.9% pair pods (18 of 22) in which sex was identified, were male-female, two pairs were male-male and two female-female.

Franklin *et al*. (2011) reported that 51.9% of singleton pods occurred in the first four weeks of the season when calves were rarely seen. Furthermore, they reported that 69.1% of 3 and 4+ larger pods with no calves present also occurred in the first four weeks of the season. Overall, in Hervey Bay singletons and pairs predominated in the formation of newly associated pods (Table 4.1). The social interactions occurring among singletons early in the season is reflected in the markedly higher probability of observing two singletons forming pairs in newly associated pods involved in non-agonistic social behaviour (Fig. 4.1C). Therefore, the presence of socially active immature males and females, and mature males and females either as singletons or pairs and in larger pods are likely to contribute to the higher rate of newly associated pods during the first four weeks of the season.

Dawbin (1966, 1997) reported that lactating females followed the migration of early pregnant and resting females south by about a month. In Hervey Bay the mother-calf class represents the largest proportion of pod types from September onwards, with the proportion of mother-calf pods in relation to other pod types increasing rapidly towards the end of the season, and with mothers spending 69.4% of their time alone with their calves (Franklin *et al.* 2011). The predominance of mother-calf pods and the time they spend alone with their calves is likely to contribute to the significantly lower rates of newly associated pods during the last six weeks of the season. Furthermore, the departure early in the season of immature and non-lactating mature females, may also contribute to a lower rate of associations in the latter half of the season.

The joint significance of both pod size and newly associated pods reported in this study indicate that there was a significant increase in the probability of observing competitive groups and non-agonistic social behaviour pods in newly associated pods, over and above the increase in pod size alone. Previous studies have reported increased surface activity with pod size (Herman 1978, Tyack 1982, Tyack and Whitehead 1983) with the exception of Silber

(1986), who reported a negative correlation between group size and surface activity. In Hervey Bay some of the larger pods that were not seen to associate while under observation, may have only recently associated and already lost members through disassociations.

### *4.5.2 Social interactions among lactating females and other conspecifics*

Clapham (2000) summarised the sparse reports of female-female associations in the Northern Hemisphere feeding and breeding grounds and reported that lactating females appear to avoid each other in all areas. Clapham and Mayo (1987) reported that in Massachusetts Bay groups containing more than a single calf were rare in summer. Weinrich (1991) reported that adult females involved in cooperative feeding were the most consistent members of stable foraging groups in the Gulf of Maine and appeared more frequently in stable groups when pregnant. While in southeastern Alaska, Baker (1985) and Perry *et al*. (1990) reported non-competitive foraging groups of humpback whales consisting of either all males, all females or both sexes, which were on occasion cooperative. Although there were dense aggregations of lactating females in Hervey Bay during the second half of the season, for the most part they remained alone with their calves (Franklin *et al*. 2011), and were involved in limited interactions with other conspecifics. However, when pods that included a calf did associate, they were significantly more likely to associate with pods in which a calf or calves were present. Franklin *et al*. (2011) suggested that Hervey Bay was a suitable stopover for mothers to engage in maternal activity with older calves during the early stages of the southern migration.

When lactating females were observed interacting with other conspecifics, they were predominantly involved in non-agonistic social interactions with only a small proportion involved in pods displaying agonistic behaviour such as competitive groups or mother-calf escort pods involving repulsion or avoidance of an escort (Table 4.2, 4.3 and 4.4). Lactating

females in Hervey Bay are predominantly involved in non-agonistic social interactions rather than agonistic competitive social interactions.

### *4.5.3 Competitive behaviour occurs throughout the season*

Competitive groups involve intrasexual competition among males for access to sexually mature females who may be in estrous (Darling *et al.* 1983, Tyack and Whitehead 1983, Baker and Herman 1984*b*, Clapham *et al*. 1992, Clapham 2000). However, Clapham (1996 p.37) qualifies the above definition because the onset and duration of oestrous in humpback females is not known and that the Principal Escort in a competitive group may well be "...competing for a female in the hope of subsequently mating with her, or is practising the post-copulatory mate guarding behaviour...and that some competitive groups...consisted entirely of males...that he...tentatively interpreted as dominance sorting." Herman *et al*. (2011) reported a male-biased sex ratio in the Hawaiian breeding grounds and suggested that newly pregnant females leave the breeding grounds earlier while males tend to linger; thus as the season progresses females become a limited resource for which males compete.

Only a low proportion of pods in Hervey Bay were competitive groups (6.3%, Table 4.5). The probability of observing competitive groups in Hervey Bay was at its lowest during the first two weeks of the season and increased significantly throughout the season. Franklin *et al*. (2011) reported that pod characteristics early in the season in Hervey Bay were consistent with the presence of immature males and females (also see Fig. 5.1, Chapter 5). Dawbin (1966, 1997) reported that immature males and females were accompanied by non-lactating females, either resting or newly pregnant are the first classes of humpback whales to travel south. It has been suggested that females may either be newly pregnant or in a temporary condition preceding ovulation (Chittleborough 1954, Nishiwaki 1959, Craig *et al*. 2003).

Consequently the presence of some mature females may attract a small number of mature males seeking potential estrous females, resulting in low levels of competitive groups in early August. As the immature class decreases towards the end of August and is replaced by an increasing proportion of mature males and females (Dawbin 1966, 1997), this is likely to contribute to the probability of observing increased competitive groups during late August and early September (Fig. 4.2A).

Although the probability of observing competitive groups was highest from mid-September onward, the number of pods available to engage in competitive groups was relatively small, as the majority of pods were composed of mothers alone with their calves (Franklin *et al.* 2011). Chittleborough (1958, 1965) reported that post-partum estrous may occur in a minority of cases (8.5%, 8 of 94, Chittleborough 1958), that this would likely occur one month after parturition, and that August is the peak-birthing month. However, mothers with calves are rarely present in Hervey Bay during August, and begin moving into the bay in early September (Franklin *et al*. 2011). Consequently the occurrence of competitive groups from September onwards is likely due to the presence of potentially estrous mature females, and the possibility of some lactating females involved in post-partum estrous events (Fig. 4.2). Baker and Herman (1984a) and Craig *et al.* (2002) reported increased competitive activity towards the end of the season in the Hawaiian breeding grounds related to the declining numbers of non-lactating estrous females. The potential decline in availability of non-lactating estrous females in Hervey Bay as the season progresses is likely to be a major factor influencing male behaviour leading to an increased rate of occurrence of competitive groups towards the end of the season (Craig *et al*. 2002).

In this study, in 72.7% of pods (24 of 33, Table 4.2) in which both competitive group behaviour and non-agonistic social behaviour were observed, non-agonistic social behaviour preceded competitive group behaviour. Furthermore, 60.6% of these pods (20 of 33, Table

4.3) were newly associated pods. Whitehead (1985) suggested that surface behaviours, such as pectoral slapping, might have a communicatory function. Clapham (2000) discussed the idea supported by personal observations, that females may use surface displays to 'call in' males or solicit competition in order to displace an unwanted companion**.** The result reported here suggests a relationship between at least some non-agonistic surface social behaviours and the occurrence of competitive group behaviour and the formation of newly associated pods.

### *4.5.4 Hervey Bay: a resource for males seeking to maximise mating opportunities*

It has been reported that the reproductive success of long-lived mammals occurs over many breeding seasons and individual male humpback whales may behave to maximize their reproductive success over a lifetime (Clapham 1996, Boness *et al.* 2002). Although Hervey Bay is south of the putative breeding ground of eastern Australian humpback whales (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999) it is a habitat where aggregations of females occur (Franklin *et al.* 2011*)*. The rate of competitive groups in Hervey was low (6.3% of pods) and the rate did not vary significantly over years. This suggests that some males migrating south from the breeding grounds may take advantage of further mating opportunities with females aggregating in Hervey Bay.

It has been suggested the presence of many singing humpback whales in an area where females aggregate may be a form of communal display (Herman and Tavolga 1980). Singing occurs in Hervey Bay and has been recorded throughout the season (W. and T. Franklin unpublished data). Early studies suggested that the mating system of the humpback whale may have some features characteristic of lek societies (Herman and Tavolga 1980, Mobley and Herman 1985). The criteria for a traditional lek includes; absence of parental care by males, existence of a mating arena, lack of resources in male territories and opportunities for

females to select males (Clapham 1996). However, Clapham (1996) noted that the humpback mating system had all the characteristics of a 'classical lek' except for the rigid spatial structuring of male territories, and suggested the term 'floating lek'. Emlen and Oring (1977, p. 219) suggested that "If female movements or concentrations are predictable, encounter rates would be high for males that position themselves in these areas..". The predictability of the presence of non-lactating females in Hervey Bay early to mid-season and lactating females from mid-season onwards, may represent a feature of a 'floating lek', which provides an annual resource for males seeking to maximize the number of potential mates.

### *4.5.5 Non-agonistic social behaviour predominates in early to mid-season*

There was significant variability in the occurrence of non-agonistic social behaviour pods both over years and within season. Franklin *et al*. (2011) reported a significant growth in pods with 3+ whales over years in Hervey Bay. They suggested that as the population increased larger groups became more common, and was likely to have generated a skewed distribution in the population towards younger whales. The proportion of eastern Australian humpback whales entering Hervey Bay may range from 30% to 50% (Chaloupka *et al*. 1999). Therefore the variability of non-agonistic social behaviour over years may be related to the relative proportions of age, sex and maturational classes of humpback whales entering Hervey Bay in any given year.

As noted above, in the early part of the season the highest proportion and numbers of pods were pairs, followed by singletons (Franklin *et al*. 2011) and were related to the presence of immature males and females early in the season and mature males and females mid-season (Dawbin 1966, 1997). In the North Atlantic, Clapham (1994) reported that juveniles (which he defined as sexually immature whales less than five years old) exhibit increasing sociality

with age, and that as they attain sexual maturity around the age of five years their social development parallels reproductive or courtship-related behaviour of mature adults.

In this study the probability of observing non-agonistic social behaviour pods predominantly occurred during the first four weeks of the season, and increased with the number of whales in the pod. Corkeron *et al*. (1994) reported from aerial surveys conducted in Hervey Bay that pods were not randomly distributed, but tended to aggregate in clusters, which may be related to social factors. Franklin *et al*. (2011) suggested that because whales enter and leave Hervey Bay from the north, the density and movements of whales increased the likelihood of interactions among pods, contributing to the formation of larger pods or to the probability of encountering recently aggregated pods. Consequently, the higher levels of non-agonistic social behaviour pods observed during the first four weeks of the season is likely to be related to the social interactions among immature males and females early in the season, and mature males and females in mid-season.

Compared to pods involved in non-agonistic social behaviour (11.8%), the majority of pods in Hervey Bay were involved in other behaviour (82.8%). Unlike competitive groups, both non-agonistic social behaviour pods and other behaviour pods have no obvious competitive component. A possible negative bias could arise from incorrectly classifying non-agonistic social behaviour pods as other behaviour pods. However, there is little likelihood for non-agonistic social behaviour pods to be classified in other behaviour as other behaviour pods are predominantly involved in surface travelling, resting and occasional surface behaviours (e.g. lob-tailing and breaching). Whereas, non-agonistic social behaviour pods involve observation of a clearly defined set of surface social behaviours, occurring in a small spatial area (see Definitions 4.3.2 above).

Hervey Bay offers a convenient habitat early in the southern migration for social activity among individuals within the above maturational classes. In non-agonistic social behaviour

pods immature males and females are more likely to be involved in social interactions related to the establishment of social bonds and juvenile development (Clapham 1994). In non-agonistic social behaviour pods mature males and females are more likely to be involved in courtship-related behaviour. The social behaviour of both classes may be reflected in the higher frequency of non-agonistic social behaviour pods in newly associated pods and as pod size increases (Fig. 4.3).

### *4.5.6 Relative proportions of non-agonistic and competitive behaviour*

Competitive group behaviour has been well documented in the Northern Hemisphere (Darling *et al.* 1983, Tyack and Whitehead 1983, Baker and Herman 1984*b*, Clapham *et al.* 1992, Clapham 2000) and in the Southern Hemisphere (Brown and Corkeron 1995). Darling *et al.* (2006) noted that competitive behaviour is more conspicuous than cooperative relationships, which are more difficult to identify and confirm. Non-agonistic and cooperative behaviour has been reported in various earlier studies (Herman and Antinoja 1977, Tyack and Whitehead 1983, Clapham *et al*. 1992, Brown and Corkeron 1995). Darling *et al*. (2006) suggested that non-agonistic behaviour may be more prevalent in humpback whale interactions than has previously been reported, and that while competitive and non-agonistic relations do occur, the relative proportion of each type of behaviour in a humpback population is not known.

This study provides a measure of the relative proportion of competitive group behaviour (6.3%, Table 4.5) and non-agonistic social behaviour (11.8%, Table 4.5) of humpback whales in Hervey Bay. Overall, competitive behaviour (7.0%) occurred in competitive groups (6.3%, Table 4.5), with a small proportion of repulsion or avoidance behaviour by mothers towards escorts (0.7%). It should be noted that 82.8% of pods (Table 4.2) in Hervey Bay were involved in 'other behaviour', in which neither competitive behaviour nor non-agonistic

social behaviour was observed. Therefore, further detailed study on these other behaviours is needed, to understand the complex social behaviour of humpback whales.

### *4.5.7* Hervey Bay: a unique stopover early in the southern migration

The results of this study and Franklin *et al*. (2011) indicate that the social behaviour and pod characteristics of humpback whales utilising Hervey Bay differ in important aspects compared with studies in the Northern Hemisphere breeding grounds of Hawaii and the West Indies. Hervey Bay is located south of the putative Great Barrier Reef breeding ground for eastern Australian humpback whales, and Franklin *et al*. (2011) concluded that it is neither a calving ground nor a terminal destination. In contrast to the Northern Hemisphere breeding grounds, for example Hawaii, where there is no easily accessible stopover between the breeding grounds and the feeding grounds in Southeastern Alaska, Hervey Bay provides a unique opportunity to study the behaviour and pod dynamics of a humpback whale population after leaving the activities on the breeding ground and while preparing for the migration to their feeding areas in Antarctica.

Herman *et al*. (2011) reported a male-biased sex ratio in the Hawaiian breeding grounds of 1.82:1 males to females. They reviewed the literature on male-biased sex ratios reported in other winter breeding grounds in both the Northern and Southern Hemisphere, and discussed the issue of whether the male-bias was a sampling artefact, or whether it reflected a differential migration to the winter grounds such that fewer females than males migrate or complete the migration. They found no conclusive evidence for sampling artefact or differential migration in the reported male-biased sex ratio and suggested that newly pregnant females may leave the breeding grounds earlier while males tend to linger. Craig *et al*. (2002) suggested that in Hawaii male humpback whales preferentially associate with mature females without a calf, and towards the end of the season expend more energy in competition over

females without a calf than females with a calf. Furthermore, they found that the probability of females with a calf being accompanied by one or more escorts increased towards the end of the season. Thus in Hawaii the modal size of pods with a calf present was three (Herman and Antinoja 1977, Herman *et al*. 1980, Glockner and Venus 1983, Herman *et al*. 2011). In contrast, in Hervey Bay the last six weeks of the season is dominated by mother-calf pods and in contrast to Hawaii, the modal size of pods with calves present was two, which was related to mothers spending most of their time alone with their calf (Franklin *et al*. 2011).

Pairs were the predominant pod size during the first four weeks of the season in Hervey Bay (51.4%, 861 of 1,676; Franklin *et al.* (2011). In this study there was male-female parity in pairs in which both individuals were sex-identified. In Hervey Bay non-agonistic social behaviour pods predominantly occurred during the first four weeks of the season and have a ratio of sex-identified whales near parity (Table 4.6) but represented only 11.8% of pods (Table 4.5). In contrast, competitive groups have a ratio of sex-identified whales of just over 3:1 males to females, but represented only 6.3% of pods (Table 4.5). However, during the last six weeks of the season in Hervey Bay almost half of all pods consist of a mother alone with her calf (47.8%, 1,107 of 2,315; Table 4.4). Taken together, the above results are potentially indicative of an overall female sex-bias in Hervey Bay. Furthermore in a recent study of 361 individually identified humpback whales in Hervey Bay, the ratio of sex-identified or inferred females to males was 2.94:1 females to males (reported in Chapter 5.4, below). Therefore, in contrast to the Hawaiian breeding grounds, it is suggested that Hervey Bay may be a preferential habitat for females involving differential migration of females and males early in the southern migration.

## 4.6 CONCLUSION

The changes in seasonal social behaviour reported in this study, involving newly associated pods, competitive groups, and non-agonistic social behaviour pods, are consistent with the seasonal occurrence and timing of particular maturational and reproductive classes of humpback whales in Hervey Bay. Non-agonistic social behaviour occurs mainly during the first four weeks of the season when immature and mature males and females are present and pods with calves are rarely sighted. Very few pods with calves engaged in non-agonistic social behaviour. Competitive groups increased towards the end of the season as the availability of mature females without calves diminished and the proportion of pods including mothers with calves increased rapidly. Overall, non-agonistic social behaviour was more prevalent than competitive behaviour. Both non-agonistic social behaviour and competitive group behaviour were more common in larger groups and newly associated pods. The data are consistent with social factors, related to the presence of differing maturational and reproductive classes, influencing the seasonal social behaviour of humpback whales in Hervey Bay.

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# *Chapter 5*

# Temporal segregation and behaviour of reproductive and maturational classes of individually identified humpback whales *(Megaptera novaeangliae)* in Hervey Bay, 1992-2009

## 5.1 ABSTRACT

This study investigated the temporal segregation and behaviour of different reproductive and maturational classes of humpback whales in Hervey Bay eastern Australia, using observations from long-term resighting histories of 361 individual whales identified photographically between 1992 and 2009. Mature non-lactating females occurred mainly during August. Lactating females occurred in September and October with peak density occurring in late September, thirty-two days after that for mature non-lactating females. There was no significant difference in the peak density and observations by day within season of immature males and females and mature non-lactating females. There were very few mature males observed in August, with the main concentrations occurring in September and October; the occurrence of this class partly overlapped with that of non-lactating females but to a greater extent with lactating females. The data suggest that both non-lactating and lactating females interact with immature and maturing males and females to a greater extent than previously reported. Hervey Bay appears to be a preferential southbound stopover habitat for females on their southern migration from their winter breeding grounds. The observed temporal segregation pattern of humpback whales in Hervey Bay is consistent with the results reported by Dawbin (1966, 1997) from whaling catches made between the 1930s and 1960s. The results suggest that temporal segregation is a constant and cohesive feature of the social organisation of migrating humpback whales, which provides a predictable social framework for individuals moving through various maturational and reproductive stages.

## 5.2 INTRODUCTION

Baleen whales show temporal segregation of migration by age, sex and reproductive class (Nishiwaki 1959; Chittleborough 1965; Dawbin 1966, 1997, Swartz 1986). Dawbin (1997) undertook the most extensive investigation of such segregation in humpback whales during their migrations between summer feeding grounds and winter breeding areas in the Southern Hemisphere. Dawbin's data were obtained from 65,600 humpback whale catches in pre- and post-war whaling periods, ranging from the early 1930s to the early 1960s. Samples were obtained at coastal whaling locations and Antarctic pelagic waters between $1^0$S and $66^0$S and he reported no significant differences in trends of the timing of occurrence of the classes of whales examined within each of the separate tropical breeding grounds.

These whaling data were based on only one sighting record per individual at the time of the individual's death and consequently provided no information of individual behaviour over time and not all behaviour classes could be differentiated in that analysis. Furthermore, those data were collected at a time when the humpback whale populations were in rapid decline (Jackson *et al*. 2006, Clapham *et al*. 2009) and it is not clear if the patterns observed were influenced by this decline. More recent collaborative studies have utilised resighting histories of individuals to investigate estimates of abundance and rates of increase for the North Atlantic humpback whale population (Stevick *et al*. 2003). Resighting histories have also been used to study migratory timing and segregation of particular age, sex and reproductive classes of humpback whales during their migrations in the central North Pacific (Craig *et al*. 2003), and the resightings and social behaviour of individual humpback whales in the Hawaiian Islands were used to determine relative sight fidelity of males and females, apparent and operational sex-ratios, calving rates, females demographics and the diversity of the social/behavioural roles of males and females (Herman *et al*. 2011). Consequently, the use of

long-term resighting histories of known individuals provides an opportunity to investigate social behaviour within the context of temporal segregation.

It has been suggested that between 30% and 50% of eastern Australian humpback whales enter Hervey Bay in any one year (Chaloupka *et al.* 1999). Hervey Bay (Queensland, $25^0$S, $153^0$E) is located south of the putative breeding ground of eastern Australian humpback whales within the lagoon of the Great Barrier Reef (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999). Humpback whales do not enter Hervey Bay during the northern migration, but do so on their southern migration (Corkeron *et al.* 1994, Brown and Corkeron 1995, Franklin *et al.* 2011). Hervey Bay is neither a calving ground nor a terminal destination, but rather a migratory stopover for a portion of the population early in the southern migration (Franklin *et al.* 2011).

Significant changes in seasonal pod characteristics and seasonal social behaviour in Hervey Bay have been reported that are consistent with, and related to, the presence of different maturational and reproductive classes of humpback whales during the season (Franklin *et al*. 2011, Chapters 3 and 4 above).

Long-term resighting histories of 361 individually identified humpback whales were used to investigate the temporal segregation and behaviour of age, sex, reproductive and maturational classes of humpback whales travelling through Hervey Bay to compare these patterns to those reported from the whaling period, and to discuss the social behaviour of humpback whales in the context of temporal segregation.

## 5.3 METHODS AND DATA

### *5.3.1 Study area, fieldwork and photo-id data*

Vessel-based photo-identification of humpback whale pods was conducted in Hervey Bay (Queensland, $25^0$S, $153^0$E) from early August until mid-October each year between 1992 and 2009 (see Chapter 2.2 and Fig. 2.1 above). Fieldwork was conducted for 181 weeks, 1,014 operational days in the field and 8,122 hours of observations (Table 5.1).

Photography of the ventral fluke patterns, shape and size of dorsal fins and lateral body markings were obtained to allow identification of individual humpback whales (Katona *et al*. 1979, Katona and Whitehead 1981). Data collected during the observation of each pod included: date, time of commencement and completion of observation, pod identification code, the observed number of individuals in the pod, pod composition, pod behaviours (continuous sampling; Altmann, 1974), associations of pods and type of encounter. Information on sex-identification was obtained where possible.

Photography for each pod was analysed in conjunction with the field notes on observations of pod composition and behaviour (for detailed description of method, see Chapter 2.5). Resighting histories of individual humpback whales based on resightings over two or more years were compiled from observations recorded in the yearly fluke catalogues. A total of 578 individual histories were obtained with resightings ranging over a period of eighteen years (Table 5.1).

Each initial sighting and subsequent resightings of the 578 individual whales, within and between seasons, was examined in conjunction with photo-identification and observation notes. Information on pod composition, pod behaviour, individual behaviour and sex were reviewed to determine whether or not each initial sighting and subsequent resightings could be used to classify each whale with respect to sex, age, reproductive and maturational classes in accordance with the definitions below.

*Table 5.1.* Summary of fieldwork, observations and data: Hervey Bay from 1992 to 2009.

| Effort and observations | | | | | | Data | | |
|---|---|---|---|---|---|---|---|---|
| | | Fieldwork | | Observations | | Yearly Catalogues | | Cumulative |
| Year | First day | Last day | Field days | Pods (*n*) | Whales (*n*) | Sightings of individuals (*n*) | Sighting histories commenced | Sighting histories |
| 1992 | 10th Aug | 9th Oct | 42 | 189 | 387 | 4 | 4 | 4 |
| 1993 | 6th Aug | 15th Oct | 53 | 229 | 442 | 5 | 3 | 7 |
| 1994 | 7th Aug | 14th Oct | 50 | 163 | 380 | 47 | 36 | 43 |
| 1995 | 6th Aug | 13th Oct | 51 | 172 | 374 | 47 | 27 | 70 |
| 1996 | 4th Aug | 11th Oct | 48 | 185 | 410 | 70 | 26 | 96 |
| 1997 | 1st Aug | 17th Oct | 64 | 300 | 693 | 140 | 52 | 148 |
| 1998 | 9th Aug | 16th Oct | 58 | 410 | 934 | 190 | 56 | 204 |
| 1999 | 28th Jul | 15th Oct | 63 | 399 | 929 | 210 | 43 | 247 |
| 2000 | 6th Aug | 13th Oct | 58 | 380 | 815 | 206 | 50 | 297 |
| 2001 | 12th Aug | 19th Oct | 57 | 432 | 954 | 234 | 43 | 340 |
| 2002 | 11th Aug | 17th Oct | 59 | 409 | 968 | 268 | 56 | 396 |
| 2003 | 10th Aug | 17th Oct | 56 | 390 | 928 | 270 | 42 | 438 |
| 2004 | 5th Aug | 15th Oct | 60 | 419 | 952 | 303 | 49 | 487 |
| 2005 | 30th Jul | 14th Oct | 61 | 448 | 1,050 | 376 | 43 | 530 |
| 2006 | 3rd Aug | 13th Oct | 58 | 420 | 984 | 341 | 23 | 553 |
| 2007 | 30th Jul | 11th Oct | 60 | 399 | 945 | 297 | 14 | 567 |
| 2008 | 7th Aug | 17th Oct | 61 | 508 | 1,283 | 407 | 11 | 578 |
| 2009 | 6th Aug | 16th Oct | 55 | 396 | 901 | 317 | 0 | 578 |
| | | Totals | 1,014 | 6,248 | 14,329 | 3,732 | 578 | |

### *5.3.2 Definitions*

***Male sex identification***: was determined by either unequivocal observation and or photography of their genital area, or the whale was inferred as a male when observed in the social role of escort to a lactating female (see definition below), a singer, a Principal Escort or a Challenging Escort in a competitive group (Tyack 1981, Glockner and Venus 1983, Baker *et al* 1984*b*, Clapham *et al*. 1992, Herman *et al*. 2011). The presence of extensive vertical and

horizontal scratch marks on the left and right lateral body, were also used in conjunction with the behavioural observations, to infer that an individual was a male (Chu and Nieukirk 1988).

***Males observed both as escorts, and not in the role of escorts***: males were identified as escorts when observed accompanying a female with calf and were classified 'with lactating female'. When the same males were observed either within or between seasons in pods with no calves present they were classified as 'not with lactating females'.

***Male maturational status - mature or unknown maturity:*** males were presumed to be socially and sexually mature if the time between first sighting and subsequent resightings exceeded six-years and were therefore classified as 'mature' (Chittleborough 1965, Clapham 1992, Gabriele *et al*. 2007 see Chapter 1.3.1 above for a detailed discussion on age determination at sexual maturity). If the time between first sighting and subsequent resightings of a male was less than six-years they were classified 'maturity unknown'. The rationale in using one to six years to infer immaturity relies on the Chittleborough (1965) and Clapham (1992) results which report humpback whale sexual maturity at an average age of five years in both the northern and southern hemisphere and provides a conservative estimate of age at sexual maturity.

***Female sex identification:*** was determined by either unequivocal observation and or photography of their genital area and the presence of a hemispherical lobe posterior to the genital slit (True 1904, Glockner 1983), or the whale was inferred as female when observed in a constant and close relationship with a calf (Tyack and Whitehead 1983, Clapham *et al*. 1999, Herman *et al*. 2011).

***Females lactating and non-lactating****:* females observed in a constant and close relationship with a calf (Tyack and Whitehead 1983, Clapham *et al*. 1999, Herman *et al*. 2011) were inferred to be lactating. When the same females were observed in other seasons in pods with

no calves present they were classified as ‘non-lactating’. If individual females were observed only in pods in a constant and close relationship with a calf throughout their resighting-histories, they were classified as ‘only lactating’. If individual females were observed only in pods with no calves present throughout their resighting-histories and were sex-identified by genital observation, they were classified as ‘only non-lactating’.

***Females maturational status - mature or unknown maturity:*** females classified as ‘lactating’ were presumed to be both socially and sexually mature and classified as ‘mature’. Females classified as ‘only non-lactating’ were presumed to be socially and sexually mature and classified as ‘mature’ if the time between first sighting and subsequent resightings exceeded six-years (Chittleborough 1955b, 1965; Clapham 1992; Best 2006, 2011: see rationale above). If the time between first sighting and subsequent resightings was less than six-years they were classified as ‘maturity unknown’.

***Known-age whales:*** were individually identified whales first observed as calves or yearlings. Yearlings were identified visually by an experienced observer, to be unambiguously small relative to adults but too large to be calves of the year (Clapham *et al.* 1999, Craig *et al*. 2003).

Known-age whales were classified as male or female from genital observations or classified as sex unknown. They were then further categorised into four age categories: sightings as calves (male, female or unknown sex); sightings as yearlings, (male, female or unknown sex); sightings as 2 to 6 year olds (male, female or unknown sex); and sightings from year seven onwards, 7+ years (male and female). Sightings of known-age individual whales (males, females and unknown sex) first sighted as calves, yearlings, or from 2 to 6 years were categorised at ‘immature’ and sightings of the same whales that exceeded six years, or if they were females observed lactating, were categorised as ‘mature’.

***Peak density:*** is the model-estimated mean day within season of each of the sex, age, reproductive and maturational classes analysed in this study.

### *5.3.3 Statistical analysis*

Analysis and modelling were undertaken on the observations of individually identified humpback whales that, from long-term resighting histories over two or more years, could be assigned to specific sub-classes of sex, age, reproductive category and/or maturational status. Data on the number of observations of the individually identified whales by sex, method of sex-identification, reproductive category and maturational status were reported. Additionally further information on more specific reproductive categories of a sub-set of individually identified females was also provided from adjacent year sightings. This information was not used in analysis or modelling but to inform the discussion of the results of the analysis and modelling of the sub-classes that were analysed.

The data were organised into eight sub-classes of interest for statistical analysis with the response variable of primary interest being day within season of each sighting. Statistics for each sub-class were reported and the observations by sub-class presented graphically.

To further investigate the above results a multilevel linear model, with day within season as the response variable, was fitted to seven of the sub-classes of whales as a fixed factor, and whale and observation of whale as nested random factors. Separate variances were fitted for the seven sub-classes in the random effects part of the model. Estimates were obtained by the Markov Chain Monte Carlo method. The model estimated mean day within season (Peak Density) for each of the seven sub-classes was reported.

To examine the mean day within season between the sub-classes, ten pairwise comparisons were undertaken and the results of the comparison tests between the selected sex, reproductive and maturational classes based on estimated marginal means were reported.

As the likelihood of encountering an individual whale in Hervey Bay may be related to their length of stay, an analysis of residency was also undertaken. The data for analysis of residency were organised as one record per year for each individual whale. Each record included the sex of the individual, whether it was lactating if female, and the dates of the first and last observations within each year the individual was observed. The number of observations, the geometric and arithmetic means and standard deviations of the observed residency times were reported by year and by sex and reproductive state.

A linear mixed effects model was fitted to the natural log of observed residency times with individual and year within individual as random factors, and with year and the sex and reproductive state categories as fixed effects and the estimated geometric means of the distributions of observed residency times of individuals by sex and reproductive state were reported. Data on the extended residency of those females and males spanning ten or more days were also reported.

Finally to inform the discussion of the results of the analysis and modelling of the sex, age, reproductive and maturational sub-classes, data on the long-term resighting histories and social interactions among different sub-classes of three known-age humpback whales were reported.

## 5.4 RESULTS

### *5.4.1 Individually identified whales and observation database*

Of the 578 individually identified whales with known resighting histories, 361 could be assigned to reproductive and known-age classes as described in the definitions above (Table 5.2). The ratio of sex-identified or inferred females to males was 2.94:1 females to males. The 2,131 observations of these whales were the database used in the analysis in this study and are summarised in Table 5.3.

*Table 5.2.* Classification of 361 individually identified humpback whales by sex, reproductive status and known-age, from resighting histories over two or more years

| Classification of individually identified whales | Number |
|---|---|
| (a) Males observed both in the role of escorts, and the same males not in the role of escorts | 77 |
| (b) Females observed lactating and the same females observed non-lactating | 126 |
| (c) Females observed only lactating | 96 |
| (d) Females observed only non-lactating | 30 |
| (e) Known-age whales: first observed as calves or yearlings | |
| I. Males | 12 |
| II. Females | 10 |
| III. Unknown sex | 10 |
| Total number of individually identified whales | 361 |

*Table 5.3.* Number of observations of individually identified whales (a, b, c and d) by sex, and method of sex-identification, reproductive category and maturational status; and known-age whales (e) by maturational status, age-class (i, ii, iii, iv) and sex.

| Class | Category or Sex | Immature | Mature | Maturity unknown | Total Obs |
|---|---|---|---|---|---|
| (a) Males observed as escorts, and the same males observed not in the role of escorts (n=77) | | | | | |
| Males: genital observation | Not with lactating females | 0 | 11 | 12 | 23 |
| Males: inferred | Not with lactating females | 0 | 126 | 98 | 224 |
| Males: genital observation | With lactating females | 0 | 7 | 0 | 7 |
| Males: inferred | With lactating females | 0 | 185 | 0 | 185 |
| Total observations of males | | | 329 | 110 | 439 |
| (b) Females observed lactating and the same females observed non-lactating (n=126) | | | | | |
| Females: genital observation | Lactating | na | 109 | na | 109 |
| Females: inferred | Lactating | na | 490 | na | 490 |
| Females: genital observation | Non-lactating | na | 60 | na | 60 |
| Females: inferred | Non-lactating | na | 203 | na | 203 |
| | Sub-total | na | 862 | na | 862 |
| (c) Females observed only lactating (n=96) | | | | | |
| Females: inferred | Lactating | na | 544 | na | 544 |
| | Sub-total | na | 544 | na | 544 |
| (d) Females observed only non-lactating (n=30) | | | | | |
| Females: genital observation | Non-lactating | na | 2 | 110 | 112 |
| | Sub-total | na | 2 | 110 | 112 |
| Total observations of females | | | 1,408 | 110 | 1,518 |
| (e) Known-age (male female or unknown sex): first observed as calves or yearlings (n=32) | | | | | |
| (i) Calves: | male | 14 | na | na | 14 |
| | female | 12 | na | na | 12 |
| | Unknown sex | 5 | na | na | 5 |
| (ii) Yearlings: | male | 33 | na | na | 33 |
| | female | 20 | na | na | 20 |
| | unknown sex | 9 | na | na | 9 |
| (iii) 2-6 years: | male | 17 | na | na | 17 |
| | female | 14 | na | na | 14 |
| | Unknown sex | 12 | na | na | 12 |
| (iv) 7+ years: | male | na | 23 | na | 23 |
| | female | na | 12 | na | 12 |
| | Unknown sex | na | 3 | na | 3 |
| Total observations of known-age whales | | 136 | 38 | na | 174 |
| Total observations of individually identified whales | | 136 | 1,775 | 220 | 2,131 |

### *5.4.2 Reproductive category of selected females based on long-term resighting histories*

Of the 252 individually identified females in the database, 111 (44.0%) had adjacent year resightings and were able to be assigned to more specific reproductive categories, which are

reported in Table 5.4. These more specific reproductive categories were not used in the statistical analysis and modeling below. The results are used when discussing the reproductive sub-classes of females lactating and non-lactating.

*Table 5.4.* Occurrences of more specific reproductive categories of 111 individually identified females derived from adjacent year resightings. Occurrences means how many times were the reproductive categories observed.

| Class | Specific reproductive category | Whales | Occurrences |
|---|---|---|---|
| (b) Females both lactating and not lactating ($n$ = 126, Table 5.3) | | | |
| | Non-lactating, resting | 16 | 18 |
| | Non-lactating, early pregnant | 36 | 44 |
| | Non-lactating, either resting or early pregnant | 21 | 22 |
| | Lactating and post-partum estrous pregnant | 17 | 26 |
| (c) Females only lactating ($n$ = 96, Table 5.3) | | | |
| | Lactating and post-partum estrous pregnant | 19 | 24 |
| (d) Females only non-lactating ($n$ = 30, Table 5.3) | | | |
| | Non-lactating, either resting or early pregnant | 2 | 2 |
| | Totals | 111 | 136 |

There were 62 occurrences of resting or early pregnant females; 49 (79.0%) in August, 12 (19.3%) in September and 1 (1.6%) in early October. There were 24 occurrences of either resting or early pregnant females; 12 (50.0%) in August, 9 (37.5%) in September and 3 (12.5%) in early October.

There were 50 occurrences of lactating and post-partum pregnant females (i.e. mature females simultaneously lactating and pregnant). Twenty-four individuals had one post-partum pregnant occurrence, 10 had two and, 2 had three. Of the 50 post-partum pregnant occurrences; 39 (78.0%) were observed during September and 11 (22.0%) were observed during October.

### *5.4.3 Statistical analysis*

The database of observations in Table 5.3 were rearranged for statistical analysis (Table 5.5), with the response variable of primary interest being the day within season (Day 1 = August 1 … October 19 = Day 80) of each sighting.

The results and statistics for each sub-class are summarised in Table 5.5 and the observations by day within season of sex, age, reproductive and maturational sub-classes are summarised in Figure 5.1, below.

*Table 5.5.* Sub-class results and statistics

| Sex, age, reproductive and maturational sub-classes | Whales (*n*) | Obs (*n*) | First day | Last day | Median | Mean | SD |
|---|---|---|---|---|---|---|---|
| (a) Males (mature, not with lactating females) | 41 | 137 | 6 | 76 | 50.0 | 49.4 | 14.28 |
| (b) Males (mature, with lactating females) | 73 | 192 | 19 | 77 | 57.0 | 56.7 | 12.32 |
| (c) Males (unknown maturity, not with lactating females) | 41 | 110 | 6 | 76 | 36.0 | 34.3 | 16.55 |
| (d) Females (lactating) | 222 | 1,143 | 13 | 80 | 57.0 | 56.8 | 12.77 |
| (e) Females (non-lactating) | 156 | 375 | 3 | 73 | 24.0 | 26.3 | 13.68 |
| (f) Calves (males and females) | 7 | 31 | 37 | 77 | 67.0 | 64.7 | 10.12 |
| (g) Males, females & unknown (1-6 years) | 32 | 105 | 1 | 62 | 22.0 | 25.3 | 13.84 |
| (h) Males & females (7+ years) | 14 | 38 | 18 | 64 | 51.5 | 45.4 | 14.83 |

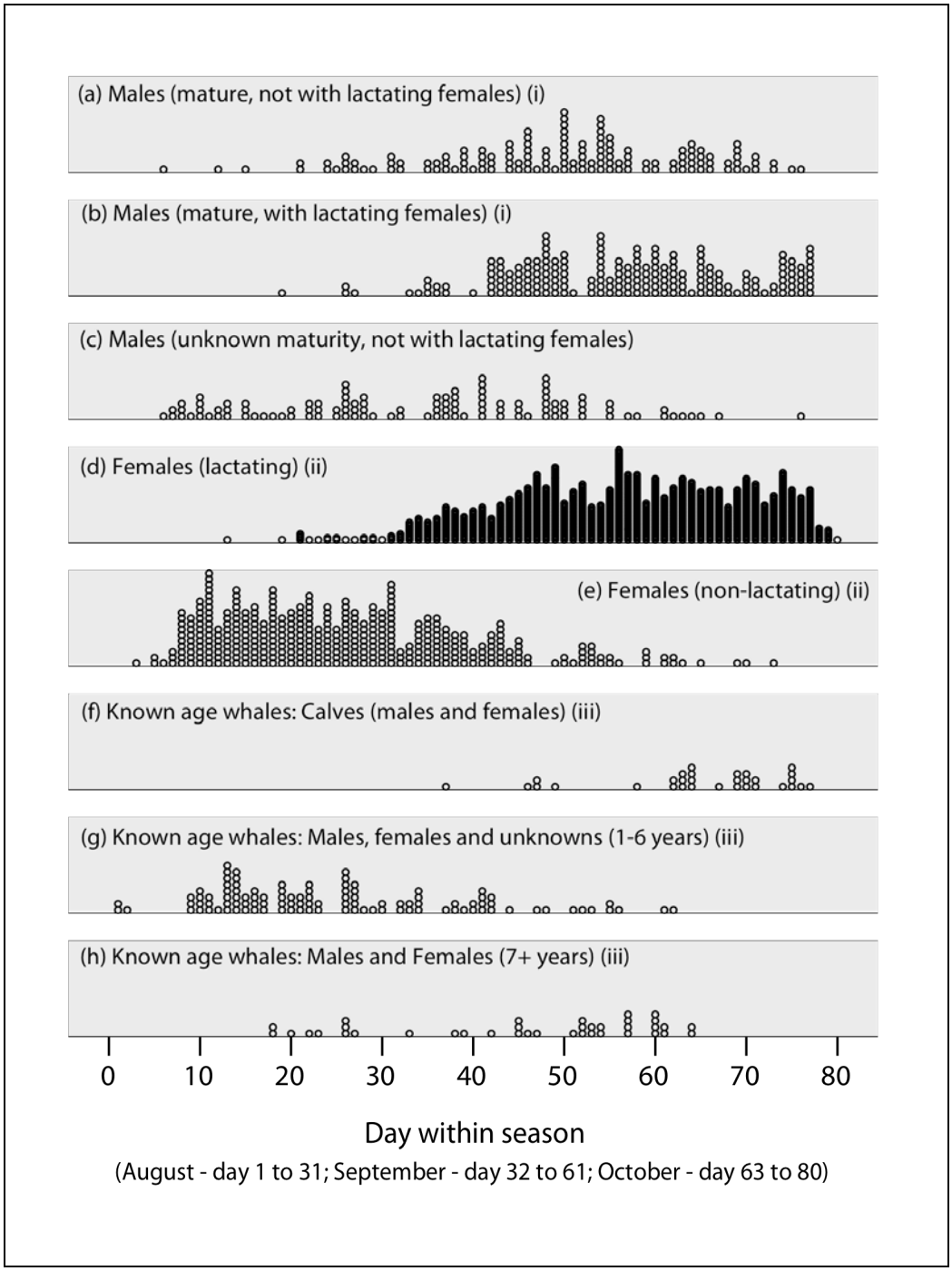


*Figure 5.1.* Observations by day within season, of individually identified whales by sex, age, reproductive and maturational sub-classes: (a) Males (mature, not with lactating females;); (b) Males (mature, with lactating females); (c) Males (unknown maturity, not with lactating females); (d) Females (lactating); (e) Females (non-lactating); (f) Calves (males and females); (g) Males, females and unknown sex (1-6 years) and (h) Males and females (7+ years).

*Note (i)*: In Figure 5.1 above, sub-class (a) and (b) represent observations of the same individually identified males.

*Note (ii)*: Of the individually identified females in sub-class (d) and (e), 126 are individuals that were observed both lactating and non-lactating (see Table 5.3).

*Note (iii)*: Sub-class (f), (g) and (h) represent observations of the same known-age individually identified whales.

Observations of mature males not with lactating females (Fig. 5.1a) were less common during August and peaked during September. As expected, observations of those same males when with lactating females (Fig. 5.1b) occurred mainly in September and early October, with very few observations in August. Males left Hervey Bay approximately 3 to 4 days before the last of the lactating females (Fig 5.1a, 5.1b and 5.1d, Table 5.5). Observations of males of unknown maturity not with lactating females occurred from early August through September and into early October (Fig. 5.1c). The extended observation period of this class suggests that it may be composed of both immature and mature whales. Observations of lactating females (Fig. 5.1d) occurred mainly in September and October and this class of whales was rarely observed in August. Observations of non-lactating females occurred predominantly in August with decreasing observations during September and very few observations in October (Fig. 5.1e). Although there is some temporal overlap of observations of lactating females (Fig. 5.1d) and non-lactating females (Fig. 5.1e) in September and less in October, there is a clear segregation and clumping of these two classes over the season.

The observations presented in Fig. 5.1f, 5.1g and 5.1h are of the same known-age individuals. The data show that calves returned to Hervey Bay as immature whales in August (Fig. 5.1f and 5.1g). Observations of immature whales (Fig. 5.1g) occurred in August and early September coinciding with the presence of the non-lactating females (Fig. 5.1e), whereas

those same immature individual whales when observed as calves, as expected, coincided with the observations of lactating females (Fig. 5.1d and 5.1f). As mature whales (7+ years) they were observed in late August through to late September (Fig. 5.1h).

### *5.4.4 Statistical model*

To further investigate the results presented in Table 5.5 and the patterns illustrated in Figure 5.1 above, a multilevel linear model, with day within season as the response variable, was fitted with the seven sub-classes of whales (calves excluded as necessarily accompanying the lactating females, Figure 5.1d and 5.1f) as a fixed factor, and whale and observation of whale as nested random factors, using MLwiN V2.25 (Rasbash *et al*. 2012). Separate variances were fitted for the seven sub-classes in the random effects part of the model. Estimates were obtained by the Markov Chain Monte Carlo method (MCMC 5,000 iterations burn in, 200,000 iterations monitoring chain length; Browne 2012).

To examine the differences in mean day within season between the sub-classes ten comparisons were planned:

(1) Females (non-lactating) v. females (lactating)

(2) Females (lactating) v. males, females and unknown sex (1-6 years)

(3) Males (mature, not with lactating females) v. females (non-lactating)

(4) Males (mature, with lactating females) v. females (non-lactating)

(5) Males (mature, not with lactating females) v. males (maturity unknown, not with lactating females)

(6) Males (mature, with lactating females) v. males (maturity unknown, not with lactating females)

(7) Males, females and unknown sex (1-6 years) v. males and females (7+ years)

(8) Males (mature, with lactating females) v. females (lactating)

(9) Females (non-lactating) v. males, females and unknown sex (1-6 years of age)

(10) Males (mature, not with lactating females) v. males and females (7+ years).

The first 7 of these comparisons were expected to yield significant mean differences, while the last 3 were not. Tests of significance for the comparisons employed Wald Chi-square tests using 1 degree of freedom (Browne 2012). Each comparison was tested against a Bonferroni-adjusted p-value of 0.005 to yield an overall alpha level of 0.05 for the ten tests.

### *5.4.5 Results of multilevel model*

In the multilevel model for mean day within season, the data were modeled as a sample of observations on each of a sample of whales. There were significant differences between the sex, age, reproductive and maturational classes (Fig. 1). As predicted the first seven planned comparisons were all highly statistically significant and the last three were not (Table 5.7), with the 7 significant tests meeting the Bonferroni-adjusted p-value of 0.005 significance level, while the 3 non-significant tests had $p > 0.106$ unadjusted. The model-estimated mean day within season (peak density of sub-class) are reported in Table 5.6 and the results of the planned comparison tests are reported in Table 5.7.

*Table 5.6.* Model estimated mean day within season (Peak Density) with 95% confidence interval for each class

| Sex, age, reproductive and maturational class | Mean | L95%CI | U95%CI |
|---|---|---|---|
| Males (mature, not with lactating females) | 51.10 | 48.37 | 53.82 |
| Males (mature, with lactating females) | 56.65 | 54.35 | 58.87 |
| Males (unknown maturity, not with lactating females) | 37.54 | 33.62 | 41.47 |
| Females (lactating) | 57.81 | 56.30 | 59.32 |
| Females (non-lactating) | 25.61 | 23.70 | 27.53 |
| Males, females & unknown (1-6 years) | 25.58 | 21.81 | 29.35 |
| Males and females (7+ years) | 45.86 | 40.13 | 51.58 |

*Table 5.7.* Results of the ten planned pairwise comparison tests between selected sexual, reproductive and maturational classes based on estimated marginal means.

| Pairwise comparisons tested | Mean Difference | L95%CI | U95%CI | $\chi_1^2$ | Two tailed *p*-value |
|---|---|---|---|---|---|
| (1) Females (non-lactating) v. Females (lactating) | -32.19 | -34.29 | -30.10 | 904.10 | 0.000 |
| (2) Females (lactating) v. Males, females and unknowns (1-6 years) | 32.23 | 28.17 | 36.29 | 241.83 | 0.000 |
| (3) Males (mature, not with lactating females) v. Females (non-lactating) | 25.48 | 22.15 | 28.82 | 223.92 | 0.000 |
| (4) Males (mature, with lactating females) v. females (non-lactating) | 31.04 | 28.04 | 34.04 | 411.88 | 0.000 |
| (5) Males (mature, not with lactating females) v. Males (maturity unknown, not with lactating females) | 13.55 | 9.45 | 17.65 | 41.97 | 0.000 |
| (6) Males (mature, with lactating females) v. Males (maturity unknown, not with lactating females) | 19.11 | 15.16 | 23.06 | 89.91 | 0.000 |
| (7) Males, females and unknowns (1-6 years) v. Males and females (7+ years) | -20.28 | -25.96 | -14.61 | 49.04 | 0.000 |
| (8) Males (mature, with lactating females) v. Females (lactating) | -1.15 | -3.90 | -1.60 | 0.68 | 0.411 |
| (9) Females (non-lactating) v. Males, females and unknowns (1-6 years) | .04 | -4.19 | 4.26 | 0 | 1.000 |
| (10) Males (mature, not with lactating females) v. Males and females (7+ years) | 5.24 | -1.11 | 11.58 | 2.62 | 0.106 |

The data presented in Figure 5.1 indicate that males (mature with lactating females) (Fig. 5.1b) leave the bay earlier than the females in the final week of the season.

### *5.4.6 Analysis of residency*

As the likelihood of encountering an individual whale in Hervey Bay may be related to their length of stay, an analysis of residency was undertaken. The data for analysis of residency were organised as one record per year for each individual whale. Each record included the sex of the individual, whether it was lactating if female, and the dates of the first and last observations within each year the individual was observed. Because there were fewer observations in the years 1992 to 1995, the 1,098 observations from 1996 to 2009 were the data selected for analysis of residency.

The distribution of observed residency times by observation (last date sighted – first date sighted + 1) included many 1-day intervals (66.5%) and was extremely right skewed. These data were transformed to their natural logarithms for further analysis. While the distribution of log intervals also included 66.5% of zero values and remained right-skewed, the distribution of residuals from the fitted model was much more symmetric, and with 1,098 observation values was considered as indicating that a normal model for the sampling distribution of the log values was appropriate. Back-transformation of an estimated mean log value yields an estimate of the geometric mean. As a descriptive statistic for a skewed distribution, the geometric mean is less influenced by extreme values than the arithmetic mean and closer to the median, and is a more ‘reasonable’ indicator of the location (central tendency) of the distribution.

The number of observations, the geometric and arithmetic means and standard deviations of the observed residency times are reported by year in Table 5.8, and by sex and reproductive state in Table 5.9. A trend of reduction over years was observed in the geometric means of

observed residency times summarized in Table 5.8, and Table 5.9 shows the geometric means reducing in the order, females lactating, males and females not lactating.

*Table 5.8.* Number of observations of individuals (N) per year, and the geometric and arithmetic means and standard deviations of observed residency times (Days)

| Year | N | Geometric Mean | Mean | Std. Deviation |
|---|---|---|---|---|
| 1996 | 35 | 2.20 | 4.26 | 5.420 |
| 1997 | 55 | 2.14 | 3.71 | 6.379 |
| 1998 | 82 | 2.10 | 3.95 | 5.715 |
| 1999 | 78 | 1.47 | 1.97 | 2.156 |
| 2000 | 74 | 1.80 | 3.12 | 4.370 |
| 2001 | 85 | 2.15 | 4.36 | 6.654 |
| 2002 | 98 | 1.89 | 3.92 | 7.577 |
| 2003 | 87 | 1.65 | 3.06 | 4.996 |
| 2004 | 97 | 2.03 | 4.05 | 6.184 |
| 2005 | 88 | 1.62 | 2.55 | 3.273 |
| 2006 | 76 | 1.44 | 2.25 | 3.250 |
| 2007 | 81 | 1.54 | 2.20 | 2.581 |
| 2008 | 92 | 1.25 | 1.55 | 2.221 |
| 2009 | 70 | 1.53 | 2.67 | 4.406 |
| Total | 1,098 | 1.73 | 3.08 | 5.020 |

*Table 5.9.* Number of observations of individuals (N) by sex and reproductive state, and the geometric and arithmetic means and standard deviations of observed residency times (Days)

| Sex and reproductive state | N | Geometric Mean | Mean | Std. Deviation |
|---|---|---|---|---|
| Females, not lactating | 265 | 1.29 | 1.63 | 1.824 |
| Females, lactating | 543 | 2.02 | 3.47 | 4.452 |
| Males | 290 | 1.67 | 3.66 | 7.271 |
| Total | 1,098 | 1.73 | 3.08 | 5.020 |

### 5.4.7 Statistical model of observed residency

A linear mixed effects model was fitted to the natural log of observed residency times with individual and year within individual as random factors, and with year and the sex and reproductive state categories as fixed effects. The model was initially fitted with year (1996-2009) as a categorical variable and subsequently as a linear function of the year number (1-

14) as a continuous variable. The Satterthwaite (1946) method was employed to adjust the degrees of freedom for the F tests of fixed effects, and the Bonferroni (see Abdi 2007) method was used to adjust for multiple pairwise comparison tests.

A plot of the estimated log observed residency times by year (1996-2009; not shown) displayed a quite linear declining trend and we report the model with year fitted as a linear function of the year number (1-14). Tests of the fixed effects found both year number ($F = 32.24$, $df = 1, 1093.7$, $p < 0.001$) and the sex and reproductive state categories ($F = 29.35$, $df = 2, 587.93$, $p < 0.001$) to be significant predictors. Bonferroni-adjusted multiple pairwise comparison tests found the lactating female class mean to be significantly greater than both the non-lactating female class mean ($p<0.001$) and the male class mean ($p=0.011$), and the male class mean to be significantly greater than the non-lactating female class mean ($p<0.001$).

The coefficient for year number showed a reduction of 0.04 (SE = 0.007) log observed residency time per year. The estimated mean log observed residency times (SE) for the sex and reproductive categories at year 5 (2000) were: 0.469 (0.069) days for non-lactating females, 0.981 (0.067) days for lactating females and 0.777 (0.075) days for males. Back-transformation yielded estimated geometric means of the distributions of observed residency times of individuals in 1996, 2000 and 2009 and are reported in Table 5.10.

*Table 5.10.* Estimated geometric means of the distributions of observed residency times of individuals.

| Sex and reproductive state / year | 1996 | 2000 | 2009 |
|---|---|---|---|
| Females, not lactating | 1.88 | 1.60 | 1.11 |
| Females, lactating | 3.13 | 2.67 | 1.86 |
| Males | 2.56 | 2.18 | 1.51 |

The trend over years was estimated as a linear function on the log days scale and consequently displays a regular form. The estimates presented in Table 5.10 are provided to show the estimated residency times on the natural scale (days) for the beginning, middle and end of the continuous function for each of the three classes; females not lactating, female, lactating, and males.

### *5.4.8 Extended residency*

Of the 361 resighted individual whales, there were 50 cases of extended residency observed that spanned 10 or more days. Twenty-five of these were females with calf, 3 were females without calf, and 22 were males. The sightings, including the span in days from the first day sighted to the last day sighted, and the longest interval in days between any two sightings, are summarised in Tables 5.11 and 5.12.

*Table 5.11.* Females with sightings spanning ten or more days

| UID | Sex | Year | No of days sighted | First sighting | Last sighting | Span from first to last sighting (Days) | Longest Interval between two sightings (Days) |
|---|---|---|---|---|---|---|---|
| 221 | Female | 2003 | 2 | 21/08/03 | 07/09/03 | 18 | 16 |
| 337 | Female | 1998 | 2 | 21/08/98 | 30/08/98 | 10 | 8 |
| 871 | Female | 2001 | 2 | 07/09/01 | 16/09/01 | 10 | 8 |
| 7 | Female/calf | 1998 | 6 | 16/09/98 | 25/09/98 | 10 | 3 |
| 7 | Female/calf | 2003 | 3 | 25/09/03 | 16/10/03 | 22 | 19 |
| 7 | Female/calf | 2006 | 4 | 15/09/06 | 24/09/06 | 10 | 3 |
| 157 | Female/calf | 2007 | 4 | 16/09/07 | 25/09/07 | 10 | 4 |
| 160 | Female/calf | 1996 | 4 | 16/09/96 | 02/10/96 | 17 | 13 |
| 160 | Female/calf | 2003 | 2 | 28/09/03 | 12/10/03 | 15 | 12 |
| 277 | Female/calf | 2005 | 2 | 07/09/05 | 19/09/05 | 13 | 11 |
| 279 | Female/calf | 1997 | 3 | 30/09/97 | 16/10/97 | 17 | 14 |
| 292 | Female/calf | 2005 | 4 | 23/08/05 | 02/09/05 | 11 | 4 |
| 362 | Female/calf | 2004 | 2 | 17/09/04 | 28/09/04 | 12 | 10 |
| 394 | Female/calf | 2001 | 3 | 09/09/01 | 23/09/01 | 15 | 11 |
| 396 | Female/calf | 2000 | 2 | 15/09/00 | 26/09/00 | 12 | 10 |
| 414 | Female/calf | 1998 | 4 | 24/09/98 | 08/10/98 | 15 | 10 |
| 425 | Female/calf | 2000 | 3 | 11/09/00 | 25/09/00 | 15 | 10 |
| 425 | Female/calf | 2004 | 3 | 16/09/04 | 27/09/04 | 12 | 5 |
| 440 | Female/calf | 2004 | 5 | 24/09/04 | 04/10/04 | 11 | 4 |
| 573 | Female/calf | 2001 | 7 | 10/09/01 | 26/09/01 | 17 | 7 |
| 633 | Female/calf | 2007 | 5 | 09/09/07 | 20/09/07 | 12 | 6 |
| 654 | Female/calf | 2006 | 4 | 03/10/06 | 12/10/06 | 10 | 5 |
| 879 | Female/calf | 2001 | 2 | 19/09/01 | 02/10/01 | 14 | 12 |
| 998 | Female/calf | 2002 | 4 | 27/08/02 | 10/09/02 | 15 | 6 |
| 1101 | Female/calf | 2006 | 7 | 14/09/06 | 29/09/06 | 16 | 4 |
| 1101 | Female/calf | 2008 | 2 | 10/09/08 | 30/09/08 | 21 | 19 |
| 1105 | Female/calf | 2002 | 2 | 24/09/02 | 04/10/02 | 11 | 9 |
| 1272 | Female/calf | 2003 | 2 | 05/09/03 | 15/09/03 | 11 | 9 |

The range of the time period between first and last day of sighting for females in Hervey Bay was 10 to 22 days and the range of the longest interval between any two sightings was 3 to 19 days. The median span from the first to the last sighting of females was 12.5 days (Mean 13.6, Median 12.5, SD = 3.4) while the median interval between any two sightings was 9 days (Mean 9.0, Median 9.0, SD = 4.5).

*Table 5.12.* Males with sightings spanning ten or more days

| UID | Sex | Year | No of days sighted | First sighting | Last sighting | Span from first to last sighting (Days) | Longest Interval between two sightings (Days) |
|---|---|---|---|---|---|---|---|
| 40 | Male | 1997 | 3 | 10/08/97 | 21/09/97 | 43 | 37 |
| 43 | Male | 2003 | 3 | 11/09/03 | 23/09/03 | 13 | 10 |
| 471 | Male | 2005 | 5 | 12/09/05 | 25/09/05 | 14 | 6 |
| 74 | Male | 1998 | 2 | 26/08/98 | 04/09/98 | 10 | 8 |
| 106 | Male | 2001 | 8 | 12/09/01 | 09/10/01 | 28 | 8 |
| 161 | Male | 1996 | 4 | 16/09/96 | 02/10/96 | 17 | 12 |
| 161 | Male | 2004 | 4 | 21/09/04 | 03/10/04 | 13 | 6 |
| 175 | Male | 1997 | 2 | 05/08/97 | 08/09/97 | 35 | 33 |
| 228 | Male | 1997 | 3 | 13/08/97 | 03/09/97 | 22 | 18 |
| 352 | Male | 2005 | 3 | 31/08/05 | 15/09/05 | 16 | 13 |
| 420 | Male | 1998 | 3 | 07/09/98 | 05/10/98 | 29 | 20 |
| 531 | Male | 2001 | 2 | 10/09/01 | 21/09/01 | 12 | 10 |
| 586 | Male | 2001 | 7 | 31/08/01 | 25/09/01 | 26 | 9 |
| 586 | Male | 2002 | 9 | 15/08/02 | 04/10/02 | 51 | 25 |
| 586 | Male | 2004 | 2 | 26/08/04 | 13/09/04 | 19 | 17 |
| 701 | Male | 2000 | 2 | 15/09/00 | 03/10/00 | 19 | 17 |
| 715 | Male | 2001 | 6 | 05/09/01 | 30/09/01 | 26 | 12 |
| 715 | Male | 2009 | 4 | 17/09/09 | 01/10/09 | 15 | 11 |
| 825 | Male | 2002 | 2 | 12/08/02 | 05/09/02 | 25 | 23 |
| 882 | Male | 2002 | 5 | 13/08/02 | 24/09/02 | 43 | 23 |
| 916 | Male | 2004 | 2 | 17/09/04 | 15/10/04 | 29 | 27 |
| 1314 | Male | 2004 | 3 | 14/09/04 | 05/10/04 | 22 | 18 |

The range of the time period between first and last day of sighting for males was 10 to 51 days and the range of the longest interval between any two sightings was from 6 to 37 days. The median span from first to last sighting of males was 22 days (Mean 24.0, Median 22.0, SD = 11.1) while the median longest interval between any two sightings was 15 days (Mean 16.5, Median 15.0, SD = 8.7).

### *5.4.9 Timing and changes in maturational and reproductive status of known-age whales*

To illustrate the timing and changes in maturational and reproductive status of known-age whales (Table 5.3e; Figure 5.1f, g and h) and the type of social interactions with other classes of whales (Fig. 5.1) in which they were engaged, the resighting history of a known-age male from a calf to an eleven year old, UID-176; a known-age female from a calf to a six year old, UID-1193, and a known-age female from a yearling to a seven year old, UID-1100, are summarised in Tables 5.13 and 5.14.

*Table 5.13.* Timing and changes of maturational and reproductive status of known-age male: observation number (Obs), date of sighting, age, number of pods, pod size, number of calves present, number of known females present, behavior in pod, pod composition and notes, with times in brackets.

| Obs | Date | Age | Pods | Size | Calves | Females | Behavior [1] | Pod composition and notes (time) |
|---|---|---|---|---|---|---|---|---|
| Known age male (Universal-id: 176. Mnemonic name: 'Floppy', from calf to eleven year old) | | | | | | | | |
| 1 | 16-Sep-96 | Calf | 4 | 8 | 4 | 4 | Other | Alone with mother (0850), then associated with three mother-calves. |
| 2 | 16-Sep-96 | Calf | 2 | 4 | 2 | 2 | Other | Alone with mother (1020), then associated with one mother-calf. |
| 3 | 18-Sep-96 | Calf | 1 | 2 | 1 | 1 | Other | Alone with mother (1120). |
| 4, 5 | 1-Oct-96 | Calf | 1 | 2 | 1 | 1 | Other | Alone with mother (1120); Alone with mother (1400). |
| 6, 7 | 2-Oct-96 | Calf | 1 | 2 | 1 | 1 | Other | Alone with mother (0600); Alone with mother (0700). |
| 8 | 2-Oct-96 | Calf | 3 | 6 | 3 | 3 | Other | Alone with mother (1545) then associated with two mother-calves. |
| 9, 10 | 26-Aug-97 | Yearling | 1 | 3 | 0 | 0 | Other | With two immatures (0745); With same two immatures (0900). |
| 11 | 26-Aug-97 | Yearling | 2 | 5 | 0 | 2 | Non-agonistic social | With previous two immatures (1025), then a pair associated, one a known mother (non-lactating) and one female yearling. |
| 12 | 26-Aug-97 | Yearling | 3 | 7 | 0 | 1 | Non-agonistic social | With two immatures (one a female) then associated with three matures and a further singleton male yearling (1230). |
| 13 | 26-Aug-97 | Yearling | 2 | 5 | 0 | 0 | Other | With two immatures (1500), then associated with two more immatures. |
| 14 | 19-Aug-99 | Three | 2 | 3 | 0 | 2 | Non-agonistic social | With female yearling (1001) then with another female yearling (1018). |
| 15 | 21-Aug-01 | Five | 3 | 6 | 0 | 0 | Competitive group | In competitive group (0922), then paired off with known female. |
| 16 | 21-Aug-01 | Five | 3 | 4 | 1 | 0 | Non-agonistic social | With previous known female (1115) then two singletons associated. |
| 17 | 23-Aug-01 | Five | 3 | 4 | 0 | 0 | Competitive group | In a pair, then two singletons associated (1516). |
| 18 | 23-Aug-02 | Six | 2 | 4 | 0 | 0 | Competitive group | In a pair (1048), joined another pair then split into two pairs again. |
| 19 | 29-Sep-03 | Seven | 1 | 4 | 1 | 1 | Other | With mother-calf and mature escort - disassociated from mother-calf and escort, when mother went into feeding pattern. |
| 20 | 29-Sep-03 | Seven | 3 | 7 | 1 | 1 | Competitive group | With mother-calf and two escorts (1025), then two singletons associated. |
| 21 | 29-Sep-03 | Seven | 3 | 6 | 1 | 1 | Other | Singleton (1109) joined with mature pair, then a mother-calf, escort. |
| 22 | 29-Sep-03 | Seven | 2 | 2 | 0 | 0 | Other | Singleton (1435) associated with another singleton. |
| 23 | 21-Sep-04 | Eight | 2 | 4 | 1 | 0 | Other (Singing) | Singleton singing (1115) joined with a mother-calf and yearling escort. |
| 24 | 23-Sep-04 | Eight | 2 | 6 | 2 | 2 | Other | Escort to mother-calf (1022), a further mother-calf, escort associated. |
| 25,26 | 26-Sep-04 | Eight | 1 | 4 | 1 | 1 | Other | Escort to known mother ('Aime', UID 422) with calf and an immature escort (1155); second resighting same group (1204). |
| 27 | 3-Oct-04 | Eight | 3 | 5 | 1 | 1 | Competitive group | Singleton then on periphery of a mother-calf, and two escorts (1050). |
| 28,29 | 18-Aug-05 | Nine | 1 | 2 | 0 | 1 | Non-agonistic social | In pair with mature female (0940); with same female (1540). |
| 30 | 11-Sep-06 | Ten | 2 | 2 | 0 | 0 | Other (Singing) | Singleton singing (0730), then joined with another singleton. |
| 31 | 14-Sep-06 | Ten | 2 | 4 | 1 | 1 | Non-agonistic social | Initially in pair with an immature (1003) and continually pectoral slapping with both pectoral fins, a mother with calf then joined the pair. |
| 32 | 14-Sep-06 | Ten | 1 | 3 | 1 | 1 | Non-agonistic social | Still escort to previous mother and calf (1130), and still pectoral slapping. |
| 33 | 23-Sep-07 | Eleven | 1 | 4 | 1 | 1 | Non-agonistic social | Escort to known mother ('Aime', UID 422) with calf and pectoral-slapping yearling escort (1553) positioned, between mother and yearling escort. |

[1] See Chapter 4 for report on social behavior in Hervey Bay

***Maturational status: male UID-176 (Calf)***

The male (catalogue number UID-176) was resighted on eight occasions as a calf during September and October. On five of these resightings he was alone with his mother. The other three resightings involved associations with multiple mother-calf pods (Table 5.13). The timings are consistent with the presence of lactating females in Hervey Bay (Fig. 5.1d).

***Maturational status: male UID-176 (1-6 years)***

As an immature male UID-176 was observed in mid- to late-August associating with numerous immature and mature whales over a period ranging from a yearling to three years old, and was involved in non-agonistic social behaviour pods. At the age of five and six, male UID-176 was resighted in three competitive groups and one non-agonistic social behaviour pod (Table 5.13).

***Maturational status: male UID-176 (7+ years)***

As a seven and eight year old, UID-176 returned to Hervey Bay in late September predominantly in pods with calves present and was only resighted in two competitive groups as a secondary escort. He displayed no aggressive behaviour towards the presence of immature escorts in mother-calf pods. He was heard singing as an eight year old.

In 2005 as a nine year old, UID-176 was resighted in Hervey Bay in mid-August and was observed on two occasions in the company of the same mature female in non-agonistic social behaviour pods. As a ten and eleven year old, he was again observed in the bay in mid-September in pods with a calf present. In the last observation of UID-176 as an eleven-year old in 2007, he was observed escorting the same known mother UID-422 with a new calf, that he had been an escort to as an eight year old in 2004 (Table 5.13).

*Table 5.14.* Timing and changes of maturational and reproductive status of known-age females: observation number (Obs), date of sighting, age, number of pods, pod size, number of calves present, number of known females present, behavior in pod, pod composition and notes, with times in brackets.

| Obs | Date | Age | Pods | Size | Calves | Females | Behavior[1] | Pod composition and notes (time) |
|---|---|---|---|---|---|---|---|---|
| Known age female (Universal-ID: 1193. Mnemonic name: 'Hodda', from calf to seven year old) | | | | | | | | |
| 1 | 9-Oct-02 | Calf | 1 | 2 | 1 | 1 | Other | Alone with mother (1130). |
| 2 | 9-Oct-02 | Calf | 1 | 2 | 1 | 1 | Other | Alone with mother (1308). |
| 3 | 10-Oct-02 | Calf | 1 | 2 | 1 | 1 | Other | Alone with mother (1544). |
| 4 | 15-Oct-02 | Calf | 1 | 3 | 1 | 1 | Other | Calf and mother with escort (0916). |
| 5 | 16-Oct-02 | Calf | 1 | 2 | 1 | 1 | Other | Alone with mother (1058). |
| 6 | 27-Aug-03 | Yearling | 1 | 3 | 0 | 1 | Other | With two mature whales. |
| 7 | 9-Aug-04 | Two | 2 | 5 | 0 | 1 | Non-agonistic social | With a yearling and a mature whale, then associated with two matures. |
| 8 | 23-Aug-06 | Four | 3 | 4 | 0 | 1 | Other | In a pair with an immature, which disassociated. Then a singer/joiner pair associated. |
| 9 | 26-Aug-08 | Six | 2 | 11 | 0 | 2 | Non-agonistic social | In a pod of four with two matures and one immature (0805), which associated with a pod of seven matures (0818). |
| 10 | 26-Aug-08 | Six | 1 | 5 | 0 | 1 | Other | In a pod of five with four matures (1134). |
| 11 | 26-Aug-08 | Six | 1 | 11 | 0 | 1 | Non-agonistic social | In a pod of eleven matures (1409). |
| 12 | 27-Aug-08 | Six | 2 | 5 | 0 | 1 | Other | In a pod of three with one mature and one immature, which associated with a pair of immatures (1308). |
| Known age female (Universal-ID: 1100. Mnemonic name: 'Klina', from yearling to seven year old) | | | | | | | | |
| 1 | 3-Sep-02 | Yearling | 2 | 3 | 0 | 1 | Non-agonistic social | Initially a singleton (0757) pectoral slapping and rolling over belly up, then associated with a mature pair. |
| 2 | 3-Sep-02 | Yearling | 1 | 2 | 0 | 1 | Non-agonistic social | In pair with a mature whale (1022). |
| 3 | 3-Sep-02 | Yearling | 1 | 5 | 0 | 1 | Non-agonistic social | With another immature and two matures (1150). |
| 4 | 10-Aug-03 | Two | 1 | 3 | 0 | 2 | Non-agonistic social | With two matures (1355) one was a known mature female observed with calf in 2004. |
| 5 | 11-Aug-03 | Two | 1 | 4 | 0 | 2 | Non-agonistic social | With one mature female and two immatures (0730). |
| 6 | 27-Aug-04 | Three | 1 | 5 | 0 | 1 | Non-agonistic social | With four matures (0815) unknown gender. |
| 7 | 25-Sep-06 | Five | 2 | 3 | 1 | 1 | Other | Initially alone with her calf (1032) a yearling associated, then later repulsed after performing a strong side-lobtail near the calf. |
| 8 | 26-Sep-08 | Seven | 1 | 2 | 1 | 1 | Other | Alone with her calf (0651). |
| 9 | 26-Sep-08 | Seven | 2 | 4 | 2 | 2 | Other | Associated with another mother and calf. |

1 See Chapter 4 for report on social behavior in Hervey Bay

***Maturational status: female UID-1193 (Calf)***

The female UID-1193 was resighted in October on five occasions as a calf. On four of these resightings she was alone with her mother and on one resighting a single escort was present (Table 5.14).

***Maturational status: female UID-1193 (1-6 years)***

As a yearling to two year old, UID-1193 was resighted on two occasions during August associating with immature and mature whales and involved in one non-agonistic social behaviour pod. From the age of four to six years, UID-1193 was resighted on five occasions in late August, associating with mature whales.

***Maturational and reproductive status: female UID-1100 (1-6 years & 7+ years)***

Female UID 1100 as a yearling to three year old was resighted on six occasions from early August to early September associating with immature and mature whales in non-agonistic social behaviour pods (Table 5.14). However, at the age of five years old UID-1100 was resighted in late September initially alone with a new calf and then with a yearling escort, which she later repulsed. Finally as a seven-year old UID-1100, was resighted once again with a new calf. She was initially alone with her calf and later associated with another mother-calf pair (Table 5.14).

## 5.5 DISCUSSION

### *5.5.1 Temporal segregation: a stable inherent feature of migrating humpback whales*

In this study using individually identified live whales temporal segregation in Hervey Bay was found to be consistent with the temporal segregation pattern reported by Dawbin (1996, 1997) utilising whaling data. Non-lactating females, either resting or newly pregnant, were

first to arrive accompanied by immature males and females. Mature males followed about 10 days later preceding the arrival of mature lactating females by about 6 days. The interval in Hervey Bay, between non-lactating females leading the migration and lactating females at the end of the migration was 32.2 days (Table 5.7 above). Dawbin (1966, 1997) reported that, except for females who changed their timing in the migration related to their reproductive status, there were no significant differences in the timing and temporal segregation of the different sex, age, reproductive and maturational classes in each of the breeding areas and at the localities in his study, based on samples from the early 1930s to the early 1960s. On the southbound migration Dawbin (1966, 1997) reported that the first class of humpback whales to travel south were resting and newly pregnant females together with immature males and females, who preceded mature males by about 10 days. Mothers with calves followed these classes 6 days later and the interval between the passage of non-lactating females and lactating females was hypothesised to be approximately one month.

The southbound data on temporal segregation presented in Dawbin (1966, Fig 4, p.158) involved a very small and biased sample (1,881 whales) compared to the northbound data (22,275 whales) (Fig. 5.5.1.1). Dawbin reported that the southbound data were difficult to interpret, because there were no southward whaling data from Cook Strait; that eastern Australian whaling operations had already filled their quotas and ceased operations before the beginning of the southward migration; and that there were a lack of data on the direction of travel of overlapping late northward and early southward migrating whales. Dawbin also reported from the uncorrected catch data, that during the southward migration mixed females occur first, followed by immature whales, mature males and females in early lactation 3, 13, and 19 days later respectively (Fig. 5.5.1.1), and suggested for the above reasons that these intervals should be increased. Furthermore, Dawbin (1966) hypothesised that “If the true interval before the arrival of immature whales is of the same order as for the northbound

whales (twelve days), then there is close agreement between the timing southward and the timing northward, and the interval between the passage of mixed and pregnant females and that of lactating females is approximately one month." The evidence presented from the sample analysed in this study (361 whales, Table 5 and 6) confirms Dawbin's hypothesis that the interval between the southbound categories of mature mixed females and lactating females is approximately one month (Figure 5.5.1.1).

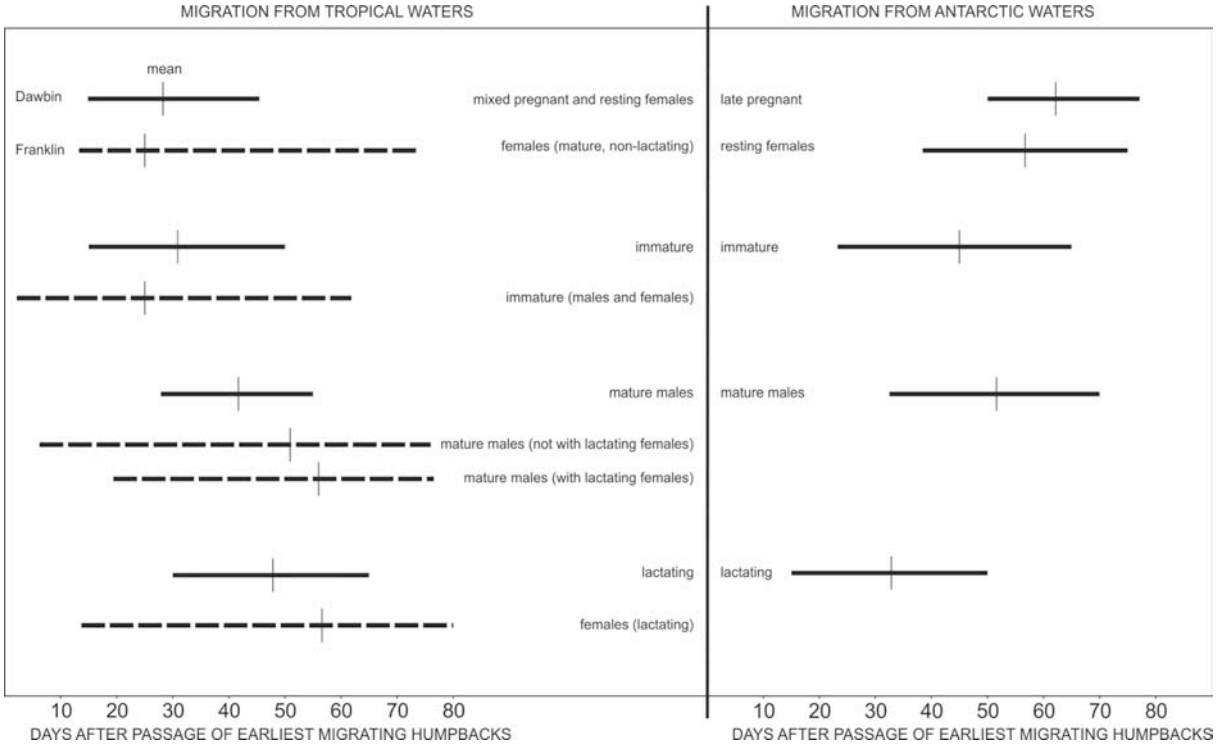


*Figure 5.5.1.1* Temporal segregation of specified categories of humpback whales from Dawbin (1966, Fig 4, p 158) and Franklin (Table 5.5 and 5.6 above). Migration from tropical waters (left) and from Antarctic waters (right) by days after passage of earliest migrating humpback whales, showing mean value for each category.

In 1963, when the IWC declared complete protection for Southern Ocean humpback whales, it was estimated that there may have been fewer than 100 survivors in the eastern Australian population (Paterson *et al*. 1994). During the thirty years from 1962 to 1992, the eastern

Australian humpback whale population was estimated to have increased to only 1,900 whales (95% CI, 1,650-2,150, Paterson *et al.* 1994). By 2005 the population was estimated to have increased to just over 7,000 humpback whales (Noad *et al*. 2006, Paton *et al*. 2011). Using a growth rate of 10.6% per annum (Noad *et al*. 2006), it is estimated that by 2009 the eastern Australian humpback whale population may have increased to approximately 10,500 humpback whales. Thus, following a period of intensive and rapid depletion during the 1930s to the 1960s and after approximately forty-seven years of partial recovery, the population continues to exhibit the migratory temporal segregation intervals as reported by Dawbin. Consequently, the timing and segregation of the age, sex, reproductive and maturational classes of humpback whales during the annual migrations may result from underlying evolutionary pressures and are likely to be an inherent and constant feature of the social organisation of humpback whales.

### *5.5.2 Reproductive status of mature females changes early in the southern migration*

In this study observations of mature non-lactating females in Hervey Bay predominantly occurred during August, with fewer observations in September and very few in early October (Table 5.5 and Fig. 5.1e). The peak density of this class occurred in late August (day within season 25.6, Table 5.6). Long-term adjacent year resightings of known individual females revealed that there were some newly pregnant and resting females among the mature non-lactating females (Table 5.4). Consequently a proportion of the previously northbound late-lactating females changed reproductive status, becoming the newly pregnant and resting females among the mature non-lactating females at the vanguard of the southern migration

Dawbin (1997) had difficulty determining the timing and reproductive status (resting or newly pregnant) of mature females early in the southern migration because of sampling limitations. He reported that most of the Southern Hemisphere shore-based commercial whaling was

concentrated on northbound whales, also that it was difficult to distinguish between northbound and southbound females during the cross-over period in August and that detection of early small foetuses was hindered by the brief examination time available at many shore stations.

Craig *et al*. (2003) questioned the classification of resting females in Dawbin (1997) and suggested that many of the mature females classified as 'resting' were likely to be newly pregnant females. Chittleborough (1954) and Nishiwaki (1959) considered 'resting' to be a temporary condition preceding ovulation. Chittleborough (1954) further reported that during June on the northern migration off western Australia, 70% of mature females with ovaries in a resting state were in the late stages of lactation, and by mid-July the proportion of resting females ready to ovulate reached a maximum, with a secondary increase in early August.

### *5.5.3 Immature males and females travel in the company of mature non-lactating females*

In this study, immature males and females observed from 1 to 6 years old were predominantly observed during August, with fewer observed during September and very few observed in early October (Figure 5.1g) with the peak density occurring in late August (day within season 25.6, Table 5.6). There were no significant differences in the mean day of observations within season (peak density) of immature males and females compared to mature non-lactating females (Tables 5.6 and 5.7; Fig. 5.1e and 5.1g).

Franklin *et al*. (2011) reported significant differences in pod characteristics during August in Hervey Bay compared to later in the season. Pairs were the predominant pod size early in the season with the highest proportion of singletons occurring throughout August. There was a significantly higher rate of pod associations during August in Hervey Bay, with significantly more non-agonistic social behaviour occurring throughout August compared with later in the

season (see Chapter 4 above). Pods with calves present were rarely sighted during August and both the pod characteristics and behaviour of humpback whales in Hervey Bay were consistent with the presence of immature males and females early in August and mature males and females in late August (Franklin *et al*. 2011, Chapter 4 above). The data presented in this study suggests that immature males and females while migrating through Hervey Bay are embedded among a phalanx of mature non-lactating females, which is clearly illustrated in the resighting histories of a known age male and two known age females presented in Tables 5.13 and 5.14 above. These immature whales are interacting not only with immature male and female whales but are also interacting with mature non-lactating females during their concurrent passage through Hervey Bay mainly in August and some in early September (Fig. 5.1 and Table 5.7).

### *5.5.4 Migratory timing of known-age individuals varies with changes in maturational and reproductive status*

Male and female humpback whales may reach sexual and social maturity as early as five years (Clapham 1992), although a recent study suggests it could be ten or more years in some populations (Gabriele *et al.* 2007, Best 2011). The reproductive success of long-lived mammals normally occurs over many breeding seasons and therefore individual male humpback whales may behave to maximise their reproductive success over their lifetime (Clapham 1996, Boness *et al*. 2002). Clapham (1992) suggested that many male humpback whales may not be able to reproduce until they are large enough or experienced enough to successfully compete with other males.

The social interactions and timing of observations of male UID-176 (Table 5.13) are consistent with the temporal segregation of maturational and reproductive classes reported by

Dawbin (1997) and with the results presented in this study. As a calf, (UID-176) was resighted in Hervey Bay over a period of sixteen days, from mid-September until the beginning of October. From a yearling to six year old he was observed in the bay during August among and interacting with immature and mature whales, and as a seven, eight, ten and eleven year old he was observed in the bay in September among and interacting with lactating females. As a nine year old he was present in the bay in mid-August with a mature female. Up to the age of eleven years there was no evidence of male UID-176 participating in competitive groups as a primary escort or as a challenging escort. The resighting history of male UID-176 (Table 5.13) is consistent with Clapham's (1992) suggestion that male humpback whales require time and experience before successfully competing with other mature males.

The resighting histories of females UID-1193 and UID-1100 are also consistent with the timing and segregation of classes presented in this study (Fig. 5.1). As a calf female UID-1193 was resighted in Hervey Bay over a period of eight days from the 9$^{th}$ to the 16$^{th}$ of October among lactating females. On four of the five resightings in October, she was alone with her mother. From a yearling to a six year old she was resighted in Hervey Bay on seven occasions during August interacting with immature and mature whales predominantly in larger non-agonistic social behaviour pods (Table 5.14)

As a yearling to a three-year old female UID-1100 was also observed in Hervey Bay among and interacting with immature and mature whales in August, and was predominantly involved in larger non-agonistic social behaviour pods. In contrast to UID-1193, at the age of five and seven years UID-1100 was observed with a new calf in each year, among and associating with lactating females in late-September (Table 5.13). The transition of UID-1100 from an immature to a mature lactating female is consistent with the timing and segregation of lactating females entering Hervey Bay during September and October.

### *5.5.5 Migratory timing of mature males allows for the changes in the reproductive status of mature females*

In this study there were very few observations of known mature males during August with the main concentrations of mature males occurring in September and October. The peak density of known mature males not with lactating females was in mid-September (day within season 51.1, Table 5.6 and Fig. 5.1a) and the peak density of the same known mature males with lactating females was in late-September (day within season 56.7, Table 5.6 and Fig. 5.1b).

Dawbin (1997) reported that mature males commence their northern migration an average of 20 days after the late-lactating females with weaning calves, followed by the mature resting females three days later, with the late-pregnant females being the last to leave on average 32 days after the late-lactating females and 11 days after the mature males. Chittleborough (1954, 1958) reported that the ovulatory period for mature female humpback whales ranged from June to November. He noted that the maximum frequency of ovulations occurred in late July with considerable numbers of ovulations in August and September and that by the peak period of ovulations in late July and August most calves from the previous season would have been weaned. Chittleborough (1955*a*) also reported that spermatogenesis in mature male humpback whales peaks in late-July and August, with lower rates in September coinciding with the ovulatory cycle of mature female humpback whales. It would appear that the migratory timing of the mature males leaves enough time for the late-lactating females to complete the weaning of their last season's calves and allows for the change in reproductive status of those females as they approach the breeding grounds in late July. Thus, the mature males would be well positioned for mating opportunities in the breeding grounds north of Hervey Bay, prior to the arrival of the mature non-lactating resting females. The data presented in this study suggest that most mature males are likely to be located further north in the breeding grounds during August and gradually move south, with some moving through

Hervey Bay, following the non-lactating mature females in late August and early September, and with their peak density being slightly ahead of the lactating females.

As reported in Chapter 4 above, in Hervey Bay there was a low probability of observing competitive groups during the first two weeks of August; the rate with which such groups were observed increased during the last two weeks of August and the first week of September. However, there was a high probability of observing competitive groups during the rest of September through to mid-October. Consistent with those results, in this study there were very few observations of mature males during August with the main concentrations of mature males occurring in September and October.

In this study, lactating females were observed in Hervey Bay from day 13 (mid-August) to day 80 (mid-October) within season, with peak density occurring at day 57.8 (late-September) within season (Table 5.6). Whilst the peak densities in Hervey Bay of lactating and non-lactating females are separated by on average 32.2 days, there is a clear overlap of these two classes during September (Figure 5.1d and e). Parturition in humpback whales occurs from June to November with the peak birthing month being August (Chittleborough 1954, 1965). Franklin *et al.* (2011) reported that lactating females begin arriving in Hervey Bay by late August and the proportion of pods with a calf present escalates steeply from late August (3.6%) through to mid-October (92.8%). In Hervey Bay lactating females spend an average of 69.4% of their time alone with their calves (Franklin *et al.* 2011) and when they do associate with other whales they are significantly more likely to associate with other mother-calf pods (see Chapter 4 above). Although the primary focus of lactating females is maternal care in Hervey Bay, the attraction for mature males in Hervey Bay is the possibility of mating opportunities with post-partum estrous lactating females.

In this study, mature males observed for ten or more days were resighted over longer intervals than mature females and the longest interval between sightings was almost twice that of mature females. Burns *et al*. (in press), reported that mature males during the southern migration off Ballina, northern NSW were resighted over longer intervals than females and suggested that some males may circle northward to maximise mating opportunities. The longer intervals between resightings of mature males may indicate that some mature males circle northwards from and to Hervey Bay in search of estrous females.

There are very few mature males in Hervey Bay during August when some mature non-lactating females are present. The main concentrations of mature males coincides with the presence of mature non-lactating females in September but more so with the lactating females in September and October. In this study, utilising long-term adjacent year resightings of known individual females there were 36 lactating females involved in 50 post-partum estrous pregnancies, i.e. they had calves two years in a row (Table 5.4). Although mature males remain concurrent with the lactating females they leave the bay ahead of the last lactating females in the final week of the season.

### *5.5.6 Hervey Bay: a preferential stopover for females early in the southern migration?*

Based on the selected sample of 361 individual resighting histories (262 females and 89 males), this study reports a ratio of 2.94:1 sex-identified or inferred females to males. The constant annual effort of observation and photography during this study, which involved no *a priori* selection of individuals or pods, coupled with the data on mean residency times, suggest that the reported ratio of sex-identified or inferred females to males is indicative of a real female sex-bias in Hervey Bay. The male-biased sex ratio reported in breeding grounds (reviewed by Herman *et al*. (2011)) and the male-biased sex ratio in the migratory corridor off eastern Australia (Brown *et al.* 1995) may be indicative of greater mating opportunities for

males in the eastern Australian breeding grounds to the north of Hervey Bay and along the main southerly migratory corridor, compared with habitats in Hervey Bay.

Heterogeneity of capture probabilities of different reproductive and maturational classes of humpback whales, particularly females with calves and mature males, may result in some unintentional sampling biases. As well, the decreasing residency in Hervey Bay over years may reflect decreasing capture probabilities as the population recovers. Therefore, further studies of heterogeneity of capture probabilities of selected maturational and reproductive classes of humpback whales is needed in order to identify and quantify any potential sampling biases and likely error rates.

Adult humpback whales may use deeper water to facilitate breeding behaviour, whereas females with calves use shallower water to avoid harassment from sexually active males who may cause injury to calves (Smultea 1994, Ersts and Rosenbaum 2003). The diving depths of individuals in competitive groups are reported to range between 10 m to 298 m (Herman *et al*. 2008) and Hervey Bay is on average less than 18 m deep (Vang 2002). Hervey Bay is a stopover early in the southern migration, with low levels of competitive behaviour (6.3% of pods, see Chapter 4 above) and only 10.8% of pods had escorts present (Franklin *et al*. 2011). Therefore, Hervey Bay provides mothers with older calves a suitable sheltered and convenient habitat for maternal care in the early stages of the southern migration (Franklin *et al*. 2011).

In this study few known mature males were observed in August, and immature males and females together with mature females were observed early in the season with peak density occurring in late August (Fig. 5.1a, e and g). In contrast, mothers with calves, who spend 69.4% of the time alone with their calves in Hervey Bay, dominated the last six-weeks of the season (Franklin *et al*. 2011). Consequently, the ratio of sex-identified or inferred females to males reported in this study indicates that Hervey Bay is a preferential habitat selected by southbound non-lactating females accompanying both immature males and females early in

the season, and by lactating females with older calves later in the season. These results suggest that there are subtle but ecologically significant differential migration patterns and routes of females, a higher proportion of which enter Hervey Bay, compared to the majority of males that remain along the coastline migratory corridor during this stage of the migration off eastern Australia.

### *5.5.7 Temporal segregation provides a predictable social framework as individuals move through different maturational and reproductive stages*

Boness *et al*. (2002) suggested that the yearlong period of gestation and the high rate of foetal growth in mysticetes together with highly seasonal breeding may result from the need for reproductive timing to coincide with annual patterns of prey availability. Alternatively, predator avoidance in high latitudes has been hypothesised as a factor influencing winter migrations to low-latitude breeding grounds (Corkeron and Connor 1999). However, in response to this hypothesis, Clapham (2001) speculated that for "humpback whale calves, energy conserved in low-latitude warm waters during the first months of life...may translate into larger size in adulthood and may in turn result in higher reproductive success." Dawbin (1956, 1966) examined the factors influencing migratory timing and pathways of humpback whales in the Southern Ocean and concluded that the primary factors were feeding behaviour in Antarctica and breeding behaviour in temperate tropical coastal waters.

There is general agreement that beyond the mother-calf association, which lasts for 11 to 12 months, the social organisation of humpback whales is characterised by small unstable groups, involving brief associations lasting for periods of a few hours or less, with some associations lasting over several days or (rarely) over longer periods (Herman and Antinoja 1977, Tyack and Whitehead 1983, Baker and Herman 1984*a*, Mobley and Herman 1985,

Mattila *et al*. 1994, Clapham 2000). Valsecchi *et al*. (2002) reported that with the exception of the mother-calf relationship, there was an absence of kin-relatedness within small groups of humpback whales. They suggested that if any social organisation does exist in the humpback whale population it is formed transiently when needed, rather than being a constant feature of the population.

Several genetic and photo-identification studies have documented evidence of maternally directed fidelity to migratory destinations (Martin *et al*. 1984, Clapham and Mayo 1987, Baker *et al*. 1990, Katona and Beard 1990, Clapham *et al*. 1993, Palsboll *et al*. 1997). Ersts and Rosenbaum (2003) suggested that patterns of habitat preference on wintering grounds, particularly those of mothers with calves appear to be guided by social organisation.

The coherent annual structure of temporally segregated maturational and reproductive classes of humpback whales is consistent with maternally directed fidelity to winter breeding grounds and summer feeding areas. The mature non-lactating females are at the vanguard and the mature lactating females at the rearguard of the southern migration, while in contrast on the northern migration, the late-lactating females with weaning calves lead the migration and the pregnant females are the last to leave the Antarctic feeding areas (Dawbin 1997). Moreover the peak densities of non-lactating females and lactating females are separated by 32 days during both the southern migration from the breeding grounds and northern migration from the feeding areas. It is interesting to note that the immature males and females follow closely behind the mature females at the vanguard of both the southern and northern migrations. Mothers returning with weaning calves on the northern migration lead their yearlings to the opposite end of the migration and leave them with the immature cohort in the early part of the southern migration. Similarly, mature males fit in with the migratory timing and reproductive status of mature females and also remain in the same position in both the southern and northern migration.

Clutton-Brock (1989) reported that several studies of species where non-breeding adults or sub-adults assist in rearing the young show that the survival of juveniles increases in relation to the number of adults that help to rear them. Furthermore, he suggested that the reasons for female clumping in mammals such as ungulates and other groups may be totally unrelated to reproduction and pointed out that the benefits of clumping may include information exchange, efficiency by observational learning or cultural transmission of learned habits. The use of long-term resighting histories of known individuals in this study revealed the timing and behaviour of the different age, sex, reproduction and maturational classes across the season in Hervey Bay. In particular the data suggest that known immature males and females were accompanied by and interacted with known non-lactating mature females from early to mid-season (see resighting histories in Table 5.13 and 5.14, and Fig. 5.1e and g). It is reported in Chapter 4 above, that whilst lactating females were primarily involved in maternal activities alone with their calves, when they did socialise they were significantly more likely to interact with other mother-calf pods. This study confirms that temporal segregation and behaviour by age, sex and reproductive classes during the annual migrations is a constant inherent feature of the social organisation of humpback whales and also shows that the social interactions of singletons and unstable groups occurred within the broader context of a stable predictable and orderly migratory procession.

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# *Chapter 6*

# Thesis synthesis, summary of general conclusions and conservation issues

## 6.1 GLOBAL RESEARCH CONTEXT

The study of humpback whales prior to the 1970s was largely a by-product of, and focussed by, commercial whaling and the establishment of the International Whaling Commission (IWC) in 1946. From the mid-1940s to the mid-1970s commercial whaling was extensively conducted in the Northern Hemisphere in the North Pacific and in the Southern Hemisphere at coastal whaling stations in temperate waters and aboard pelagic whaling factory ships in Antarctic waters (True 1904; Mathews 1937; Mackintosh 1942; Nishiwaki 1959; Chittleborough 1965; Dawbin and Falla 1949; Dawbin 1956; 1966). Data from these and other studies yielded extensive information on humpback whale morphology, physiology, reproduction, diet, distribution and movements (Chittleborough, 1954; 1955a; 1955b; 1958a, 1958b; 1959a; 1959b; Dawbin 1964, 1997; Chapter 1 above).

From the 1970s the emergence worldwide of non-lethal techniques including photo-identification, genetics, satellite tagging and acoustics stimulated extensive individual and collaborative studies of the ecology of humpback whales in tropical breeding grounds as well as in temperate and polar feeding areas. These studies extended scientific knowledge of humpback whale populations in all ocean basins and the linkages within and between feeding areas and breeding grounds as well as social behaviour and social organisation (see Chapter 1.4 for a summary of these studies). This research phase culminated in two major ocean-

basin-wide studies involving extensive collaborations, which were undertaken in the Northern Hemisphere: Years of the North Atlantic Humpback Whale (YONAH) (Smith *et al*. 1999) and Structure of Populations, Levels of Abundance and Status of Humpback Whales in the North Pacific; (SPLASH) (Calambokidis *et al*. 2008). In the Southern Hemisphere the South Pacific Whale Research Consortium (SPWRC) has coordinated research over the last decade on humpback whale breeding grounds across the South Pacific and linkages with eastern Australia and Antarctic feeding grounds (Garrigue *et al*. 2007, 2011a and b; Franklin *et al*. 2012.

Studies undertaken during the period of lethal whaling of humpback whales in Australia provided a foundation for subsequent non-lethal methods of investigation of humpback whales on both the western and eastern coastlines of Australia. However the data obtained on individual humpback whales provided only one record of each whale, at the time of its death.

The Australian coastlines provide excellent opportunities for long-term research on humpback whales throughout much of their annual migration and breeding periods. This context was noted by Dawbin (1956 p. 190) who made the observation that "The great length of the east Australian coastline situated in the tropics…provides a much more extended area of coastal conditions suitable for breeding humpbacks than is available near Pacific Islands…and that many more humpback whales pass close to this coastline than occur near any of the Pacific Islands."

During their annual migration between winter breeding grounds and summer feeding areas eastern Australian humpback whales traverse the full length of the continental shelf from $12^0$ S (northeastern Queensland, Chaloupka and Osmond 1999) to approximately $43^0$ S (southeast Tasmania, Gales *et al*. 2009). South of the putative tropical breeding ground ($16^0$ to $23^0$ S), eastern Australian humpback whales travel offshore past Stradbroke Island, ($27^0$ S, Brown and Corkeron 1995, Noad *et al*. 2011), Byron Bay and Ballina ($29^0$ S, Paton *et al*. 2011), and

Eden ($37^0$ S, Gales *et al.* 2009). It has been noted that humpback whales, after leaving the putative breeding ground in northeastern Queensland, continue to display social behaviours along the eastern coastline of Australia (Brown and Corkeron 1995).

During their southern migration some humpback whales divert west of the primary coastal migratory pathway and enter and leave Hervey Bay from the north ($25^0$ S, Paterson 1991, Franklin *et al*. 2011, Fig 1.6.1 above). Research conducted in Hervey Bay prior to this study established that humpback whales aggregate on the eastern side of Hervey Bay during the southern migration (Corkeron 1993, Corkeron *et al*. 1994). The research outlined above provides the context for this present study, which aimed to address the question 'What is the social and ecological significance of Hervey Bay for eastern Australian humpback whales?' To address this question long-term observations and photo-identification of humpback whales were undertaken involving constant effort across the season during the southern migration (see Figure 3.1, Chapter 3). The extensive data obtained (see Chapter 2), were used to investigate pod characteristics and composition (Chapter 3), social behaviour (Chapter 4), and temporal segregation of reproductive and maturational classes of humpback whales (Chapter 5). These investigations revealed that Hervey Bay is utilised by different maturational and reproductive classes of humpback whales as the season progresses, that it is a unique stopover in the early part of the southern migration and that it provides an important habitat for some eastern Australian humpback whales. The study also provided important insights into the social behaviour and social organisation of humpback whales in Hervey Bay. These general conclusions are synthesised in section 6.2 below.

## 6.2 SYNTHESIS AND GENERAL CONCLUSIONS

### *6.2.1 Hervey Bay as a stopover is different from traditional breeding grounds*

Humpback whales migrate annually over long distances between summer feeding areas in near-polar waters and winter breeding grounds in tropical and near-tropical waters (Baker *et al*. 1990, Rasmussen *et al.* 2007). In the northern hemisphere traditional breeding grounds are located between $16^0$ and $23^0$ north in the offshore waters near the West Indies and Hawaiian Islands (Whitehead and Moore 1982, Baker and Herman 1981), while in eastern Australia the breeding grounds for humpback whales are considered to be between $16^0$ and $23^0$ south (Smith *et al*. 2012). Hervey Bay is located at $25^0$, south of the putative breeding grounds and is an accessible stopover utilised by certain classes of humpback whales early in the southern migration prior to leaving for feeding areas in Antarctica (Figure 1.6.1, Chapter 3).

The present study shows that there are differences in social behaviour in Hervey Bay compared to breeding grounds in the Northern Hemisphere (Chapter 4). The proportion of lone mother-calf pods in Hervey Bay (Table 3.2) was greater than has been reported for other regions (Hawaii: Mobley and Herman 1985, Herman and Antinoja 1977; West Indies: Mattila and Clapham 1989, Mattila *et al.* 1994). One of the major differences between the Hervey Bay and Hawaiian studies was that the modal size for pods having a calf present was three, mother-calf and escort (Herman and Antinoja 1977, Herman *et al.* 1980, Glockner and Venus 1983). By contrast, in Hervey Bay in pods with calves present the modal size was two, because of the significantly higher proportion of mothers alone with their calf (Table 3.4c). This difference in pod size and composition may be related to Hawaii being a breeding destination whereas Hervey Bay is a migratory stopover early in the southern migration for mothers with older calves (Franklin *et al.* 2011, Chapter 3 above). It has been suggested that adult humpback whales may use deeper water to facilitate breeding behaviour, whereas

females with calves use shallower water to avoid harassment from sexually active males who may cause injury to calves (Smultea 1994, Ersts and Rosenbaum 2003). Hervey Bay is on average less than 18 m deep (Vang 2002) and there were low levels of competitive behaviour and few escorts recorded (see Chapter 4 and Franklin *et al*. 2011), hence Hervey Bay is not a traditional breeding ground.

### *6.2.2 Seasonal changes in social behaviour*

This study shows that the seasonal social behaviour of humpback whales is intimately linked not only with pod characteristics but also with the seasonal changes of different classes of whales moving through Hervey Bay on their southern migration (Chapter 3). Data on pod characteristics demonstrate a significant increase of pods of 3 plus whales over years (Fig. 3.3a), coinciding with a trend of rapidly increasing abundance (Noad *et al*. 2011, Paton *et al*. 2011) and partial recovery of the eastern Australian population. Observations by Dawbin (1956) of humpback whales displaying social behaviour in coastal waters and in semi-tropical waters prompted him to suggest that humpback whales probably require some period in coastal waters for breeding behaviour. Dawbin (1956, p. 191) concluded that "an intensive study of environmental conditions and humpback behaviour in the breeding areas may well prove to be more productive in furthering an understanding of their migratory movements than any similar study of humpbacks on passage or in the feeding grounds."

### *6.2.3 Timing and social behaviour of classes of humpback whales utilising Hervey Bay*

The seasonal pod characteristics and social behaviour of humpback whales in Hervey Bay show significant differences in the first four weeks of the season compared to the last six weeks of the season (Chapter 3 and 4). Pairs and singletons were the predominant pod size

during the first four weeks, while pods with calves were rarely sighted. Non-agonistic social behaviour occurred mainly during the first four weeks. Pod characteristics and behaviour in the first four weeks are related to the presence of immature and mature males and females involved in social interactions.

Mothers with calves predominated during the last six weeks of the season with the proportion of pods with a calf present escalating rapidly towards the end of the season (Fig. 3.2b). Overall, there were low levels of competitive behaviour with the highest frequency of competitive behaviour occurring towards the end of the season (Fig. 4.2c).

It has been reported that mother and calf pods rarely associate with other mother-calf pods in winter breeding grounds (Herman and Antinoja 1977, Baker and Herman 1984a, Mobley and Herman 1985). In contrast in Hervey Bay, although the proportion of pods with more than one calf present is low, interaction between mother-calf pods does occur. By mid-to-late season in Hervey Bay, when the calves are more mature and mother-calf bonds are well established, mothers may be more comfortable mixing with other mother-calf pods. When mothers were not alone with their calves, they were either accompanied by an escort or escorts, or were mixing with other females with calves (Table 3.3, 3.4c). However, it would appear that mothers with calves in Hervey Bay are mainly left alone, which gives them ample time for maternal activities involving training, nurturing and feeding their calves. In addition, mothers were often observed resting on the surface of the water with their calves and were mostly left alone by male humpback whales, and by whale-watching tour operators, that mainly seek out active pods.

### *6.2.4 Temporal segregation of reproductive and maturational classes*

Using long-term and adjacent year resighting histories of individually identified humpback whales; this study was able to compare the differing reproductive status and timing of mature non-lactating females throughout the season in Hervey Bay (Chapter 5). Known mature non-lactating females occurred in August with peak density occurring in late August and fewer in September and very few in early October. The study data also showed that there was no significant difference in the peak density and observations by day within season of immature males and females compared to mature non-lactating females (Table 5.7). Detailed observations of timing and behaviour of three particular individuals showed that immature males and females interact with non-lactating, resting or newly pregnant females (Tables 5.13 and 5.14). Known non-lactating females also overlap with lactating females in September, with peak density occurring in late September, on average thirty-two days later than the mature non-lactating females (Table 5.7).

Burns (2010) reported the regularity of timing of particular known individual humpback whales during their migration past Ballina northern NSW over years and raised the question as to which other individual whales they may be likely to encounter over years. In contrast to mature females who change their position in the migration sequence according to their reproductive status, mature males do not change the timing of their occurrence in the migratory procession (Dawbin 1966, 1997). Therefore there may be a higher probability of migrating mature males encountering individuals that they have encountered in previous years.

Few known mature males are observed in August in Hervey Bay, with the main concentrations in September and October (Fig. 5.1). The peak density of known mature males when they were not in the company of lactating females occurred in mid-September, a week

earlier than the peak density in late September of known mature males observed with lactating females (Fig. 5.1, Table 5.7).

It is interesting to note that male UID-176 changed his residency timing in Hervey Bay as he matured, but was resighted with a known mother with calf UID-422 on 26th September 2004 and again with the same mother on 23rd September 2007 (Table 5.13). Therefore, within the context of the temporal segregation and behaviour of humpback whales, further research and investigation is needed to provide insight into the question of whether or not there are long-term repeated associations between known individuals.

### *6.2.5 Female bias and differential migration of males and females in Hervey Bay*

A female-biased sex ratio of 2.94:1 sex-identified or inferred females to males is evident from the 361 individual resighting histories in this study (Chapter 5). This contrasts strongly, with the male-biased sex ratio reported in the migratory corridor off eastern Australia (Brown *et al*. 1995) and the male-biased sex ratio reported in the breeding grounds in Hawaii and other regions globally (reviewed by Herman *et al*. 2011). Coupled with the data on mean residency times (Chapter 5), this strongly suggests that the reported ratio of sex-identified or inferred females to males in Hervey Bay is a real phenomenon. However, heterogeneity of capture probabilities of different reproductive and maturational classes of humpback whales, particularly females with calves and mature males, may result in some unintentional sampling biases. Furthermore, the decreasing residency in Hervey Bay over years may reflect decreasing capture probabilities as the population recovers. Therefore, further studies of heterogeneity of capture probabilities of selected maturational and reproductive classes of humpback whales are needed in order to identify and quantify any potential sampling biases and error rates.

In their global review of humpback whales, Fleming and Jackson (2011) reported a number of resting areas and potential resting areas for humpback whales en route to terminal destinations. Bannister and Hedley (2001) and Jenner *et al*. (2001) reported that during the southern migration south from the breeding area in the Kimberley region on the western Australian coastline, humpback whales use Exmouth Gulf and Shark Bay as resting nursery regions. Further research is needed in these areas to determine whether differential migratory routes occur for particular classes of whales, such as mother with calves, immature males and females, and mature males seeking potential mating opportunities away from the direct migratory coastlines.

### 6.2.6 *Temporal segregation a consistent and coherent feature of social organisation*

The timing and spacing of different reproductive and maturational classes of humpback whales in Hervey Bay (Chapter 5) is fully consistent with the temporal segregation reported by Dawbin (1966, 1997). The data suggest that mature non-lactating and lactating females interact with, and are involved in, the social development of immature and maturing males and females (Tables 5.13 and 5.14). Hervey Bay provides a safe environment for resting mothers and calves; it is an area where immature male and female humpback whales can develop their social skills and potentially learn from and interact with mature females. In addition, the predictability of females in different maturational and reproductive stages frequenting the bay throughout the season provides mature males with potential mating opportunities across the migratory season in Hervey Bay. Burns *et al*. (in press) suggested that some males during the southern migration off Ballina northern NSW may circle back to maximise mating opportunities. The residency data presented in this study, showing that some males visit Hervey Bay early and subsequently return later in the season (Table 5.12), suggest that a similar motive may underlie these occurrence patterns.

This study suggests that temporal segregation is a constant and cohesive feature of the social organisation of migrating humpback whales, which provides a predictable social framework for individuals moving through various maturational and reproductive stages as they age.

### *6.2.7 Increase in abundance may have density dependent effects on humpback whales in Hervey Bay*

Over the period of this study the eastern Australian humpback whale population has shown a near linear trajectory increase in abundance from approximately 2,000 in 1992 (Paterson *et al*. 1994) to approximately 13,000 in 2009 (Noad *et al*. 2004, 2011; Fig.1.5.4.1). Consequently, the possible density dependent effects on humpback whales visiting Hervey Bay should be considered. In this study it is suggested that the significant increase over years in groups of 3+ whales (Fig. 3.3) may be related to the increasing proportion of socially active and interacting immature and mature males and females, aggregating in the bay. Furthermore, the significantly higher rate of pod associations (Fig. 4.1b) during the first four weeks of the season and the relatively higher frequency of non-agonistic social behaviour early in the season (Fig. 4.3b) may be related to the density and movement into and out of Hervey Bay of an increasing proportion of immature and mature males and females over years. Finally, the rapid increase of mothers alone with their calves in the latter half of the season and the fact that when mothers with calves associate they are significantly more likely to associate with other mother calf pods (see 4.4.8.1 above) may be related to the increasing density of mother calf pods in Hervey Bay.

### *6.2.8 Benefits outweigh costs for humpback whales utilising Hervey Bay*

Hervey Bay is not a traditional breeding ground. It is neither a calving area nor a terminal destination. After spending time in the breeding grounds to the north of Hervey Bay some humpback whales make a diversion from the primary migratory pathway and enter Hervey Bay (Fig. 1.6.1 above). There are substantial physiological pressures on humpback whales to initiate the migration towards summer feeding areas (Locker 1984). Consequently, the costs in energy in diverting from the primary migratory pathway and spending time in Hervey Bay must be outweighed by the benefits from time spent in Hervey Bay. There are potential risks for humpback whales entering and leaving Hervey Bay. Humpback whales have to negotiate extensive sand-spits and contend with strong tidal conditions in shallow waters moving into and out of the bay (Fig. 1.6.1 above).

In contrast to the wide dispersal of humpback whales throughout the breeding area to the north (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999, Smith *et al*. 2012), in Hervey Bay dense aggregations of whales occur in a limited and relatively shallow area (Fig.1.6.1 above). Mature females that are either resting or in the early stage of pregnancy accompany and interact with immature males and females in pairs and larger groups and may benefit from socialising opportunities during the first half of the season. Mature males and females involved in both non-agonistic social behaviour and competitive groups provide opportunities for social bonding and possibly breeding. Mothers with older calves have the opportunity to rest in Hervey Bay after the initial birthing period, but also benefit from the opportunities for maternal and social activities with low levels of interference from mature males.

The long migration between their feeding areas in Antarctica and their breeding ground within the Great Barrier Reef appears to be a maternally directed learned experience. There is a rhythm and order, which binds the whole group in an annual orchestrated movement

(Chapter 5). Mothers with weaning calves lead the northern migration closely followed by the immature males and females then by the mature males and females and finally the last to leave the Antarctic feeding areas are the expectant mothers (Fig. 5.5.1.1.). While on the southern migration from the breeding ground in the Great Barrier Reef, resting and newly pregnant mature females lead the way south followed closely by the immature males and females, then the mature males and females, while the last to leave Hervey Bay are the mothers with this season's calves (Fig. 5.1, and Fig. 5.5.1.1). Thus the mature females are at the vanguard and rearguard of the migration both northwards and southwards.

Hervey Bay's place in the annual rhythm of the orchestrated migratory movement of eastern Australian humpback whales appears to be a 'Cavanbah', a safe annual social meeting place (see: http://arakwal.com.au/cavanbah/).

## 6.3 FUTURE RESEARCH

The long-term dataset of resighting histories of individual males and females used in this study provides opportunities to investigate further questions on the social behaviour of humpback whales. These include; Do breeding females form long-term relationships? Similarly do mature males form long-term relationships? Are there any long-term patterns in the timing of resightings and site fidelity of individual mature males utilising Hervey Bay? Do mature male escorts entering Hervey Bay exhibit other social functions beyond escorting lactating females? To what degree do mature males socially interact with immature males?

Future research of long-term capture histories of individually identified humpback whales using robust design modelling could provide estimates of probability of entry and survival by week within season and over years, together with estimates of abundance within season and

over years, site fidelity, residency, as well as birthing rates. These estimates could contribute to better understanding of density dependent effects in Hervey Bay.

The availability of GIS data in conjunction with long-term sightings provides the basis for investigating the spatial utilisation of the Hervey Bay habitat by both individual and classes of humpback whales and to address the following questions. Have there been any changes over years in the spatial utilisation of the bay by classes of humpback whales? Do particular classes of humpback whales exhibit differences in the spatial utilisation of the Hervey Bay habitat? Has the increasing population of humpback whales using the bay influenced spatial utilisation? Can changes in spatial use of the bay over the long-term provide the basis for a predictive model of future use of the bay by the eastern Australian humpback whales?

## 6.4 CONSERVATION ISSUES

Humpback whales in Queensland waters are protected under the Nature Conservation Act 1992 and are listed as 'Vulnerable' in the Nature Conservation (Wildlife) Regulation 2006. Eastern Hervey Bay was the first site to be specifically declared for the protection of humpback whales within a single 'general use zone' designated as a 'Whale Management and Monitoring Area' within the Hervey Bay Marine Park declared in 1989. Since 1997 humpback whales have been managed under the Nature Conservation (Whales and Dolphins) Conservation Plan 1997 (Vang 2000). The Great Sandy Marine Park was established in 2004 incorporating the former Hervey Bay Marine Park. Current regulations related to commercial and recreational whale-watching within a designated whale management and monitoring area are set out in the Marine Parks (Great Sandy) zoning plan 2006. These regulations provide for movement of commercial and recreational vessels in close proximity to whales and provisions for the protection of whales within the Marine Park.

Hervey Bay and Fraser Island are also the focus of an international and domestic tourism industry and a commercial and recreational fishing and boating industry. Furthermore, there is an established and expanding aquaculture industry. Human activities within the Hervey Bay region are increasing, coinciding with the rapidly expanding humpback whale population along eastern Australia. Therefore, it is likely that interactions between humpback whales and human activities are going to increase substantially in future, which will require careful management to ensure that Hervey Bay continues to provide a suitable habitat for these whales.

During August and September, Hervey Bay is clearly an important habitat for mature non-lactating females (newly pregnant and resting), as well as for immature males and females. Later in the season it is an important stopover for lactating females involved in maternal care with older calves. Therefore, it is imperative to ensure the long-term viability of Hervey Bay as a habitat important to the reproductive success of these eastern Australian humpback whales. There is clearly the possibility of future increased anthropogenic disturbances of the migrating humpback whales and their habitat in Hervey Bay from increased boat traffic, pollution, aquaculture development and habitat degradation. Therefore it is important that long-term monitoring of this habitat and its use by different classes of migrating humpback whales is continued into the future.

Moreover, it is essential that an integrated environmental research, monitoring and management plan be created for Hervey Bay. Such a plan should include an adaptive management framework to mitigate impacts from increased human activities, as well as provisions for monitoring the interactions and effects of these activities on humpback whales. The monitoring data should then be regularly reviewed to evaluate and adapt the planning processes, in order to better manage human activities in this important whale habitat for the future.

# *Chapter 7*

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# *Chapter 8*

# Appendix:

# Summary of relevant Authored and Co-authored publications

Franklin, T., W. Franklin, L. Brooks, P. Harrison, P. Baverstock and P. Clapham. 2011. Seasonal changes in pod characteristics of eastern Australian humpback whales (Megaptera novaeangliae), Hervey Bay 1992-2005. *Marine Mammal Science, 27(3): E134–E152 (July 2011) ©2010 by the Society for Marine Mammalogy. DOI: 10.1111/j.1748-7692.2010.00430.x*.

Franklin, T. and D. Burns. 2005. A Southern Right Whale, (Eubalaena Australis), In Hervey Bay, Qld and Ballina, N NSW. *Memoirs of the Queensland Museum* **51 (2): 308**.

Franklin, W., Franklin, T., Brooks, L., Gibbs, N., Childerhouse, S., Smith, F., Burns, D., Paton, D., Garrigue, C., Constantine, R., Poole, M.M., Hauser, N., Donoghue, M., Russell, K., Mattila, D.K., Robbins, J., Oosterman, A., Leaper, R., Harrison, P., Baker, S.C. and Clapham, P. (2012) Antarctic waters (Area V) near the Balleny Islands are a summer feeding area for some Eastern Australian (E (i) breeding group) Humpback whales (Megaptera novaeangliae). Journal of Cetacean Research and Management 12, 321-327.

Franklin, W., T. Franklin, N. Gibbs, S. Childerhouse, C. Garrigue, R. Constantine, L. Brooks, D. Burns, D. Paton, M. M. Poole, N. Hauser, M. Donoghue, K. Russell, D. K. Mattila, J. Robbins, M. Anderson, C. Olavarria, J. Jackson, M. Noad, P. Harrison, P. Baverstock, R. Leaper, S. C. Baker and P. Clapham. (In press*b*). Photo-identification

confirms that humpback whales (Megaptera novaeangliae) from eastern Australia migrate past New Zealand but indicates low levels of interchange with breeding grounds of Oceania. *Journal of Cetacean Research and Management*.

Franklin, W., T. Franklin, L. Brooks, C. Jenner, M. Jenner, L. Goncalves, R. Leaper, L. Brooks and P. Clapham. 2008. Photo-identification comparison of humpback whale (Megaptera novaeangliae) flukes from Antarctic Area IV with Western and Eastern Australian fluke catalogues *Paper SC/60/SH1 presented to the International Whaling Commission Scientific Committee. (Unpublished) 13pp. [Available from the office of this Journal]*.

Anderson, M., D. Steel, W. Franklin, T. Franklin, D. Paton, D. Burns, P. Harrison, P. Baverstock, C. Garrigue, P. Baverstock, C. Olavarria, M. Poole, N. Hauser, R. Constantine, D. Theile, P. Clapham, M. Donoghue and S. Baker. 2010. Microsatellite genotype matches of eastern Australian humpback whales to Area V feeding and breeding grounds. *Paper SC/62/SH7 presented to the Scientific Committee of the International Whaling Commission, Agadir, Morocco, 30th May - 11th June 2010.11pp. (Unpublished). [Available from the office of this Journal]*

Burns, D., L. Brooks, P. Harrison, T. Franklin, W. Franklin, D. Paton and P. Clapham. in press. Migratory movements of individual humpback whales photographed off the eastern coast of Australia. *Marine Mammal Science*.

Garrigue, C., T. Franklin, R. Constantine, K. Russell, D. Burns, M. Poole, D. Paton, N. Hauser, M. Oremus, S. Childerhouse, D. Mattila, N. Gibbs, W. Franklin, J. Robbins, P. Clapham and C. S. Baker. 2011. First assessment of interchange of humpback whales between Oceania and the east coast of Australia. *Journal of Cetacean Research and Management (Special Issue) 3***:** 269-274.

Jackson, J. A., M. Anderson, D. S. Steel, L. Brooks, P. Baverstock, D. Burns, P. Clapham, R. Constantine, W. Franklin, T. Franklin, C. Garrigue, N. Hauser, D. Paton, M. M. Poole and S. C. Baker. 2012. Multistate measurements of genotype interchange between East Australia and Oceania (IWC breeding sub-stocks E1, E2, E3 and F2) between 1999 and 2004. *Paper SC/64/SH22 presented to the Scientific Committee of the International Whaling Commission. 16pp. (Unpublished). [Available from the office of this journal]*.

Gregory Kaufman, Douglas Coughran, Judy M. Allen, Daniel Burns, Chris Burton, Cristina Castro, Simon Childerhouse, Rochelle Constantine, Trish Franklin, Wally Franklin, Paul Forestell, Rosemary Gales, Claire Garrigue, Nadine Gibbs, Curt Jenner, David Paton, Michael Noad, Jooke Robbins, Elisabeth Slooten, Franz Smith and P. Stevick. 2011. Photographic Evidence of Interchange Between East Australia (BS E-1) and West Australia (BS – D) Humpback Whale Breeding Populations. *Paper SC63/SH11 presented to the Scientific Committee of the International Whaling Commission. 16pp. (Unpublished). [Available from the office of this Journal]*.

Paton, D. A., L. Brooks, D. Burns, T. Franklin, W. Franklin, P. Harrison and P. Baverstock. 2011. First abundance estimate of east coast Australian humpback whales (*Megaptera novaeangliae*) utilising mark-recapture analysis and multi-point sampling. *Journal of Cetacean Research and Management (Special Issue) 3***:** 253-259.

Rochelle Constantine, Judy Allen, Peta Beeman, Daniel Burns, Simon Childerhouse, Michael C. Double, Paul Ensor, Trish Franklin, Wally Franklin, Nick Gales, Claire Garrigue, Emma Gates, Nadine Gibbs, Amanda Hutsel, Curt Jenner, Micheline Jenner, Greg Kaufman, Anne Macie, David K. Mattila, Adrian Oosterman, David Paton, Jooke Robbins, Peter Stevick, Natalie Schmitt, Alden Tagarino and K. Thompson. 2011. Comprehensive photo-identification matching of Antarctic Area V humpback whales.

*Paper SC/63/SH16 presented to IWC Scientific Committee. 11pp.(unpublished). [Available from the office of this Journal]*.

Steel, D., N. Schmitt, M. Anderson, D. Burns, S. Childerhouse, R. Constantine, T. Franklin, W. Franklin, N. Gales, C. Garrigue, N. Gibb, N. Hauser, D.Mattila, C. Olavarria, D. Paton, M. Poole, J. Robbins, J. Ward, P. Harrison, P. Baverstock, M. Double and C. S. Baker. 2011. Initial genotype matching of humpback whales from the 2010 Australia/New Zealand Antarctic Whale Expedition (Area V) to Australia and the South Pacific. *Paper SC/63/SH10 presented to the Scientific Committee of the International Whaling Commission. 8pp. (Unpublished). [Available from the office of this Journal]*.