Abundance, population dynamics, reproduction, rates of population increase and migration linkages of eastern Australian humpback whales (*Megaptera novaeangliae*) utilising Hervey Bay, Queensland

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A thesis submitted to the School of Environment, Science and Engineering in fulfillment of the requirements for the degree of

Doctor of Philosophy

**SOUTHERN CROSS UNIVERSITY**

November 2014
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).

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ABSTRACT

Hervey Bay is located to the south of the putative breeding and overwintering grounds of the eastern Australian humpback whale population in the Great Barrier Reef. Previous research has established that large numbers of humpback whales stopover in Hervey Bay during the early stages of the southern migration to Antarctic summer feeding areas.

In this study robust design modeling of long-term capture histories of individual humpback whales and analysis of photo-identification data – obtained during observations of humpback whales in Hervey Bay over 21 years (1992 to 2012) and from other locations across the Pacific, eastern Australia, western Australia, east Africa and Antarctic Area IV and V feeding areas - are used to address a core question: What is the role and function of Hervey Bay during the migration of eastern Australian (Group E1) humpback whales? The data are used to investigate the specific questions: how many humpback whales use Hervey Bay within season and over years; how long do humpback whales using Hervey Bay stay in the Bay; is there site-fidelity to Hervey Bay; what proportion of eastern Australian humpback whales are using Hervey Bay, what is the rate of reproduction and rates of population increase of humpback whales using Hervey Bay; and what patterns are evident for migratory movements and interchange with other regions, including potential feeding areas in Antarctica.

The estimated yearly abundance of humpback whales visiting Hervey Bay increased from 791 in 1997 (95% CI, 407-1176) to 4406 in 2009 (95% CI, 3343-5470). The trajectory of increase in estimated abundance over the 17 years was near linear and slightly greater than the trajectory of increase in the estimated abundance of the whole eastern Australian humpback whale population. A relatively constant
proportion of eastern Australian humpback whales visited Hervey Bay each year (mean = 34%, standard deviation = 5.3%).

Between years apparent survival was estimated to be relatively constant over years at 95% (SE = 0.012, 95% CI, 0.918:0.966) and near to the upper limits of biologically plausible survival levels for humpback whales. The near constant proportion of whales occurring in Hervey Bay from the eastern Australian population and the very high site-fidelity of some of those whales in Hervey Bay, suggest that the same cohorts of humpback whales return regularly to Hervey Bay. This study provides the first evidence that a specific sub-group from the eastern Australian humpback whale population uses Hervey Bay and that the sub-group is growing at a greater rate than the eastern Australian population.

Between week entry probabilities display a regular form over years, with variation in the proportion of yearly visitors present prior to the beginning of sampling in each season (mean = 17%, SD = 6.5%), which may be related to the shifts in the timing of the migration. Within season abundance is heavily skewed to the first half of the season, with approximately 83% of entries occurring in the first five weeks of the season and 17% of entries occurring during the last five weeks of the season. There are two distinct peaks in abundance within season; the highest in week 3 and the second highest abundance occurs in week 8 each year. The lowest probability of entry (1.2%, 95% CI, 0.0004-0.028) and the lowest between week apparent survival (1.3%, 95% CI, 0.062-0.262) occurs between weeks 5 and 6. These results coincide with the mid-season departure of the mature female, immature and older male, and female cohorts, and the arrival of lactating females with older calves and accompanying mature male escort cohorts that dominate the latter half of the season.
Temporary emigration was estimated to be constant over years at 14.1% (SE = 0.038; 95% CI, 0.081:0.234) and is consistent with a hypothesis that two cohorts – each comprising of breeding females depending upon their breeding status - visit Hervey Bay in alternate years. The typical residency time of humpback whales visiting Hervey Bay is about 1.4 – 2.0 weeks (mean = 1.6 weeks, SD = 0.34).

The observed proportion of calves to whales in Hervey Bay (weekly average 1997 to 2009 = 17.9%) is consistent with the estimated growth rate of the eastern Australian population and calf survival of humpback whales that utilise Hervey Bay may be higher than for the eastern Australian population as a whole. Modelling of the population trajectory of humpback whales utilising Hervey Bay reveals that observed abundance estimates exhibit a logistic trend with a faster growth rate in the mid-1970s, near linear growth during the early and mid-2000s and a slightly decreasing growth rate by 2009. The average rate of increase in abundance of humpback whales utilising Hervey Bay between 1997 and 2009 was estimated at 14.2% (95%CI 11.1% to 15%).

The analysis of all natural marks - including ventral tail fluke marks, dorsal fin shapes and lateral body marks - observed on 79 individual humpback whales over long time-spans ranging from 2 to 21 years, showed very low levels of change in primary and secondary natural marks, no significant difference in the proportion of changes in the natural marks on ventral tail flukes compared the dorsal fin shapes and to the natural lateral body marks. The use of dorsal fin shapes and lateral body marks in conjunction with ventral tail fluke natural marks provides a reliable mechanism to minimise and manage misidentification in large humpback whale photo-identification datasets.
Analysis of photo-identification data of fluke matches between New Caledonia and Hervey Bay revealed low levels of intermingling between eastern Australia and New Caledonia, consistent with these populations being discrete breeding populations. Matches between eastern Australia and New Zealand provided the first evidence that eastern Australian humpback whales are travelling through southern New Zealand waters en-route to and from Antarctic feeding areas.

Analysis of photo-identification data of fluke matches between the Balleny Islands and Hervey Bay supports the hypothesis that Antarctic Area V waters, in the vicinity of the Balleny islands, is a summer feeding area for some eastern Australian humpback whales, including at least some whales resighted in Hervey Bay. While matching of fluke catalogues from Antarctic Area IV with fluke catalogues from Eastern Australia, Western Australia and East Africa provided evidence that the humpback whales photographed in the Antarctic Area IV feeding area are from a different population to the African and Australian populations. There was weak evidence supporting the hypothesis that the whales photographed in Antarctica are from the Western Australian population. Photo-identification photography data also showed that humpback whales from eastern Australia do not always travel directly to Antarctic Area V to feed and may exhibit a diverse range of feeding destinations after leaving Australian coastal waters.

This study presents the first evidence that the humpback whales utilising Hervey Bay may be a sub-group of the eastern Australian (E1) humpback whale population. Hervey Bay provides a unique stopover for extended residency early in the southern migration for mature females, either early pregnant or resting, accompanying immature males and females, and lactating females with new calves during the latter season. Humpback whales from Hervey Bay use complex migratory pathways to and from Antarctic feeding areas and are involved in low levels of migratory interchange.
with nearby Pacific populations. This study provides the first evidence that eastern
Australian humpbacks use the southern waters of New Zealand en-route to and from
Antarctic feeding areas. Data presented in this study suggests that utilising Hervey
Bay as a stopover may contribute to the social development and high survival rates
of calves and younger humpback whales. This may provide a reproductive advantage
to these eastern Australian humpback whales and be a factor in the relatively high
rates of increase in abundance observed in humpback whales using Hervey Bay
compared to the eastern Australian breeding populations and to other humpback
populations.
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XXXII
Chapter 1

General Introduction

1.1 HUMPBACK WHALE (*Megaptera novaeangliae*)

1.1.1 Taxonomy

Humpback whales (*Megaptera novaeangliae*) are one of the large baleen whales that belong to the Order Cetacea (now included in Order Cetartiodactyla), Suborder Mysticeti and Family Balaenopteridae (Clapham and Mead 1999). The genus is considered mono-typic and was first described from a specimen on the coast of New England by Borowski (1781). *Megaptera novaeangliae* is the accepted taxonomic classification of the humpback whale (Clapham and Mead 1999).

1.1.2 Evolution

Fossil records reveal that the first cetaceans were evident around 55 million years ago (Bajpai and Gingerich 1998, Berta *et al.* 2006, Montgelard *et al.* 2007). The nearest groups to Cetacea still in existence are the artiodactyls (cows, pigs and hippopotamuses; even-toed ungulates), (Geisler and Uhen 2003), and recent molecular studies suggest that Cetacea and extant artiodactyls are monophyletic (Nikaido *et al.* 1999; Arnason *et al.* 2000; Madsen *et al.* 2001; Murphy *et al.* 2001; Geisler and Uhen 2003, 2005; Berta *et al.* 2006; Montgelard *et al.* 2007). The hippopotamus is considered the closest living relative of cetaceans (Madsen *et al.* 2001, Murphy *et al.* 2001, Geisler and Uhen 2003, Montgelard *et al.* 2007). Although the two clades, Cetacea and Artiodactyla were recently combined into a
single order, Cetartiodactyla (Montgelard et al. 2007), the issue is still under considerable debate (Price et al. 2005, Agnarsson and May-Collado 2008, Spaulding et al. 2009, Perrin 2010) and the Infraorder Cetacea remains in common use (Rice 2009). However, the Society for Marine Mammalogy recognise the inclusion of Cetaceans in Cetartiodactyla in their list of Marine Mammal Species and Subspecies (SMM 2014).

Fossil and molecular information indicate that Odontoceti and Mysticeti shared a common archaeocete ancestor around 35 million years ago (Berta et al. 2006). The Infraorder Cetacea is made up of the toothed whales, Odontoceti; and the filter feeding or baleen whales, Mysticeti (Rice 2009). Odontoceti have one blowhole and in contrast Mysticeti have two blowholes (Bannister 2002, Berta et al. 2006).

The Mysticeti consist of four families: the Balaenidae (right whales), Neobalaenidae (pygmy right whales), Eschrichtiidae (gray whales) and Balaenopteridae (rorquals) (Bannister 2002, Rice 2009). Ventral throat pleats and a dorsal fin distinguish the Balaenopterids and the name “rorqual” is Norse for “whale with pleats in its throat” (Bannister 2002, Berta et al. 2006). The pleats run from under the rostrum to the navel button and expand as the whale takes in large amounts of prey with water to feed (Lillie 1915, Winn and Reichley 1985, Clapham and Mead 1999, Bannister 2002). The Family Balaenopteridae includes the humpback whale and seven other species including the largest of all the whales, the blue whale (Balaenoptera musculus), which grows up to 33 m and weighs up to 190 tonnes (Slijper 1962, Yochem and Leatherwood 1985, Berta et al. 2006). The other six rorqual species are the fin whale (Balaenoptera physalus), sei whale (B. borealis), Bryde’s whale (B. brydei and B. edeni), Omura’s whale (B. omurai), and two species of minke whale (B. acutorostrata and B. bonarensis).
Both the fossil record and evolutionary genetics suggest that existing humpback whale lineages are of ancient origin, possibly dating back to the Miocene period between 23 to 5 million years ago (Baker et al. 1993, Demere et al. 2005).

1.1.3 Morphology

Humpback whales are morphologically unique amongst the extant 89 species of Cetacea (plus 1 species possibly extinct) (Clapham and Mead 1999, SMM 2014), having pectoral fins longer than any other species. The pectoral fins measure approximately a third the length of their body size (True 1904). They also have unique tubercles on their upper and lower rostrum and leading edge of the pectoral fins, which have hydrodynamic form and function related to feeding (True 1904, Whitehead 1981, Fish and Battle 1995, Miklosovic et al. 2004).

The ventral surface varies from all black to all white, while the colouration of the dorsal surface is usually black (True 1904, Lillie 1915, Matthews 1937, Omura 1953, Tomilin 1957, Nishiwaki 1959, Chittleborough 1965, Glockner and Venus 1983, Allen et al. 1994, Rosenbaum et al. 1995, Rosenbaum et al. 1995, Clapham and Mead 1999). The colouration of ventral flukes also differs by region (Rosenbaum et al. 1995). Another feature is the serrated posterior margin of the fluke, and the dorsal fin is highly variable in shape and size, ranging from high set and falcate to low-set and rounded (Katona and Whitehead 1981, Clapham and Mayo 1990). The ventral fluke serrations, the individual variation in the patterns of black and white pigmentation on the ventral flukes together with the shape and colouration of dorsal fins and variation in the patterns of lateral body markings, provide a robust means of individual identification supported by photo-identification (Katona and Whitehead 1981, Shane and McSweeney 1990, Clapham and Mead 1999, Calambokidis et al.
2008, Kniest et al. 2010). Photo-identification has been the basis of many long-term studies of individually identified humpback whales (Clapham and Mead 1999).

Compared to other rorqual whales, humpback whales are relatively short and stout and unlike other rorquals whales, they have relatively few ventral throat grooves; 12 to 36 compared to 38 to 100 (True 1904, Clapham and Mead 1999). They have from 270 to 400 baleen plates within the mouth (Matthews 1937, Tomilin 1957, Clapham and Mead 1999, Clapham 2002). The baleen plates are mainly black with some white along the front and during feeding the baleen plates function as a filtering curtain (True 1904). The ventral grooves, which run from the ventral rostrum to the navel - as in other balaenopterids - expand during feeding allowing enlargement of the mouth cavity to take in prey with water prior to using the baleen plates and tongue to filter the food from the water (True 1904).

Females can be distinguished from males through the presence of a hemispherical lobe at the posterior terminus of the genital slit, which is absent in males (True 1904, Glockner 1983), and the anal and genital slits are closer together in females than males (Matthews 1937). Males are generally smaller than females by about 1m to 1.5m (Chittleborough 1965, Clapham and Mead 1999) and it is suggested that the observed sexual dimorphism may be an adaptation resulting from the increased energy demands on females from pregnancy and lactation (Ralls 1976, Clapham 1996, Ralls and Mesnick 2002).

The overall average length of humpback whales is considered to range from 12 m to 15 m and it is suggested that pre-whaling populations may have had some very large individuals from 17 m to 19 m in length (Matthews 1937, Tomilin 1957, Chittleborough 1965, Clapham et al. 1997, Clapham and Mead 1999).
The average weight of humpback whales is from 24 to 35 tons up to a maximum of 48 tons (Mackintosh 1942, Watson 1985, Winn and Reichley 1985, Perry et al. 1999). Tomlin (1957) reported that humpback whales have from 51 to 54 vertebrae. The fusion of vertebrae has been used as an indicator of physical maturity in humpback whales (Chittleborough 1955b).

1.1.4 Foraging and diet


Feeding behaviour of humpback whales is characterized as ‘gulp feeding’ where, making use of the ventral pleats, they take in one very large mouthful of prey at a time (Watkins and Schevill 1979, Hain et al. 1982, Clapham 2000). Observed feeding behaviours include: swimming, lunging and bubble netting (Jurasz and Jurasz 1979, Hain et al. 1982, Goldbogen et al. 2008). Humpback whales either feed by themselves, in pairs or sometimes in cooperating groups (Whitehead 1983; Baker and Herman 1984a; Perry et al. 1990; Strailey 1990; Baker et al. 1992; Clapham 1993, 2000).
Different feeding techniques in different ocean basins have been observed (Clapham 2000). Certain feeding behaviours may involve cultural transmission throughout a population (Weinrich et al. 1992) and changes in feeding behaviours have been reported at the same time as changes in prey behaviour (Friedlaender et al. 2009).

1.2 DISTRIBUTION

Humpback whales are found in all oceans of the world in both the Northern and Southern Hemisphere. They migrate annually over long distances between tropical and temperate breeding grounds and high latitude polar feeding areas (Baker 1990, Rasmussen et al. 2007). Genetic research has shown that there are three major groups of humpback whales: The North Atlantic and North Pacific populations and the Southern Hemisphere population (Baker et al. 1993, Baker and Medrano-Gonzalez 2002, Fleming and Jackson 2011).

1.2.1 Northern Hemisphere

In the North Pacific and the North Atlantic Humpback whale populations are widely distributed across the two ocean basins, while in the North Indian Ocean there is a single isolated population (Clapham 2000, Fleming and Jackson 2011).

1.2.1.1 North Pacific

There are complex linkages between breeding grounds and feeding areas in the North Pacific with strong maternal fidelity to both breeding grounds and feeding areas and low levels of interchange between separate sub-populations (Calambokidis et al. 2008). Humpback whales migrate between the North Pacific feeding areas with overwintering and breeding grounds in offshore Mexico, Central America and mainland Mexico, Hawaii and Asia (Calambokidis et al. 2008). The Hawaiian Islands
are considered the primary breeding grounds for North Pacific humpback whales (Calambokidis et al. 2008, Herman et al. 2011).

In the eastern North Pacific feeding areas occur off California and Alaska and in the western North Pacific as far west as Russia (Clapham 2000, Calambokidis et al. 2008, Fleming and Jackson 2011).

The California coast along with the Oregon coast and the northern Washington coast are the most easterly feeding areas in the North Pacific (Baker et al. 1994, 1998a, 2008; Calambokidis et al. 1996, 2000, 2008; Darling et al. 1996). Further north, dense feeding areas are found across the Alaskan region in the eastern and western Gulf of Alaska, southeastern Alaska and further west in the Bering Sea and the eastern Aleutian Islands (Baker et al. 1985, 1990, 1992, 1994, 1998b, 2008; Perry et al. 1990; Calambokidis et al. 1996, 2008). In the western North Pacific, feeding areas have been identified at the western end of the Aleutian Islands, Kuril Islands, Commander Islands and the east side of Kamchatka with the most westerly feeding areas in Russian waters in the Gulf of Anadyr (Baker et al. 2008, Calambokidis et al. 2008).

Hawaiian breeding grounds are located in the main Hawaiian Island of 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, 1998, 2008; Calambokidis et al. 2008; Herman et al. 2011). In Asia breeding grounds are in 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 Mexican breeding grounds include 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). Interchange of individual humpback whales between the breeding grounds in Japan and Hawaii has also been reported (Darling and Cerchio 1993, Salden et al. 1999).

1.2.1.2 North Atlantic

Humpback whales feeding across the North Atlantic Ocean migrate annually to breeding grounds located 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).

North Atlantic feeding areas have been reported in the eastern North Atlantic at 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); in the western North Atlantic at West Greenland, Newfoundland and Labrador in Canada and the Gulf of St Lawrence (Whitehead 1983; Katona and Beard 1990; Palsboll et al. 1995, 1997; Smith et al. 1999; Stevick et al. 2003, 2006); and 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 only mid-ocean stopover location reported is Bermuda, where the western North Atlantic humpback whales may feed in deep waters around Bermuda during the stopover (Stone et al. 1987)
1.2.1.3  Indian Ocean

A unique population of humpback whales is located in the Oman Sea, off the Arabian Peninsula, which is non-migratory and remains year-round in temperate waters (Reeves et al. 1991, Mikhalev 1997, Minton 2004, Rosenbaum et al. 2009, Minton et al. 2011). Photo-identification and genetic analysis have confirmed that this is an isolated population (Minton 2004, Rosenbaum et al. 2009, Minton et al. 2011). It is a small, endangered population (< 100 individuals, Minton et al. 2011) and is threatened by a range of environmental and anthropogenic impacts (Baldwin et al. 2010, Braulik et al. 2010, Corkeron et al. 2011, Minton et al. 2011).

1.2.2  Southern Oceans

The International Whaling Commission recently initiated a comprehensive assessment of Southern Hemisphere humpback whale populations (IWC 2011). They identified relatively discrete breeding groups off the coasts of South America, Africa, western and eastern Australia and in the Pacific. They also documented known or hypothesised linkages with Antarctic feeding areas. The results are summarised in Figure 1.2.2.1 (IWC 2011).
Figure 1.2.2.1. Southern Hemisphere humpback whale 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 2011).

Breeding aggregations in the Southern Hemisphere occur in the Pacific Ocean off eastern Australia (breeding Group E1, Fig 1.2.2.1), across the South Pacific (breeding Groups E2, E3, F1 and F2, Fig 1.2.2.1) and off the western coast of Central America and South America (breeding Group G, Fig 1.2.2.1). In the Atlantic Ocean off eastern South America along the Brazilian coast (breeding Group A, Fig 1.2.2.1) and off West Africa (breeding Group B, Fig 1.2.2.1). In the Indian Ocean off East Africa (breeding Group C, Fig 1.2.2.1) and off Western Australia (breeding Group D, Fig 1.2.2.1).
1.2.2.1 South America (Breeding Groups G and A)


Group (G) humpback whales migrate 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). Humpback whales breeding in Central America primarily feed in the Magellan Strait whereas humpback whales breeding off the northwestern coast of South America feed in areas off the western Antarctic Peninsula (Olavaria et al. 2006a, Acevedo et al. 2008b).

Group (A) humpback whale breeding locations are 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, 2006b; 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). The Group (A) humpback whales migrate to feeding areas in offshore waters of the South Sandwich Islands, off
the western Antarctic Peninsula and of South Georgia (Zerbini et al. 2006, Engel et al. 2008, Engel and Martin 2009).

1.2.2.2 South Africa (Breeding Groups B and C)

The Group (B) breeding grounds off the West Africa coast are found in the Gulf of Guinea (breeding Group B1); in the Bight of Benin, Togo, the Sao Tome and Principe Archipelago and north at Pagalu (Aguilar 1985; Van Waerebeek 2003; Rosenbaum and Mate 2006; Picanco et al. 2009), and also further south 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). A separate genetic sub-population has been found migrating in waters off Namibia and west South Africa (B2, Fig. 1.2.2.1) but the breeding location of this sub-population is yet to be located (Barendse et al. 2006, 2011; Rosenbaum and Mate 2006; Rosenbaum et al. 2009).

West African humpback whales also migrate to waters off Bouvet Island, southwest of Africa (Rosenbaum and Mate 2006, Engel and Martin 2009) and to the waters of St Helena in the southeastern Atlantic (Macleod and Bennett 2007).

Feeding areas for West African humpback whales have been found south of the Walvis Ridge off Namibia and the waters of Saldanha Bay southwest Africa (Best et al. 1995; Barendse et al. 2006, 2011).

Three separate breeding aggregations have been identified for Group (C) humpback whales off the East African coast. The coastal waters of Madagascar (C3, Fig. 1.2.2.1), (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); Comoros Islands, Mayotte Island and islands and reefs of the Mozambique Channel (C2, Fig. 1.2.2.1), (Best et al. 1998; Ersts et al. 2006, 2011; Kiska et al. 2007; Rosenbaum et al. 2009;
Findlay et al. 2011) and the Seychelles, Tanzania and Mozambique (C1, Fig. 1.2.2.1), (Reeves et al. 1991, Best et al. 1998, Hermans and Pistorious 2008, Rosenbaum et al. 2009, Findlay et al. 2011). The putative feeding areas of Group (C) are unknown and may be in Antarctic Area III from $5^0$ E and $60^0$ E (IWC 2011, Tynan 1998, Fig. 1.2.2.1).

1.2.2.3 Western Australia (Breeding Groups D)

Breeding aggregations for Group (D) off the west coast of Australia occur at Camden Sound and in the Kimberley Region (Bannister and Hedley 2001, Jenner et al. 2001) with resting areas located further south at Exmouth and Shark Bay (Bannister, 1994, Bannister and Hedley 2001, Jenner et al. 2001).

Feeding areas for Group (D) humpback whales are in Antarctica above $56^0$S and between $80^0$E and $110^0$E (Area IV, Fig 1.2.2.1) (Rayner 1940; Chittleborough 1959a, 1965; Gill and Burton 1995; Matsuoka et al. 2006; Franklin et al. 2008). It has been suggested that some eastern Australian (E1) and western Australian (D) humpback whales may intermingle during summer feeding in Antarctic Area IV (Chittleborough 1965, Gales et al. 2009).

1.2.2.4 Eastern Australia and South Pacific (Breeding Groups E and F)

Humpback whales off eastern Australia (Breeding Group E1) are the focus of this research. The putative breeding and overwintering grounds of the eastern Australian (E1 breeding group) is within the lagoon of the Great Barrier Reef between $16^0$S and $23^0$S (Simmons and Marsh 1986, Chaloupka and Osmond 1999, Gales et al. 2010, Smith et al. 2012a, Fig. 1.6 and Fig. 1.7.1 below). The E1 breeding Group migrates annually to feeding areas within Antarctic Area V (Chittleborough 1965, Dawbin 1966, Rock et al. 2006), (Fig. 1.2.2.1 above) and early discovery tagging indicated
low levels of interchange with breeding Group D in Antarctic Area IV (Chittleborough 1965). During the annual migrations between breeding grounds in the Great Barrier Reef and Antarctic feeding Areas E1 humpback whales are observed along the eastern coastline of Australia off Eden, Ballina, Byron Bay, Stradbroke Island and the Gold Coast Bay during both the southern and northern migration (Chittleborough 1965, Dawbin 1966, Patterson 1991, Burns 2010, Paton et al. 2011, Gales et al. 2009, Meynecke et al. 2013) and in Hervey Bay during the southern migration (Patterson 1991, Corkeron et al. 1994, Chaloupka et al. 1999, Franklin et al. 2011, Franklin 2012).

Breeding aggregations in the South Pacific occur in the waters off (see Fig. 1.6 below): New Caledonia (163-169°E 18-23°S) (Garrigue and Gill 1994, Garrigue et al. 2001, Garrigue et al. 2010, Garrigue et al. 2011b); Vanuatu (168°E, 17°S) (Garrigue et al. 2004); Fiji (178°E 18°S) (Paton and Clapham 2002, Gibbs et al. 2006; Tonga (173-177°W, 15-23°S) (Dawbin 1966, Abernethy et al. 1992); Samoa and American Samoa (173-170°W, 13°S) (Noad et al. 2006, Robbins and Mattila 2006); Cook Islands (8-23°S 156-167°W) (Hauser et al. 2000, Hauser and Clapham 2006). No inter-annual re-sightings, only a few within season re-sightings and movements of satellite-tagged humpback whales suggest the Cook Islands may be a migratory corridor for humpback whales travelling towards Tonga (Hauser and Clapham 2006, Hauser et al. 2010, Garrigue et al. 2011a) and French Polynesia (8-27°S 134-155°W) (Gannier 2000, 2004; Poole 2002, 2006).

‘Discovery’ mark tagging during commercial whaling provided early evidence of linkages between eastern Australian and Oceania breeding grounds and Antarctic Area V and VI feeding areas (Chittleborough, 1959; Dawbin, 1964, Paton and Clapham, 2006). Investigation of migratory movement of humpback whales in the
Western Pacific led Dawbin (1949, 1956) to consider that the Balleny Islands and the Ross Sea were the putative summer destination for humpback whales that travel along the coasts of eastern Australia and other parts of the Pacific and through New Zealand waters. Prior to this study, only three individual photo-ID matches have been reported between humpback whales that migrate along the eastern Australian coast (E (i) Breeding Stock) and Antarctic Area V feeding areas in the vicinity of the Balleny Islands and the Ross Sea (Kaufman et al., 1990; Rock et al., 2006). No photo-ID matches have been reported between any of the Oceania breeding grounds and Area V or Area VI Antarctic feeding areas. However, one recent genotype match was reported between New Caledonia and the Antarctic Area V feeding area, and a small number of genotype matches have been reported between Oceania breeding grounds and Antarctic Area I and VI feeding areas (Steel et al. 2008).

During the 1950s a comprehensive study was undertaken of the migration of humpback whales through New Zealand waters (Dawbin and Falla, 1949; Dawbin, 1956; Dawbin, 1966) and the breeding ground destinations of humpbacks travelling through New Zealand waters were considered to be the eastern Coral Sea. Including the Chesterfields and New Caledonia, and the Tongan Group of islands (Dawbin and Falla 1949).

1.3 MIGRATION

Humpback whales occur in every ocean of the world and migrate very long distances of up to 16,000 to 18,800 km a year between winter breeding grounds in tropical and near tropical waters and summer feeding areas in cold temperate or near-polar waters (Baker et al. 1990, Rasmussen et al. 2007, Robbins et al. 2011). The timing of the migrations in each of the Northern and Southern hemisphere is asynchronous around the equator; so that when Northern Hemisphere humpbacks are in high
latitude feeding areas in the boreal summer the Southern Hemisphere humpback whales are in low-latitude tropical breeding grounds during the austral winter. Conversely when Northern Hemisphere humpbacks are in low-latitude tropical breeding areas in winter, Southern Hemisphere humpbacks are in Antarctic feeding areas during the austral summer (Omura 1953; Dawbin 1956, 1966; Chittleborough 1965; Baker et al. 1990; Clapham 2000). Humpback whales require some period in suitable semitropical coastal waters for normal breeding behaviour with waters temperatures in the range of $24^\circ$C to $28^\circ$C (Dawbin 1966, Whitehead and Moore 1982, Herman and Antinoja 1977). Limited equatorial spatial overlap occurs between Southern and Northern hemisphere humpback whales, in breeding areas off Central America and off the Gulf of Guinea West Africa, (Acevedo and Smultea 1995, Van Waerebeek 2003, Stevick et al. 2004, Best 2008). It has been suggested that the overlap may be related to regional water temperatures either side of the equator for breeding activity (Rasmussen et al. 2007).

1.3.1 Why do humpback whales migrate

Migratory evolution in a species may be related to the maximization of fitness in a seasonal environment (Alerstam et al. 2003). In the case of the Mysticeti whales there are two primary hypotheses for the drivers of migration, which involve selective advantage for pregnant females and their calves:

(a) Migrating to low-latitude tropical waters for breeding reduces the risk of predation from Orca whales, particularly for neonatal calves (Corkeron and Connor 1999, Connor and Corkeron 2001).

(b) The birthing of calves in warm low-latitude waters provides an advantage to calves, enabling them to devote more energy on development and growth rather than on survival, as would be the case in cold polar waters. Thus birthing in warm
low-latitude waters may produce an overall higher rate of reproductive success 

Orca whales do prey upon humpback whales with calves being relatively more 
vulnerable to predation (Naessig and Lanyon 2004, Mehta et al. 2007, Reeves et al. 
2006, Ford and Reeves 2008, Steiger et al. 2008) and the abundance of Orca is 
higher towards the poles compared to the tropics (Forney and Wade 2007), which is 
consistent with hypothesis (a) above.

However, water temperature appears to be a fundamental factor for the selection of 
breeding grounds with humpback whale populations migrating to breeding areas 
where water temperature is at least 25°C within the range 24°C to 28°C (Dawbin 
2007). Some populations cross the equator to travel to areas with warmer waters 
(Stone et al. 1990, Rasmussen et al. 2007). The importance of water temperature in 
breeding grounds supports hypothesis (b) above.

Whilst the debate on why baleen whales migrate remains presently unresolved a 
recent study suggested a novel hypothesis that long migrations between cold polar 
waters and warm tropical water may be related to the physiological maintenance of 
skin in Orca whales and that similar physiological constraints could be a factor 
influencing the migration of large baleen whales (Durban and Pitman 2012).

1.3.2 Temporal segregation and migratory timing

Temporal segregation by age, sex and reproductive class has been shown to occur in 
baleen whale migrations (Nishiwaki 1959; Chittleborough 1965; Dawbin 1966, 
1997, Swartz 1986). To study temporal segregation in the southern oceans Dawbin 
(1997) obtained samples between 1°S and 66°S, from coastal whaling areas off the 
west and east coast of Africa, west and east coasts of Australia, from New Zealand
waters and from Antarctic commercial whaling pelagic catches, both pre and post
the Second World War (Dawbin 1966, 1997). Dawbin (1966, 1997) reported no
significant differences in trends of the timing of occurrence of the age and
reproductive classes of humpback whales examined within each of the separate
tropical breeding grounds.

During the northern migration from their Antarctic feeding areas, lactating
humpback females with calves from the previous season were first to commence
northward travel followed by immature males and females about 12 days later. Ten
days after the immatures, mature males began moving north with mature early
pregnant and resting females being the final cohort to move north separated from
the lactating females by about a month (Dawbin 1966, 1997). The first cohort to
travel south from tropical breeding grounds, are early pregnant or resting females
closely followed by immature males and females, then mature males and finally
lactating females with new calves (Dawbin 1966, 1997).

Immature males and females and mature males retain the same position within the
migratory procession during both the northern and southern migration and spend
about the same time in both feeding and breeding areas. In contrast, mature females
move between the vanguard and rearguard of the migratory procession depending
upon their reproductive status. Early pregnant females are the first to leave the
breeding grounds southbound and the first to arrive in Antarctica and they are last to
leave Antarctic feeding areas northbound. In contrast lactating females are last to
leave the breeding grounds southbound and first to leave Antarctic feeding grounds
northbound. Consequently newly pregnant females spend the longest time in
Antarctic feeding areas while lactating females spend the shortest time (Dawbin
1966, 1997).
Off the east coast of Australia, because of the timing of commercial whaling, Dawbin had a small and biased sample to investigate temporal segregation. As a consequence the results he reported underestimated the southbound intervals between age and reproductive cohorts (Dawbin 1997). Franklin (2012) using long-term photo-identification found that the temporal segregation of age and reproductive classes in Hervey Bay was consistent with Dawbin’s earlier findings. The results of both studies are summarised in figure 1.3.2.1.

Figure 1.3.2.1. Temporal segregation of specified categories of humpback whales from Dawbin (1966) and Franklin (2012). Migration from tropical waters (left) and from Antarctic waters (right) by days after the passage of the earliest migrating humpback whales, showing mean value for each category (Source, adapted from: Franklin 2012).

Eastern Australian humpback whales (E1 Group) spend approximately two months on average in the northern part of their migratory range, of which approximately 4 weeks is spent in the breeding grounds within the lagoons of the Great Barrier Reef (Smith et al. 2012a, Burns et al. 2014). On average they spend 9 weeks travelling south and north between tropical breeding grounds and Antarctic feeding areas and, 25 weeks in Antarctic feeding areas (Burns et al. 2014).

1.3.3 Breeding and feeding site fidelity and residency

Baker et al. (1990) reported segregation of mitochondrial DNA haplotypes among sub-populations 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. Long-term photo-identification studies have documented maternally directed fidelity to feeding destinations in the Northern Hemisphere (Martin et al. 1984, Clapham and Mayo 1987, Baker et al. 1990, Katona and Beard 1990, Perry et al. 1990, Clapham et al. 1993, Palsboll et al. 1997, Weinrich 1998). Fidelity to breeding grounds over multiple years has been

1.4 LIFE HISTORY AND POPULATION PARAMETERS

1.4.1 Birth, growth and age

Calves are born in sub-tropical and tropical waters during winter months after a gestation period of approximately 11 to 12 months (Clapham 2000). No humpback whale birth event has been observed and recorded (Matthews 1937; Chittleborough 1958a, 1965; Clapham 2000). At birth neonates weigh about two tons and average 4.5 m in length (Tomilin 1957, Chittleborough 1958a, 1965, Bannister et al. 1996, Clapham and Mead 1999). A few twin fetuses were observed during commercial whaling operations but there are no reports or evidence of twin births, or survival of twins, and humpback females are considered uniparous (Chittleborough 1958a, 1965; Slijper 1962; Mikhailov 1997; Clapham 2000).

Calves are fed by mothers during the first months of their life (Oftedal 1997) and remain with their mothers during most of the first year of their life. They are feeding independently by about 6 months and weaning generally occurs by the age of 12 months (Chittleborough 1958a; Baker and Herman 1984b; Clapham and Mayo 1987, 1990; Glockner-Ferrari and Ferrari 1990; Baraff and Weinrich 1993; Clapham 1993). During its first year a calf doubles in size from an average of 4.5 m to an average of 9 m (Tomilin 1957, Chittleborough 1965). Most calves are separated from their mother and independent towards the end of their natal year (Clapham et
al. 1999), with a few remaining associated with their mothers for up to another year (Baraff and Weinrich 1993).

By the average age of sexual maturity at around 4 to 5 years, females are on average 11 m to 13 m and males are 10 m to 12 m (Tomilin 1957, Chittleborough 1959a, 1965, Nishiwaki 1959, Clapham 1992). Chittleborough (1965) reported that physical maturity in humpback whales occurred about 12 years after sexual maturity and that physically mature males and females were about 13 m and 13.9 m respectively (Chittleborough 1965).

Chittleborough (1965) reported that, from his sample of 894 humpback whales collected between 1952 and 1962 there were very low levels of physical maturity, with 1.4% in males and 1.8% in females. Whereas for a mature baleen stock, the range of physically mature individuals was expected to be between 25% and 35% (Macintosh 1942). Chittleborough (1965) surmised that the most likely reason for this bias was that whalers had intentionally selected for killing larger, older humpback whales. Consequently, Chittleborough (1965) may have underestimated the lengths of humpback whales at physical maturity. This is supported by evidence of body lengths reported from earlier commercial whaling sources, which ranged from 14.2 m to 16.2 m for males and 15.5 m to 18.6 m for females (True 1904, Clapham et al. 1997, Chittleborough 1965). Clapham and Mead (1999) urged caution in interpretation of these length data and noted that while humpback whales of 17 m to 18 m long seem unlikely, some pristine populations may have contained a few individuals of this size.

The removal of most ‘old’ whales from the populations by whaling made the life expectancy of humpback whales difficult to estimate (Clapham 2000). The age of humpback whales was originally calculated by counting the laminations of light and dark layers that accumulate as waxy accretions in the auditory canal, as one growth
layer (GLG) (Chittleborough 1959b, 1965). Using an age estimate of two GLG’s accrued per annum (Chittleborough 1959b, Robins 1960) Chittleborough reported the oldest humpback whale he examined off Western Australia was 48 years old. However, a recent review of the original GLG counts, and available age calibration evidence from corpora lutea, concluded that one rather than two GLG is accrued annually (Best 2006, 2011). This suggests the likelihood that the age of Chittleborough’s oldest whale should be doubled from 48 years to 96 years. Therefore, it is possible that the maximum longevity of a mature humpback whale may be about 100 years.

1.4.2 Age at first parturition and reproduction

Ovulation in females and the presence of sperm in male testes indicates sexual maturity (Chittleborough 1954, 1955a, 1955b). The average age of sexual maturity was reported to be from 4 years to 5 years (Tomilin 1957, Chittleborough 1959a, 1965, Nishiwaki 1959, Clapham 1992). The study by Clapham (1992) in the Gulf of Maine using long-term photo-identification of known individuals reported sexual maturity at 5 years of age. However, more recent studies have reported higher ages for first calving in some populations. In southeastern Alaska, Gabriele et al. (2007a) reported an average age of 11.8 years for first calving and Robbins (2007) found the age at first calving to be 8.78 years. Reasons for the differences in the results of age at first calving reported in these studies, have not yet been determined (Best 2011).

Whilst females and males are reported to reach sexual maturity at similar ages, it has been suggested that males may not have sufficient experience to successfully compete with older males and to therefore reproduce until they approach full physical maturity around 17 years of age (Chittleborough 1965, Clapham 1992, Franklin 2012).
The peak birth month in the Northern Hemisphere is February (Herman and Antinoja 1977, Whitehead 1981) while in the Southern Hemisphere the peak birth month was found to be August (Matthews 1937; Chittleborough 1958a, 1965). The peak birth month of August for females in the Southern Hemisphere coincides with the peak of spermatogenesis in male testes during August (Chittleborough 1955a). Ovulation of females in the Southern Hemisphere occurs from June to November and generally females only ovulate once, some twice and very few ovulate three times during that period (Chittleborough 1953, 1954, 1965).

The birthing interval of females in both the Northern and Southern Hemisphere is on average a calf every two to three years (Wiley and Clapham 1993, Chittleborough 1965, Barlow and Clapham 1997, Steiger and Calambokidis 2000, Clapham and Baker 2009). Some consecutive year births of more than three years have been reported (Glockner-Ferrari and Ferrari 1984, 1990).

Average annual birthing rates reported from specific regions include: Western Australia, 0.37 (Chittleborough 1965); Alaska, 0.37 and 0.36 (Baker et al. 1987, 1992); Gulf of Maine, 0.42, 0.42 and 0.39 (Clapham and Mayo 1990, Barlow and Clapham 1997, Clapham et al. 2003); California, 0.44 (Steiger and Calambokidis 2000); Hawaiian Islands, 0.48 (Herman et al. 2011); Gulf of Maine, 0.42 (Robbins 2007). Post-partum ovulation and single-year inter birth intervals do occasionally occur (Chittleborough 1965, Clapham and Mayo 1987, Glockner-Ferrari and Ferrari 1990, Franklin 2012), which may be related to early calf mortality and or females fitness (Lockyer 1984, Clapham and Mayo 1987, Gabriele et al. 2001).

There is no evidence of cessation of reproduction with age in baleen whales and whether there is a decline in reproduction with age among female humpback whales remains unresolved (Marsh and Kasuya 1986, Robbins 2007).
1.4.3 Survivorship

Survival is an important demographic parameter, that plays an important role in the assessment of humpback whale populations (Zerbini et al. 2010). Early survival rate analysis utilised simple time-varying models (Mizroch et al. 2004). The development of the MARK program (White and Burnham 1999) allowed the generalization and parameterization of existing CJS models (Cormack 1964, Jolly 1965, Seber 1965) and provided the basis for the utilisation of more complex modeling of survival and other biological parameters (Pollock 1982; Burnham 1993; Kendall et al. 1995, 1997; Kendall and Nichols 1995; Pradel 1996; Barker 1997; Schwarz and Stobø 1997; Barker and White 2001; Kendall and Bjorkland 2001). These developments enhanced the estimation of survival from large and complex datasets (Mizroch et al. 2004).

Survival rates in humpback whales are usually reported as calf and non-calf survival, with calf survival sub-divided into 6-month survival and, 6 to 12 month survival (Zerbini et al. 2010). A summary of recent estimates of non-calf and calf survival are reported in Table 1.4.3.1, which was adapted from Zerbini et al. (2010).
Table 1.4.3.1  Estimates of non-calf and calf survival by mean, SE (where available), 95% CI, region, years and source study. (Adapted from Zerbini et al. 2010).

<table>
<thead>
<tr>
<th>MEAN</th>
<th>SE</th>
<th>95% CI</th>
<th>REGION</th>
<th>YEARS</th>
<th>STUDY</th>
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<tr>
<td>SURVIVAL – NON-CALF</td>
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<td>North Atlantic</td>
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<tr>
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<td>1979–1991</td>
<td>Barlow and Clapham (1997)</td>
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<td>Rosenbaum et al. (2002)</td>
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<td>Western Greenland</td>
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<td>6- to 18-month survival, Robbins (2007)</td>
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1.4.4 Global abundance, rates of increase (ROI) and impacts of whaling

The pre-exploitation estimate of humpback whales worldwide was conservatively thought to be greater than 120,000 whales (Johnson and Wolman 1984) and humpback whale populations became subject to commercial whaling during the late 1800s in the eastern and northern Atlantic and the North and South Pacific (Johnson and Wolman 1984, Clapham and Baker 2009). Humpback whales became a major focus of modern commercial whaling in Antarctica between 1904 and the early 1970s (Chittleborough 1965, Clapham and Baker 2009) and were severely impacted by Soviet illegal whaling between 1947 and 1973 (Clapham et al. 2009, Ivaschenko et al. 2011). The total commercial whaling catch of humpback whales, between 1900 and 2005, was reported at 213,245 whales (Clapham and Baker 2009) reducing many populations to near extinction (Baker et al. 1993). A detailed summary of impacts, exploitation and recovery of humpback whales in the South Pacific and eastern Australia is presented in Section 1.5 below.

Humpback whales have been protected in some parts of the world from 1955 and globally since 1963 and numbers have increased from a few thousand in the mid-1960s to more than an estimated 60,000 (Harrison et al. 2009, Woinarski et al. 2014). The IUCN status of humpback whales has moved from ‘endangered’ in 1986, to ‘vulnerable in 1990 and to ‘least concern’ in 2008. However some sub-populations, Oceania and the Arabian Sea, have shown low ROI and have remained on the ‘endangered’ list (Harrison et al. 2009). Estimates of ROI in humpback whale populations worldwide show wide variability (Table 1.4.4.1 below, adapted from Zerbini et al. 2010). Furthermore some estimated rates may not be plausible and
possibly inflated because of survey bias, population sub-structuring and immigration from other populations (Zerbini et al. 2010).

Table 1.4.1. Estimates of rates of increase (ROI) for some humpback whale populations worldwide (adapted from Zerbini et al. 2010)

<table>
<thead>
<tr>
<th>Region</th>
<th>Period</th>
<th>ROI (% yr)</th>
<th>Reference#</th>
</tr>
</thead>
<tbody>
<tr>
<td>North Pacific</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern Gulf of Alaska</td>
<td>1987–2003</td>
<td>6.6</td>
<td>Zerbini et al. (2006a)</td>
</tr>
<tr>
<td>West coast of the USA</td>
<td>1990–2008</td>
<td>8.0</td>
<td>Calambokidis (2009)</td>
</tr>
<tr>
<td>North Atlantic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Southern Hemisphere</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Australia</td>
<td>1978–2004</td>
<td>9.6</td>
<td>Branch (2011)</td>
</tr>
<tr>
<td>Antarctic (Circumpolar)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Western Pacific Ocean/E</td>
<td>1984–2007</td>
<td>10.9</td>
<td>Noad et al. (2008)</td>
</tr>
<tr>
<td>Australia</td>
<td>1987–1999</td>
<td>10.9</td>
<td>Paterson et al. (2001)</td>
</tr>
<tr>
<td>Antarctic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antarctic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Antarctic</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Western South Atlantic</td>
<td>1995–1998</td>
<td>7.4</td>
<td>Ward et al. (2011)</td>
</tr>
<tr>
<td>Antarctic</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

# See Zerbini et al. (2010) for a detailed discussion of these results.

Earlier estimates of maximum ROI for humpback whale populations of 14.7% and 13.4 % were based upon unrealistic assumptions and extreme parameter values (Brandao 2000, Clapham et al. 2001, Zerbini et al. 2010). Zerbini et al. (2010) reviewed available data on humpback whale life-history parameters and computed a distribution of plausible growth rates for humpback whales. They used a mean non-calf survival rate of 0.984; a mean calf survival rate of 0.669 and 0.808; a mean age at first parturition of 5.9 years and a mean birthrate of 0.41, resulting in an estimated mean ROI of 7.3 % to 8.6 % per year and a proposed maximum ROI for humpback whales of 11.8% per year.
1.5 WHALING EXPLOITATION OF HUMPBACKS AND OTHER WHALES IN THE 20TH CENTURY

British and American sailing whaling ships arrived in the Pacific in the late 18th century and initially exploited sperm and right whales, leaving humpback whales in the South Pacific relatively untouched until modern industrial whaling commenced in the 20th century (Townsend 1935, Smith et al. 2012b), (For a brief history of this period see Appendix I, page 331 below).

Two simultaneous technical innovations in the late 19th century laid the foundation for 20th century modern industrial whaling, the invention of the explosive harpoon fired from a cannon and the development of fast steam-powered whale catchers. (Harrison 1968, Clapham and Baker 2009). Modern industrial whaling developed in three phases over the first 60 years of the 20th century. The first phase was based on the model developed by Svend Foyn of well-equipped shore-based factories supported by fast catcher vessels. In the early 1900s the Norwegians invented the large floating factory ship, which could be moored in sheltered bays, supported by fast catchers and able to be moved from place to place, seeking fresh stocks of whales as needed. The final and most lethal phase was the well-equipped pelagic factory ship, with the addition of the stern slipway from 1925. By 1929 most pelagic factory ships were purpose built for whaling and the first diesel catcher was built in 1937 (Harrison 1968, Clapham and Baker 2009).

The success of the Norwegians during the late 1800s and early 1900s led to an expansion of whaling bases world-wide This stimulated Britain, Russia and Japan to engage in modern industrial whaling and finally led to industrial whaling in Antarctica. On a whaling voyage to Antarctica during the late 1890’s, Capt. L. A. Larsen reported large stocks of untouched rorqual whales. He returned to Antarctica
in 1904, to establish the first shore-based whaling station on the South Georgia Islands, supported by fast catcher vessels. By 1911 there were six shore-based whaling factories established and operating from the South Georgia Islands, all using fast catcher vessels with explosive harpoons (Harrison 1968). The Perano family commenced shore-based whaling with custom built fast catchers in the Cook Straits, New Zealand in 1911. Along with shore-based whaling at Norfolk Island and on the coast of eastern Australia, shore-based whaling continued through until the early 1960s (Dakin 1963, Grady 1982, Suter 1982). Owing to depleted stocks of right whales from earlier sailing ship whaling in the late 19th century, humpback whales were the primary species targeted by shore-based whaling in Australia, New Zealand and Antarctica between 1904 and 1964 (Matthews 1937, Daikin 1963).

The first pelagic whaling factory vessel in Antarctica was the ‘Sir James Clark Ross’, sent to the Ross Sea with catchers in 1923 (Harrison 1968). Harrison (1968) reflected that the killing ‘efficiency of the pelagic whalers and their catchers were the cause of their ruin’. By the 1930-31 season there were forty-one pelagic factory ships in Antarctica with 200 catchers and during that season alone they killed 40,000 whales (Harrison 1968). By the 1966-67 seasons, a scarcity of whales reduced the Antarctic pelagic fleet to only nine factory ships (Harrison 1968). Japan established modern industrial whaling in the early 1900s and only entered Antarctic pelagic whaling in 1934. During late 1930s they operated six factory ships, all of which were sunk during the World War II (Harrison 1968).

Overall between 1904 and 1983 a total of 2,019,000 whales were reported taken in Southern Hemisphere waters during the three phases of whaling described above (Clapham and Baker 2009). The catch by species is summarised in Table 1.5.1.
Table 1.5.1 Southern Hemisphere catch totals, 1900-2005: Source: IWC. (Reprinted from Clapham and Baker 2009).

<table>
<thead>
<tr>
<th>Species</th>
<th>Catch</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue</td>
<td>362,770</td>
<td>17.66</td>
</tr>
<tr>
<td>Fin</td>
<td>725,331</td>
<td>35.30</td>
</tr>
<tr>
<td>Sei</td>
<td>203,843</td>
<td>9.92</td>
</tr>
<tr>
<td>Humpback</td>
<td>213,245</td>
<td>10.38</td>
</tr>
<tr>
<td>Bryde’s</td>
<td>7,881</td>
<td>0.38</td>
</tr>
<tr>
<td>Minke</td>
<td>119,415</td>
<td>5.81</td>
</tr>
<tr>
<td>Right</td>
<td>4,424</td>
<td>0.22</td>
</tr>
<tr>
<td>Sperm</td>
<td>405,898</td>
<td>19.76</td>
</tr>
<tr>
<td>Other</td>
<td>11,835</td>
<td>0.58</td>
</tr>
<tr>
<td>Total</td>
<td>2,054,642</td>
<td>100.00</td>
</tr>
</tbody>
</table>

A further 45,767 humpback whales were taken illegally by the Soviet whaling fleet in Southern Hemisphere waters but not reported to the IWC (Clapham and Baker 2009, Ivaschenko et al. 2011).

Clapham et al. (2009) reviewed catches of humpback whales in the Southern Ocean after World War II between 1947 and 1973, including legal and illegal Soviet catches and other pelagic and shore-based catches, and reported that at least 72,542 humpback whales were killed in this period. Around a third of these whales (25,192), came from Antarctic Areas IV and V below Australia and New Zealand in just two seasons, 1959/60 and 1960/61. This contributed directly to the collapse of the shore-based humpback whaling industry on the east coast of Australia, Norfolk Island and at New Zealand by the early 1960s.
1.5.1 Other threats

1.6 HUMPBACK WHALE POPULATION STRUCTURE IN EASTERN AUSTRALIA AND SOUTH PACIFIC

Since the late 1980s long-term photo-identification and genetic studies of humpback whales have been conducted across the South Pacific by scientists from the South Pacific Whale Research Consortium and Southern Cross University Whale Research Group. Study sites for both photo-identification and genetic studies include: Hervey Bay (Anderson et al. 2010, Franklin et al. 2011, Franklin 2012); Byron Bay and Ballina (Anderson et al. 2010, Burns 2010, Paton et al. 2011, Burns et al. 2012); New Caledonia (Garrigue et al. 2000, 2001); Vanuatu (Garrigue et al. 2004); New Zealand (Gibbs and Childerhouse 2000, Constantine et al. 2007); Tonga (Abernethy et al. 1992); Fiji (Paton and Clapham 2002); American Samoa (Robbins and Mattila 2006); Cook Islands (Hauser et al. 2000); and French Polynesia (Poole 2002, 2006) (Figure 1.6).

The movement of individual whales between wintering grounds within Oceania and between Oceania wintering grounds and eastern Australia were assessed using photo-identification matching of flukes collected at all sites between 1999 and 2004 (Garrigue et al. 2011a, 2011b), (Figure 1.6). Although the matches suggest low levels of longitudinal intermingling of individual humpback whales between breeding grounds and relative isolation amongst breeding groups, the data did not provide conclusive evidence of stock structure across the South Pacific.
Figure 1.6. Study sites of humpback whales across the South Pacific. Double-headed arrows represent photo-id matches between sites from a match between site catalogues of flukes collected between 1999 and 2004. The numbers of matches are shown midway along the lines (Source: Garrigue et al. 2011a, 2011b).

Genetic analysis of humpback whale DNA samples from eastern Australia, New Caledonia, Tonga, Cook Islands, eastern Polynesia, Colombia and Western Australia revealed significant differentiation at both the haplotype and nucleotide level ($F_{ST} = 0.033$; $\Phi_{ST} = 0.022$) among the seven breeding grounds and for most pair-wise comparisons (Olavarria et al. 2006b, 2007). Further, the data suggested that the IWC breeding stock E (IWC 2011) should be sub-divided into three separate breeding stocks: E1, eastern Australia; E2, New Caledonia and Vanuatu and E3, Tonga and Fiji (Olavarria et al. 2006b, 2007; Anderson et al. 2010).

Matching of microsatellite genotypes between eastern Australia and Oceania breeding areas found matches between New Caledonia and Tonga consistent with
the low levels of photo-identification matches reported above (Steel et al. 2008). Migratory interchange was also detected between eastern Australia, New Caledonia and Antarctic feeding Area V, and Tonga and Antarctic feeding area IV. In addition two matches were found between Tonga and Antarctic feeding Area I, and one genetic match between Colombia and Antarctic feeding Area 1 (Steel et al. 2008, Anderson et al. 2010). Prior to this study only one previous photo-identification fluke match has been reported between eastern Australia and Antarctic feeding Area V (Rock et al. 2006).

1.6.1 Eastern Australia and Oceania: Modelling of exploitation and population recovery

Recent modelling of population trajectories for the Oceania and east Australian humpback whale populations reveals the full and devastating impact of modern industrial whaling during the 20th century (Jackson et al. 2006, 2009). The median posterior estimates for carrying capacity ($K$), growth rate ($r_{max}$), minimum abundance ($N_{min}$), rate of recovery ($N_{2009}$: $K$), with 95% Posterior probability intervals are summarised in Table 1.6.1 and the modelled population trajectories between 1900 and 2020 are illustrated in Figure 1.6.1
Table 1.6.1 Posterior estimates: Carrying capacity ($K$), Growth rate ($r_{\text{max}}$), Minimum abundance ($N_{\text{min}}$), Rate of recovery ($N_{2009}$: $K$); with 95% Posterior probability intervals (Reprinted from Jackson et al. 2009).

<table>
<thead>
<tr>
<th>Carrying capacity</th>
<th>Posterior probability</th>
<th>Growth rate ($r_{\text{max}}$)</th>
<th>Posterior probability</th>
<th>Minimum abundance ($N_{\text{min}}$)</th>
<th>Posterior probability in 2009 ($N_{2009}$: $K$)</th>
<th>Rate of recovery</th>
<th>Posterior probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>East Australia (E1)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>22,093</td>
<td>20,062 - 26,673</td>
<td>10.5</td>
<td>10.2 - 10.6</td>
<td>196</td>
<td>168 - 243</td>
<td>0.46</td>
<td>0.38 - 0.54</td>
</tr>
<tr>
<td>Oceania (E2, E3, F)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20,576</td>
<td>14,573 - 24,019</td>
<td>5.1</td>
<td>3.8 - 7.4</td>
<td>676</td>
<td>376 - 1209</td>
<td>0.23</td>
<td>0.20 - 0.54</td>
</tr>
</tbody>
</table>
Coastal and pelagic commercial whaling severely depleted the eastern Australian and Oceania populations from the 1940s to the 1970s (Clapham et al. 2009, Jackson et al. 2009, Ivaschenko et al. 2011). By the early 1960s it is estimates that only about 200 eastern Australian humpback whales survived (Patterson et al. 1994, Jackson et al. 2009) with few breeding females (Chittleborough 1965) and in Oceania only about 700 humpback whales survived (Jackson et al. 2009). Recovery in eastern Australia was very slow between the early 1960s and 1990s, with the population estimated to have only increased to 1,900 whales (95% CI, 1,659-2,159, Patterson et
al. 1994) by 1992. The eastern Australian population increased rapidly from the mid-
1990s with an overall annual rate of increase of 10.6±0.5% (95% CI) for the period
1987 to 2004 (Jackson et al. 2009, Noad et al. 2011). In contrast recovery in Oceania
has been low relative to eastern Australia with an estimated growth rate of 5.1%
(95% CI, 3.8-7.4, Jackson et al. 2009). Some regions of Oceania, including the
Chesterfields off Noumea, Fiji and New Zealand, where catches of humpback whales
occurred during the late 19th century have shown no, or little, recovery (Dawbin
Overall there has been little indication of trends in abundance in Oceania (Baker et
al. 2006, Constantine et al. 2012) and very low rates of recovery overall in Oceania
(Jackson et al. 2006, 2009; Constantine et al. 2012).

Social aggregation of some of the remaining Oceania humpback whales with the
eastern Australian whales, after the near total collapse of both populations in the
early 1960s, has been hypothesised to explain the relatively more rapid rate of
recovery of the eastern Australian population (Clapham et al. 2006, Clapham and
Zerbini 2015).

1.7 HUMPBACK WHALES IN HERVEY BAY

Hervey Bay (25°S, 152°E) is south of the putative breeding and overwintering area of
eastern Australian humpback whales within the lagoon of the Great Barrier Reef
(Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999, Smith et
al. 2012a, Figure 1.7.1). Humpback whales enter and leave Hervey Bay from the
north and aggregate on the eastern side of Hervey Bay along the western shore of
Fraser Island (Corkeron 1993, Corkeron et al. 1994, Franklin et al. 2011, Franklin
2012, Figure 1.7.1). Hervey Bay is neither a terminal destination nor a calving area
for humpback whales, but rather a stopover early in the southern migration (Franklin 
et al. 2011, Franklin 2012).

![Map of Hervey Bay and its geographic relationship to the Great Barrier Reef. The migratory pathways of humpback whales 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 panel.](image)

**Figure 1.7.1** The left panel shows the location of Hervey Bay and its geographic relationship to the putative overwintering and breeding grounds within the inter-reef lagoon of the Great Barrier Reef. The migratory pathways of humpback whales 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 panel.

It has been suggested that 30% to 50% of eastern Australian humpback whales use Hervey Bay (Chaloupka et al. 1999). Humpback whales do not enter Hervey Bay during the northern migration, but move continuously through Hervey Bay during the southern migration from late-July to late-October (Franklin et al. 2011, Franklin 2012).
The seasonal pod characteristics, social behaviour and temporal segregation of reproductive and maturational classes of humpback whales using Hervey Bay was studied during the period 1992 to 2009 (Franklin et al. 2011, Franklin 2012). Pairs and singletons predominate early in the season and consist mainly of immature males and females involved in non-agonistic social behaviour. Pods with calves present are rarely seen during the first four weeks of the season, however mothers with older calves predominate during the last six weeks of the season. Mothers spend 69.4% of their time alone with their calves involved in maternal activities and only 10.8% of pods have one or more escorts present (Franklin et al. 2011, Franklin 2012).

Overall competitive pod activity is low (6.3% of pods), and increases significantly towards the end of the season, while non-agonistic social behaviour (11.8% of pods) occurs predominantly during the first four weeks of the season and declines sharply towards the end of the season. There is clear temporal segregation and clumping of non-lactating and lactating females. Non-lactating, resting and early pregnant females are in the company of immature males and females with peak density occurring in late August, while the peak density of lactating females occurs in late September. A female biased sex ratio together with the observed seasonal pod behaviour and temporal segregation of reproductive classes, suggest that Hervey Bay is a preferential habitat for females early in the southern migration, involving differential migration of males and females along the eastern Australian coastline near Hervey Bay (Franklin et al. 2011, Franklin 2012).

Previous research in Hervey Bay has provided important information on aspects of the ecology and behaviour of humpback whales utilising Hervey Bay but did not address the important question of the role and function of Hervey Bay in the migration of eastern Australian humpback whales.
1.8 FOCUS OF THESIS AND RESEARCH OBJECTIVES

The aim of the research presented in this thesis is to determine the role of Hervey Bay to eastern Australian humpback whales, and its function for the subpopulation of migrating humpback whales that use Hervey Bay.

To address this aim long-term photo-identification data and capture histories of individual humpback whales in Hervey Bay are analysed using capture-recapture modelling to investigate the population dynamics, and fluke matches are analysed to investigate migratory movements of humpback whales utilising Hervey Bay.

The overall objective of the research is to improve the understanding of where Hervey Bay fits into the migration of eastern Australian humpback whales and, what is the function of Hervey Bay for the migration of eastern Australian humpback whales.

The specific research objectives were:

♦ To investigate abundance within season and over years of humpback whales in Hervey Bay,

♦ To estimate population parameters of humpback whales in Hervey Bay, including probabilities of apparent survival within and between seasons, probabilities of entry and capture within seasons and survivorship, residency and site fidelity,

♦ To investigate reproduction rates and trends in abundance of the humpback whales utilising Hervey Bay,
♦ To investigate temporary immigration and the relationship of humpback whales using Hervey Bay to other eastern Australian humpback whales,

♦ To analyse stability of all natural marks on humpbacks whales and the implications for the management of photo-identification misidentification errors

♦ To investigate migratory interchange of humpback whales from Hervey Bay with the Oceania and Western Australian breeding groups, and as well linkages with Antarctic feeding areas.
1.9 THESIS FORMAT

Chapter 1 provides a general review on the biology and ecology of humpback whales globally. This chapter also reviews the population structure of humpback whales, population dynamics and impacts of whaling on Australian and other subpopulation groups in the South Pacific Ocean and a review of patterns of use of Hervey Bay by eastern Australian humpback whale.

Chapter 2 describes the study methods including: study site and survey timing, vessel-based surveys, observation, photo-identification, photographic data analysis, life history data and the extraction of capture histories for this study.

Chapters 3 examines the use of natural tags to identify individual humpback whales, assesses the stability of natural marks and the management of misidentification during the photo identification process.

CHAPTER 4, 5, 6 and 7 are the main data chapters and are formatted as either published manuscripts or manuscripts in preparation for publishing. Chapter 4 presents the capture history database, the model selection and description and results on population parameter estimates and abundance within and between seasons in Hervey Bay. Chapter 5 examines the reproductive rate of females utilising Hervey Bay and investigates trends in abundance. Chapter 6 presents the results of an analysis of fluke matches with Oceania breeding grounds and New Zealand catalogues and is based on a published manuscript. The focus of Chapter 7 is ‘where do Hervey Bay whales feed’. Sub-chapter 7.1 presents the results on analysis of fluke matches with a catalogue from the Antarctic Area V feeding area near the Balleny Islands and is based on a published manuscript. Sub-chapter 7.2 presents results on an analysis of a comparison between a fluke catalogue from the Antarctica Area IV

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feeding area with fluke catalogues from eastern Australia, western Australia and east Africa. Chapter 7.2 is formatted as a manuscript in preparation for publishing. Information on the movements of two humpback whales recorded from Hervey Bay that were satellite tagged off Eden during the southern migration is included in Appendix II.

Chapter 8 provides a synthesis and general conclusions arising from the thesis.

As the chapters and sub-chapters are in manuscript form there is necessarily some repetition of the information in general methods and general introduction review sections.
1.10 LITERATURE CITED IN INTRODUCTION & APPENDIX I


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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 TOP’s Hervey Bay humpback whale research study, and the focus of this thesis on the population dynamics and migratory interchange 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 WISP03749606).
2.2 STUDY SITE AND SURVEY TIMING

Hervey Bay, formed by Fraser Island and the Australian mainland, is located at 25°S, 153°E on the eastern coast of Queensland (Fig. 2.2.1). It is a wide, shallow bay approximately 4,000 km² in area and is generally less than 16 m deep, with a sand and mud bottom (Vang 2002). Fraser Island is 126 km long, 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. 2.2.1).

![Image of map showing Hervey Bay and the Great Barrier Reef](image)

Figure 2.2.1. 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°S and 23°S (shaded) (Simmons and Marsh 1966, Paterson 1991, Chaloupka and Osmond 1999, Smith et al. 2012). The study area and the Hervey Bay Marine Park boundaries are shown on the eastern side of Hervey Bay.

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Paterson (1991) reported that the annual southern migration of humpback whales 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 1967 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 5th of August until mid-October. The study area (Fig. 2.2.1) is approximately 27.6 km from Urangan Boat Harbour, Hervey Bay. Fieldwork was planned for six days each week, leaving Urangan harbour at 0600 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 12.9-16.5 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.

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). Members of the research team constantly scanned 360° for any pods approaching the pod under observation.

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 1984a, 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 1984b; 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 that an individual was a male.

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. Sloughed-skin samples were also 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 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 identification and behavioural information of individuals in each pod were selected and 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 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 reights 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 2.5.1 and 2.5.2, Figure 2.5.2). 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 1961). The ACDC characteristics selected for the system (Table 2.5.1) were derived from a visual analysis of 26,000 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 2.5.2). A standard protocol was utilised for the allocation of ACDC codes to the filename of each fluke image (Table 2.5.1). 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 2.5.2) 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 in any given year, the ACDC filename reflects the changes 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 2.5.1. Examples of how ACDC categories display in photo-identification analysis software are presented in Figure 2.5.2.
Table 2.5.1 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.

<table>
<thead>
<tr>
<th>Code</th>
<th>Description</th>
<th>Protocol used for code assignment&lt;sup&gt;(a)&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(A) Primary Characteristics:</td>
<td>Step I</td>
</tr>
<tr>
<td>BB</td>
<td>Black Border</td>
<td>View and examine the ventral fluke photo from posterior to anterior across the horizontal plane for primary characteristics.</td>
</tr>
<tr>
<td>BC</td>
<td>Black Centre</td>
<td></td>
</tr>
<tr>
<td>BK</td>
<td>Black</td>
<td></td>
</tr>
<tr>
<td>TE</td>
<td>Trailing edge</td>
<td>Compare to examples (Fig 2.5.1) and assigned primary code or codes. If BB &amp; 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.</td>
</tr>
<tr>
<td>NT</td>
<td>Notch</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(B) Secondary Characteristics:</td>
<td>Step II</td>
</tr>
<tr>
<td>BS</td>
<td>Black Stem</td>
<td>View and examine the ventral fluke photo from posterior to anterior across the horizontal plane for secondary characteristics.</td>
</tr>
<tr>
<td>DM</td>
<td>Damaged</td>
<td></td>
</tr>
<tr>
<td>RK</td>
<td>Rake Marks</td>
<td></td>
</tr>
<tr>
<td>CR</td>
<td>Curled</td>
<td>Step IV</td>
</tr>
<tr>
<td>WP</td>
<td>White Patch</td>
<td>Compare to examples (Fig 2.5.1) and assign secondary codes from posterior to anterior for characteristics present. Separate each four digits of code by a hyphen.</td>
</tr>
<tr>
<td>BP</td>
<td>Black Patch</td>
<td></td>
</tr>
<tr>
<td></td>
<td>(C) Tertiary Characteristics:</td>
<td>Step V</td>
</tr>
<tr>
<td>SM</td>
<td>Scratch Marks</td>
<td>View and examine the ventral fluke photo posterior to anterior across the horizontal plane for any tertiary characteristics present.</td>
</tr>
<tr>
<td>DT</td>
<td>Dots</td>
<td>Step VI</td>
</tr>
<tr>
<td>RG</td>
<td>Rings</td>
<td>Compare to examples (Fig 2.5.1) 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.</td>
</tr>
</tbody>
</table>

<sup>(a)</sup> The examples (Figure 2.5.1 below) illustrate the stratification of categories from the applied ACDC codes in each fluke photograph filename.
Figure 2.5.1  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 2.5.2.

*Table 2.5.2* Number and % of flukes by primary ACDC categories in 1992-2009 fluke catalogue.

<table>
<thead>
<tr>
<th>Primary ACDC categories (1)</th>
<th>Number of Flukes</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>BBBC/BBDM/BBNT/BBRK (Black Borders plus)</td>
<td>51</td>
<td>1.8</td>
</tr>
<tr>
<td>BCBP/BCDM/BCCR/BCNT/BCRK (Black Centres plus)</td>
<td>214</td>
<td>7.6</td>
</tr>
<tr>
<td>BKDM/BKNT/BRKR/BKWP (Black plus)</td>
<td>66</td>
<td>2.3</td>
</tr>
<tr>
<td>TEBB (Trailing Edge, Black Border)</td>
<td>311</td>
<td>11.0</td>
</tr>
<tr>
<td>TEBP/TECR (Trailing Edge, Black Patch or Curled)</td>
<td>9</td>
<td>0.3</td>
</tr>
<tr>
<td>TEDM (Trailing Edge, Damaged)</td>
<td>93</td>
<td>3.3</td>
</tr>
<tr>
<td>TEHL (Trailing Edge, Holes)</td>
<td>52</td>
<td>1.8</td>
</tr>
<tr>
<td>TENT-1 (Trailing Edge (Thick), Notch)</td>
<td>372</td>
<td>13.2</td>
</tr>
<tr>
<td>TENT-2 (Trailing Edge (Medium), Notch)</td>
<td>742</td>
<td>26.3</td>
</tr>
<tr>
<td>TENT-3 (Trailing Edge (Fine), Notch)</td>
<td>696</td>
<td>24.7</td>
</tr>
<tr>
<td>TERK (Trailing Edge, Raked)</td>
<td>215</td>
<td>7.6</td>
</tr>
<tr>
<td><strong>Total Flukes 1992-2009</strong></td>
<td><strong>2821</strong></td>
<td><strong>100.0</strong></td>
</tr>
</tbody>
</table>

(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 2.5.1 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.
2.6 CAPTURE HISTORIES AND PHOTO IMAGE QUALITY

Life history information 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 capture histories were obtained with resightings of individually identified whales ranging from two to eighteen years. A summary of effort, observations and resight data is presented in Table 2.6.1.

Table 2.6.1. Summary of fieldwork, observations and resight data: Hervey Bay from 1992 to 2009.

<table>
<thead>
<tr>
<th>Year</th>
<th>First day</th>
<th>Last day</th>
<th>Field days</th>
<th>Pods</th>
<th>Whales</th>
<th>Fluke photos</th>
<th>Resighting histories</th>
<th>Cumulative Resighting histories</th>
</tr>
</thead>
<tbody>
<tr>
<td>1992</td>
<td>10th Aug</td>
<td>9th Oct</td>
<td>42</td>
<td>189</td>
<td>387</td>
<td>4</td>
<td>4</td>
<td>4</td>
</tr>
<tr>
<td>1993</td>
<td>6th Aug</td>
<td>15th Oct</td>
<td>53</td>
<td>229</td>
<td>442</td>
<td>5</td>
<td>3</td>
<td>7</td>
</tr>
<tr>
<td>1994</td>
<td>7th Aug</td>
<td>14th Oct</td>
<td>50</td>
<td>163</td>
<td>380</td>
<td>47</td>
<td>36</td>
<td>43</td>
</tr>
<tr>
<td>1995</td>
<td>6th Aug</td>
<td>13th Oct</td>
<td>51</td>
<td>172</td>
<td>374</td>
<td>47</td>
<td>27</td>
<td>70</td>
</tr>
<tr>
<td>1996</td>
<td>4th Aug</td>
<td>11th Oct</td>
<td>48</td>
<td>185</td>
<td>410</td>
<td>70</td>
<td>26</td>
<td>96</td>
</tr>
<tr>
<td>1997</td>
<td>1st Aug</td>
<td>17th Oct</td>
<td>64</td>
<td>300</td>
<td>693</td>
<td>140</td>
<td>52</td>
<td>148</td>
</tr>
<tr>
<td>1998</td>
<td>9th Aug</td>
<td>16th Oct</td>
<td>58</td>
<td>410</td>
<td>934</td>
<td>190</td>
<td>56</td>
<td>204</td>
</tr>
<tr>
<td>1999</td>
<td>28th Jul</td>
<td>15th Oct</td>
<td>63</td>
<td>399</td>
<td>929</td>
<td>210</td>
<td>43</td>
<td>247</td>
</tr>
<tr>
<td>2001</td>
<td>12th Aug</td>
<td>19th Oct</td>
<td>57</td>
<td>432</td>
<td>954</td>
<td>234</td>
<td>43</td>
<td>340</td>
</tr>
<tr>
<td>2002</td>
<td>11th Aug</td>
<td>17th Oct</td>
<td>59</td>
<td>409</td>
<td>968</td>
<td>268</td>
<td>56</td>
<td>396</td>
</tr>
<tr>
<td>2003</td>
<td>10th Aug</td>
<td>17th Oct</td>
<td>56</td>
<td>390</td>
<td>928</td>
<td>270</td>
<td>42</td>
<td>438</td>
</tr>
<tr>
<td>2004</td>
<td>5th Aug</td>
<td>15th Oct</td>
<td>60</td>
<td>419</td>
<td>952</td>
<td>303</td>
<td>49</td>
<td>487</td>
</tr>
<tr>
<td>2005</td>
<td>30th Jul</td>
<td>14th Oct</td>
<td>61</td>
<td>448</td>
<td>1,050</td>
<td>376</td>
<td>43</td>
<td>530</td>
</tr>
<tr>
<td>2006</td>
<td>3rd Aug</td>
<td>13th Oct</td>
<td>58</td>
<td>420</td>
<td>984</td>
<td>341</td>
<td>23</td>
<td>553</td>
</tr>
<tr>
<td>2007</td>
<td>30th Jul</td>
<td>11th Oct</td>
<td>60</td>
<td>399</td>
<td>945</td>
<td>297</td>
<td>14</td>
<td>567</td>
</tr>
<tr>
<td>2008</td>
<td>7th Aug</td>
<td>17th Oct</td>
<td>61</td>
<td>508</td>
<td>1,283</td>
<td>407</td>
<td>11</td>
<td>578</td>
</tr>
<tr>
<td>2009</td>
<td>6th Aug</td>
<td>16th Oct</td>
<td>55</td>
<td>396</td>
<td>901</td>
<td>317</td>
<td>0</td>
<td>578</td>
</tr>
<tr>
<td></td>
<td>Totals</td>
<td></td>
<td>1,014</td>
<td>6,248</td>
<td>14,329</td>
<td>3732</td>
<td>578</td>
<td></td>
</tr>
</tbody>
</table>
Some resightings of individual humpback whales were based on lateral dorsal and body markings, where these had been photographically related to the fluke of a particular individual utilising sequentially timed and dated photography. However the resightings using only lateral dorsal and body markings were excluded from the analysis and were not included in Table 2.6.1 above, as some of these individuals may already be included in the dataset on a fluke only basis creating potential false negatives.

A database of the capture histories of each individual humpback whale was compiled in an Excel spread sheet including the reference number of the best available fluke photograph for each sighting occasion. Each individual fluke photograph selected was assessed for photo quality against the SPLASH photo quality protocols (Calambokidis et al. 1997), which include ratings for: the proportion of fluke visible above water; horizontal and lateral angle of the fluke as it is photographed; exposure, contrast and lighting of the fluke photograph and the focus of the fluke photograph.

Only capture history sightings supported by a fluke photograph rated to have adequate quality for photo-identification matching were used in the modelling data.
2.7 LITERATURE CITED


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Chapter 3

Identification of individual Southern Hemisphere humpback whales (*Megaptera novaeangliae*) utilising all available natural marks: managing the potential for misidentification
3.1 INTRODUCTION

The use of photographs of natural markings on individual humpback whales (*Megaptera novaeangliae*) is an established technique to study the biology, behaviour and ecology of both individuals and populations of humpback whales (e.g. Shevill and Backus 1960; Emmel 1976; Jurasz and Jurasz 1979; Katona *et al.* 1979; Katona and Whitehead 1981; Baker *et al.* 1986; Baker *et al.* 1992; Clapham 1993, 2000; Whitehead 1995, 2008; Clapham and Mayo 1990; McGregor and Peake 1998; Calambokidis *et al.* 2008; Burns 2010; Franklin *et al.* 2011; Franklin 2012; Franklin *et al.* 2012).

The proportion of individuals that can be identified from natural marks varies between different cetacean species (Shane and McSweeney 1990). In the case of humpback whales, double-tagging experiments using both genetic and photo-identification data have shown that almost 100% of individual humpback whales can be identified using natural marks, provided sufficient high quality photographs of the natural marks can be obtained (Katona *et al.* 1979, Stevick *et al.* 2001, Garrigue *et al.* 2011). However natural marks can change over time, especially in immature whales (Carlson *et al.* 1990, Blackmer *et al.* 2000) leading to misidentification errors. The quality of photographs used in the process of individual identification and photo-identification matching, can also give rise to misidentification errors (Friday *et al.* 2000, Stevick *et al.* 2001).

Capture-recapture techniques, including the use of sophisticated modelling, have and are being used to estimate the size and population dynamics of humpback whale populations (Pollock 1982; Kendall *et al.* 1995, 1997; Kendall and Nichols 1995, Schwarz and Stobo 1997, Kendall and Bjorkland 2001, see Chapter 4). In an early review of the use of capture-recapture techniques, Hammond (1986) suggested
that the process of photo-identification with large numbers of photographs could be facilitated through the use of computers to digitise, store, categorise and catalogue individual whales by types of markings and by the utilisation of all available natural marks, for example ventral tail flukes, dorsal fin shapes and lateral body marks.

Misidentification errors in capture-recapture studies related to quality of photographs (non-evolving natural tags), and changes in natural marks (evolving natural tags), have recently been investigated and modelled (Yoshizaki 2007). A simulation study, using a misidentification mechanism and a framework for modelling the effect of misidentification, showed that conventional estimators could seriously overestimate population size when errors due to misidentification are ignored (Yoshizaki et al. 2009).

This study investigates and examines the stability and or changes in all available natural marks on humpback whales, including ventral tail flukes, dorsal fin shapes and lateral body marks. Using a sample of 79 individual humpback whales resighted in 2 to 11 different years, over timespans ranging from 2 to 21 years, the utilisation of all-available natural marks in photo-identification of individual humpback whales and, the minimisation and management of misidentification in the photo-identification process are evaluated.
3.2 METHODS

Photo-identification of humpback whales was undertaken in Hervey Bay (Chapter 2, Fig. 2.2.1 above) between 1992 and 2009. A full description of the study site, vessel surveys, timing of sampling, observations conducted, data collected and photo-identification methodology are provided in Chapter 2.

As well as high-resolution digital photography of ventral tail flukes, systematic high-resolution photography of dorsal fin shapes and lateral body marks were also obtained for each of the individuals in each pod photographed (Katona et al. 1979, Katona and Whitehead 1981, Hammond 1986, Clapham and Mayo 1990). To facilitate matching of dorsal fin shapes and lateral body marks with the ventral tail flukes of particular individuals, ‘marker’ shots were consistently taken (of the expedition vessel hand-rail) to indicate that the preceding sequence of photographs of dorsal fin shapes, lateral body marks and ventral tail flukes were of the same individual whale.

Photo-identification analysis of individual whales was undertaken using a propriety matching system based on categorisation of ventral tail flukes utilising an Array of Coded Discrete Characteristics (ACDC), applied to the file name of each ventral fluke photograph The ACDC system, applied to ventral tail flukes, is fully described in Chapter 2 (See Chapter 2, Section 2.5, Table 2.5.1 and 2.5.2, Figure 2.5.1). In this study the incorporation of the left and right dorsal fin shapes and lateral body natural marks into the ACDC photo-identification matching system is described. The utilisation of dorsal fin shapes and lateral body natural marks in conjunction with ventral tail fluke natural marks provides valuable additional information for use in the photo-identification process. As with the ventral tail flukes the ACDC categories for dorsal fin shapes and lateral body natural marks were based on individually unique
dorsal fin shapes and stable patterns of black and white pigmentation on the dorsal fins and lateral body marks (Katona et al. 1979, Katona and Whitehead 1981, Hammond 1986, Clapham and Mayo 1990). The combined ACDC characteristics, for ventral tail flukes as well as dorsal fin shapes and lateral body marks, selected for the photo-identification matching process were derived from an empirical visual analysis of a selection of 26,000 ventral tail flukes, dorsal fin shapes and lateral body marks in photographs taken between 1992 and 2003 and are summarised in Table 3.1.

All photography of each individual whale in each pod was analysed prior to the matching process described in Chapter 2 (see Section 2.5) and, the ACDC codes were applied to the filename for each photograph of an individual whale’s ventral tail fluke as well as the left and/or right dorsal fin shape and lateral body marks. Analysis outcomes were logged in a consolidated Filemaker Pro™ ‘Whale Analysis’ log. The ACDC characteristic codes used to describe natural marks on the ventral tail fluke, dorsal fin shape and lateral body marks of individual humpback whales are summarised in Table 3.1 below.
Table 3.1. Array of Coded Discrete Characteristics (ACDC) for categorisation of Ventral Tail Flukes, Dorsal Fin Shapes and Lateral Body Marks used for individual identification and photo-identification matching

<table>
<thead>
<tr>
<th>Ventral Tail Flukes</th>
<th>Dorsal Fin Shape &amp; Lateral Body Marks</th>
</tr>
</thead>
<tbody>
<tr>
<td>(A) Primary Characteristics:</td>
<td>(A) Primary Dorsal Fin Shapes:</td>
</tr>
<tr>
<td>BB</td>
<td>Black Border</td>
</tr>
<tr>
<td>BC</td>
<td>Black Centre</td>
</tr>
<tr>
<td>BK</td>
<td>Black</td>
</tr>
<tr>
<td>TE</td>
<td>Trailing edge</td>
</tr>
<tr>
<td>NT</td>
<td>Notch</td>
</tr>
<tr>
<td>TC</td>
<td>Truncated</td>
</tr>
<tr>
<td>CP</td>
<td>Chipped</td>
</tr>
<tr>
<td>HK</td>
<td>Hook</td>
</tr>
<tr>
<td>(B) Secondary Characteristics:</td>
<td>(B) Secondary Lateral Body Characteristics:</td>
</tr>
<tr>
<td>BS</td>
<td>Black Stem</td>
</tr>
<tr>
<td>DM</td>
<td>Damaged</td>
</tr>
<tr>
<td>RK</td>
<td>Rake Marks</td>
</tr>
<tr>
<td>CR</td>
<td>Curled</td>
</tr>
<tr>
<td>WP</td>
<td>White Patch</td>
</tr>
<tr>
<td>BP</td>
<td>Black Patch</td>
</tr>
<tr>
<td>(C) Tertiary Characteristics:</td>
<td>(C) Tertiary Lateral Body Characteristics:</td>
</tr>
<tr>
<td>SM</td>
<td>Scratch Marks</td>
</tr>
<tr>
<td>DT</td>
<td>Dots</td>
</tr>
<tr>
<td>RG</td>
<td>Rings</td>
</tr>
<tr>
<td>RM</td>
<td>Rub Marks*</td>
</tr>
<tr>
<td>GS</td>
<td>Grey Spine*</td>
</tr>
<tr>
<td>PK</td>
<td>Peduncle Knobs*</td>
</tr>
</tbody>
</table>

*These marks were usually observed on females with calves present.

* Peduncle knobs are observable on whales with reduced body mass.
Between 1992 and 2009, 6,248 pods involving 14,329 whales were observed and photographed in Hervey Bay. After photo-identification matching between each yearly ACDC ventral tail fluke catalogue a total of 578 resight histories of individual humpback whales were derived (Chapter 2, see Table 2.6.1).

To examine the stability and or changes in natural marks on ventral tail flukes as well as dorsal fin shapes and lateral body marks, a sample of 79 resight histories of individual humpback whales were selected, consisting of: 44 females resighted in 5 to 12 different years, with resightings spanning 7 to 21 years; 20 males resighted in 4 to 10 different years, with resightings spanning 7 to 16 years; and 15 immature whales (3 females, 3 males and 9 of unknown gender) resighted in 2 to 4 different years, with resightings spanning 2 to 9 years [the ‘immature’ whales were selected based on resightings occurring predominantly during August or in early September when the immature cohort is present in Hervey Bay (Franklin et al. 2011). The resighting histories of some of these immature whales, extended beyond their immature years].

The best photograph of an individual whale’s ventral tail fluke as well as left and/or right dorsal fin shape and lateral body marks, for each sighting, from the first sighting to the last resighting, were selected and placed in sequential order in a Mac OS X™ finder window. The filename for each sequential photograph was examined and any changes in the ACDC codes were noted and recorded. The photographs were then visually displayed in Preview™ (an Apple photo display program) in time-sequential order and systematically examined, each with the same viewing protocol as follows: the viewing protocol for ventral fluke photographs was from posterior to anterior (Table 2.5.1 above) while the viewing protocol for dorsal fin shapes and lateral body marks was from dorsal to ventral. Firstly each of the primary ACDC characteristics were examined, then each of the secondary ACDC characteristics and
finally the tertiary ACDC characteristics (Table 3.1). Any observed changes in the ventral tail fluke ACDC primary, secondary and tertiary characteristics were noted and recorded and as well any changes in the dorsal fin shape and secondary and tertiary lateral body marks were noted and recorded.
3.3 RESULTS

The outcomes of the analysis of natural marks from the systematic photography of the life history of the 79 individual humpback whales are summarised below in Tables 3.2 (44 females), Table 3.3 (20 males) and Table 3.4 (15 immature whales).

Changes in primary characteristics of the ventral tail flukes were observed in 6 of the 79 (7.6%) individual whales (Tables 2 to 4). Changes in secondary characteristics of the ventral tail flukes were observed in 4 of the 79 (5.1%) individual whales (Tables 3.2 to 3.4). There were 4 of 79 (5.1%) cases where changes occurred to both the primary and secondary characteristics of the ventral tail flukes of an individual whale (Tables 3.2 to 3.4). Changes were observed in the tertiary marks of the ventral tail flukes on 26 of 79 (32.9%) individual whales (Tables 3.2 to 3.4).

Changes in the primary dorsal fin shape and/or secondary lateral body marks were observed in only 2 of the 79 (2.5%) individual whales (Tables 3.2 to 3.4) while changes in the tertiary marks on the lateral body were observed in 36 of 79 (45.6%) individual whales (Tables 3.2 to 3.4).

A binary logistic mixed effects model on a pair-matched sample of the 79 ventral tail flukes natural marks as well as the dorsal fin shapes and lateral body natural marks of the same individual whales; found no significant differences in the proportions of ventral tail fluke natural marks and dorsal fin shapes and lateral body natural marks, that displayed changes in primary and/or secondary characteristics over time (F=0.939, df=1/156, p =0.334).
Table 3.2. Changes in Characteristics of Ventral Tail flukes, Dorsal Fin Shapes and Lateral Body Marks in forty-four females sighted in five or more years.

<table>
<thead>
<tr>
<th>Mnemonic Name</th>
<th>UID*</th>
<th>Gender</th>
<th>Years Resighted (With Calf)</th>
<th>Span of Years</th>
<th>Array of Coded Discrete Characteristics (ACDC)</th>
<th>Dorsal Fin Shape &amp; Lateral Body Marks</th>
<th>Scratches, Dots, Rings &amp; Rub marks on Lateral Body</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Agathea</td>
<td>0326</td>
<td>Female</td>
<td>8 98,99,00,02,03,04,07,09</td>
<td>12 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>2 Alchemy</td>
<td>1128</td>
<td>Female</td>
<td>5 02,04,06,08,10</td>
<td>9 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>3 Alexandria</td>
<td>0559</td>
<td>Female</td>
<td>6 99,03,0,05,07,09</td>
<td>11 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>4 Amity</td>
<td>0185</td>
<td>Female</td>
<td>6 97,00,02,04,06,08</td>
<td>12 NC</td>
<td>NC</td>
<td>C</td>
<td>NC</td>
</tr>
<tr>
<td>5 Bluebell</td>
<td>0232</td>
<td>Female</td>
<td>5 97,03,05,07,11</td>
<td>15 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>6 Buttons</td>
<td>0573</td>
<td>Female</td>
<td>6 99,01,03,07,0,12</td>
<td>14 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>7 Coda</td>
<td>0248</td>
<td>Female</td>
<td>11 97,98,99,00,01,02,03,04,05,06,07</td>
<td>11 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>8 Ester</td>
<td>0158</td>
<td>Female</td>
<td>6 96,98,00,03,06,09</td>
<td>14 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
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<tr>
<td>9 Dover</td>
<td>0865</td>
<td>Female</td>
<td>5 01,03,05,07,12</td>
<td>12 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>10 Hodda</td>
<td>1116</td>
<td>Female</td>
<td>5 02,03,04,06,08</td>
<td>7 NC</td>
<td>NC</td>
<td>C</td>
<td>NC</td>
</tr>
<tr>
<td>11 Iceberg</td>
<td>0221</td>
<td>Female</td>
<td>8 97,98,99,03,05,07,10,12</td>
<td>16 NC</td>
<td>NC</td>
<td>NC</td>
<td>C</td>
</tr>
<tr>
<td>12 Ionus</td>
<td>1101</td>
<td>Female</td>
<td>6 02,04,06,08,10,12</td>
<td>11 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
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<tr>
<td>13 Italy</td>
<td>0663</td>
<td>Female</td>
<td>5 99,00,06,08,11</td>
<td>13 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>14 Kline</td>
<td>1017</td>
<td>Female</td>
<td>5 02,03,04,06,08</td>
<td>7 NC</td>
<td>NC</td>
<td>C</td>
<td>NC</td>
</tr>
<tr>
<td>15 Lahaina</td>
<td>0293</td>
<td>Female</td>
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<td>12 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
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<tr>
<td>16 Magneta</td>
<td>0149</td>
<td>Female</td>
<td>9 96,98,99,01,03,04,06,08,10</td>
<td>15 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>17 Mallard</td>
<td>0016</td>
<td>Female</td>
<td>6 94,97,01,05,08</td>
<td>15 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>18 My Auntie</td>
<td>0037</td>
<td>Female</td>
<td>7 94,97,98,01,02,05,06</td>
<td>13 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>19 Nala</td>
<td>0007</td>
<td>Female</td>
<td>12 92,96,97,98,99,02,03,06,08,09,10,12</td>
<td>21 NC</td>
<td>NC</td>
<td>NC</td>
<td>C</td>
</tr>
<tr>
<td>20 Nouveau</td>
<td>0164</td>
<td>Female</td>
<td>8 96,98,99,04,06,07,08,09</td>
<td>14 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>21 Nummer</td>
<td>0574</td>
<td>Female</td>
<td>5 99,01,04,06,08</td>
<td>10 NC</td>
<td>NC</td>
<td>NC</td>
<td>C</td>
</tr>
<tr>
<td>22 Papoose</td>
<td>0425</td>
<td>Female</td>
<td>9 98,99,00,01,02,03,04,06,08</td>
<td>11 NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
</tbody>
</table>

*UID = Universal Identification Number in Fluke Catalogue. ^NC = No Change observed C = Change observed

*Life-history extended with sightings between 2010 and 2012.
Table 3. 2 (Continued). Changes in Characteristics of Ventral Tail flukes, Dorsal Fin Shapes and Lateral Body Marks in forty-four females sighted in five or more years.

<table>
<thead>
<tr>
<th>Mnemonic Name</th>
<th>UID</th>
<th>Gender</th>
<th>Years Resighted</th>
<th>Span of Years</th>
<th>Array of Coded Discrete Characteristics (ACDC)</th>
<th>Dorsal Fin Shape &amp; Lateral Body Marks</th>
<th>Scratches, Dots, Rings &amp; Rub marks on Lateral Body</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>(Number of Years)</td>
<td>(With Calves)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>23 Paulita*</td>
<td>1452</td>
<td>Female 6</td>
<td>04,05,06,08,09,10</td>
<td>7</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>24 Pendant*</td>
<td>0654</td>
<td>Female 6</td>
<td>00,03,04,06,09,12</td>
<td>13</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>25 Pele</td>
<td>0414</td>
<td>Female 5</td>
<td>98,99,00,02,08</td>
<td>11</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>26 Pinto*</td>
<td>0247</td>
<td>Female 6</td>
<td>97,99,02,07,09,11</td>
<td>15</td>
<td>NC, NC, NC, C, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>27 Pixie*</td>
<td>1053</td>
<td>Female 5</td>
<td>02,06,08,09,12</td>
<td>11</td>
<td>NC, NC, NC, NC, NC</td>
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<td>C</td>
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<tr>
<td>28 Quaver</td>
<td>0093</td>
<td>Female 5</td>
<td>95,96,97,03,07</td>
<td>13</td>
<td>NC, NC, NC, NC, NC</td>
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<td>NC</td>
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<tr>
<td>29 Raindrop*</td>
<td>0089</td>
<td>Female 5</td>
<td>95,96,97,00,11</td>
<td>17</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
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<tr>
<td>30 Rama</td>
<td>0417</td>
<td>Female 6</td>
<td>98,99,00,01,02,05</td>
<td>8</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>31 Reiki</td>
<td>0157</td>
<td>Female 8</td>
<td>96,98,00,01,06,07,08,09,</td>
<td>14</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>32 Ruby</td>
<td>0102</td>
<td>Female 8</td>
<td>95,97,98,00,02,03,07,08,</td>
<td>14</td>
<td>NC, NC, C, NC, NC</td>
<td>C</td>
<td>C</td>
</tr>
<tr>
<td>33 Sapphire</td>
<td>0891</td>
<td>Female 5</td>
<td>01,03,05,07,09</td>
<td>9</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>34 Sundance*</td>
<td>0165</td>
<td>Female 6</td>
<td>96,98,02,05,07,11</td>
<td>16</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>35 Tasco*</td>
<td>0721</td>
<td>Female 6</td>
<td>00,05,06,09,10</td>
<td>11</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>C</td>
</tr>
<tr>
<td>36 Timantha</td>
<td>0092</td>
<td>Female 8</td>
<td>95,96,99,00,01,02,04,06</td>
<td>12</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>37 Tolerance</td>
<td>0022</td>
<td>Female 6</td>
<td>94,98,00,03,05,09</td>
<td>16</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>38 Venus*</td>
<td>0114</td>
<td>Female 6</td>
<td>95,98,99,01,05,10</td>
<td>16</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>C</td>
</tr>
<tr>
<td>39 Wedgewood</td>
<td>0152</td>
<td>Female 7</td>
<td>96,98,00,02,04,06,08</td>
<td>13</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>40 Wendy*</td>
<td>0409</td>
<td>Female 8</td>
<td>98,00,01,02,03,05,08,11</td>
<td>14</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>41 White Wings</td>
<td>0428</td>
<td>Female 6</td>
<td>98,00,02,04,08,09</td>
<td>12</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>42 White Wolf*</td>
<td>0006</td>
<td>Female 11</td>
<td>92,94,97,98,99,01,04,05,07,09,12</td>
<td>21</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>43 Yolanda</td>
<td>0160</td>
<td>Female 8</td>
<td>96,98,00,02,03,05,06,07</td>
<td>12</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>44 Zipper</td>
<td>0014</td>
<td>Female 5</td>
<td>94,97,01,04,09</td>
<td>16</td>
<td>NC, NC, NC, NC, NC</td>
<td>NC</td>
<td>NC</td>
</tr>
</tbody>
</table>

*UID = Universal Identification Number in Fluke Catalogue. ^NC = No Change observed  C = Change observed

* Life-history extended with sightings between 2010 and 2012
There were no changes observed to the primary and secondary natural marks on the ventral tail flukes of the 44 females and there were no changes observed to the primary dorsal fin shape and secondary lateral body marks of the 44 females (Table 3.2). The only changes observed in the natural marks on the 44 females were the tertiary marks (scratches, dots and rings) on 6 (13.6%) of the ventral tail flukes (Table 2) and the tertiary marks (scratches, dots, rings & rub marks) on 10 (22.7%) of the lateral body marks (Table 3.2).

Figure 3.1 and Figure 3.2 below illustrate the long-term stability of ventral tail fluke natural marks as well as dorsal fin shape and lateral body natural marks of two breeding females observed and photographed over a timespan of twenty-one years.
Figure 3.1. Whale UID 0006 [White Wolf] (Resight history Table 3.2 above): Photography of ventral tail fluke, left and right dorsal fin and lateral body marks (top to bottom) in 1994, 1997, 2007 and 2012. The ACDC categorisation of this ventral tail fluke is TENT (Trailing edge and notch). A total of 64.2% of the ventral tail flukes in the Hervey Bay catalogue (1810 of 2821, 64.2%) exhibit these characteristics (Chapter 2, see Fig 2.5.1 and Table 2.5.2). Hence in a large ACDC category such as TENT, the use of dorsal fin shape and lateral body natural marks are very useful and provide valuable additional identification information to minimise and manage potential misidentification. Notice fresh tertiary rub mark on dorsal fin in both 2007 and 2012. Appliance of the strict ACDC viewing protocol for flukes, dorsal fins and lateral body marks aids individual identification while tertiary marks usually don't interfere with individual identification.
Figure 3.2. Whale UID 0007 [Nala] (Resight history Table 3.2 above): Photography of ventral tail fluke, left and right dorsal fin shape and lateral body marks (top to bottom) in 1996, 2003, 2008 and 2012. While there is no change in the ventral fluke natural marks and ACDC categories overtime, use of the dorsal shape provides confirmation of individual identity. Note variation in tertiary grey spine mark over years, associated with the presence of a calf, while of interest such tertiary marks do not influence individual identification.
Table 3.3. Changes in Characteristics of Ventral Tail flukes, Dorsal Fin Shapes and Lateral Body Marks in twenty males sighted in four or more years.

<table>
<thead>
<tr>
<th>Mnemonic Name</th>
<th>UID</th>
<th>Gender</th>
<th>Years Resighted</th>
<th>Span of Years</th>
<th>Resightings (Number of Years)</th>
<th>Array of Coded Discrete Characteristics (ACDC)</th>
<th>Dorsal Fin Shape</th>
<th>Lateral Body Marks</th>
<th>Scratches, Dots &amp; Ringss on Lateral Body</th>
</tr>
</thead>
<tbody>
<tr>
<td>Excalibur</td>
<td>0074</td>
<td>Male</td>
<td>5</td>
<td>8</td>
<td>94,95,96,98,01</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>C</td>
</tr>
<tr>
<td>Floppy</td>
<td>0161</td>
<td>Male</td>
<td>10</td>
<td>12</td>
<td>96,97,99,01,02,03,04,05,06,07</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>NC, C</td>
</tr>
<tr>
<td>Gatch</td>
<td>0040</td>
<td>Male</td>
<td>8</td>
<td>12</td>
<td>94,96,97,98,99,02,04,05</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>C</td>
</tr>
<tr>
<td>Glen QC</td>
<td>0352</td>
<td>Male</td>
<td>8</td>
<td>12</td>
<td>98,02,03,04,05,07,08,09</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>NC, C</td>
</tr>
<tr>
<td>Hockey Stick a</td>
<td>0300</td>
<td>Male</td>
<td>3</td>
<td>13</td>
<td>98,99,10</td>
<td>C</td>
<td>NC</td>
<td>NC</td>
<td>NC, C</td>
</tr>
<tr>
<td>Jambo</td>
<td>0012</td>
<td>Male</td>
<td>5</td>
<td>12</td>
<td>93,95,99,01,04</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>NC, C</td>
</tr>
<tr>
<td>Kristallos</td>
<td>0278</td>
<td>Male</td>
<td>8</td>
<td>12</td>
<td>97,98,99,00,02,03,07,08</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>NC, C</td>
</tr>
<tr>
<td>Matra a</td>
<td>0400</td>
<td>Male</td>
<td>6</td>
<td>14</td>
<td>98,00,01,05,07,11</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>Moon Shark a</td>
<td>0586</td>
<td>Male</td>
<td>10</td>
<td>13</td>
<td>99,00,01,02,04,05,06,07,08/11</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>C, C</td>
</tr>
<tr>
<td>Orsen Welles</td>
<td>0418</td>
<td>Male</td>
<td>5</td>
<td>9</td>
<td>98,99,03,05,06</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>C, NC</td>
</tr>
<tr>
<td>Owl Claw</td>
<td>0043</td>
<td>Male</td>
<td>8</td>
<td>12</td>
<td>94,95,96,97,98,00,03,05</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>Peru a</td>
<td>0715</td>
<td>Male</td>
<td>9</td>
<td>12</td>
<td>00,01,02,04,05,06,07,09,11</td>
<td>C</td>
<td>NC</td>
<td>NC</td>
<td>NC, C</td>
</tr>
<tr>
<td>Picollo</td>
<td>0984</td>
<td>Male</td>
<td>4</td>
<td>7</td>
<td>02/06/07/08</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>C</td>
</tr>
<tr>
<td>Rune</td>
<td>0420</td>
<td>Male</td>
<td>5</td>
<td>9</td>
<td>98,00,01,03,06</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>C</td>
</tr>
<tr>
<td>Scorpio a</td>
<td>0730</td>
<td>Male</td>
<td>7</td>
<td>13</td>
<td>00,01,02,03,04,10,12</td>
<td>C</td>
<td>NC</td>
<td>NC</td>
<td>NC, C</td>
</tr>
<tr>
<td>Spiral</td>
<td>0049</td>
<td>Male</td>
<td>5</td>
<td>7</td>
<td>94,96,97,98,00</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>NC, C</td>
</tr>
<tr>
<td>Trident a</td>
<td>0470</td>
<td>Male</td>
<td>4</td>
<td>14</td>
<td>99,00,02,12</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>NC, C</td>
</tr>
<tr>
<td>Two Forks a</td>
<td>0237</td>
<td>Male</td>
<td>6</td>
<td>16</td>
<td>97,01,04,05,06,12</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>Yelo a</td>
<td>0531</td>
<td>Male</td>
<td>4</td>
<td>13</td>
<td>99,00,01,11</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>NC, C</td>
</tr>
<tr>
<td>Zephyrus a</td>
<td>1507</td>
<td>Male</td>
<td>5</td>
<td>7</td>
<td>04,05,08,09,10</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
</tbody>
</table>

*UID = Universal Identification Number in Fluke Catalogue. ^NC = No Change observed C = Change observed

* Life-history extended with sightings between 2010 and 2012
Changes were observed in the primary characteristics on 2 of the 20 (10%) of male ventral tail flukes (Table 3.3) and changes were observed in the secondary characteristics of 1 of the 20 (0.5%) male ventral tail flukes (Table 3.3), while changes were observed in the tertiary characteristics of 5 of the 20 (25%) male ventral tail flukes (Table 3.3).

Changes were observed in 2 of the 20 (10%) male primary dorsal fin shapes and/or secondary lateral body characteristics (Table 3.3) while changes were observed in the lateral body tertiary marks of 15 of the 20 (75%) males (Table 3.3). There were no changes to both the primary and secondary ventral tail fluke natural marks and the primary dorsal fin shape or secondary lateral body marks of any individual male (Table 3.3).

Figure 3.3 and Figure 3.4 illustrate the use of dorsal fin shape to avoid false positives when damage occurs to the primary trailing edge and the variation in horizontal and vertical scratch marks evident in 75% of male lateral body marks.
Figure 3.3. Whale UID 0300 [Hockey Stick] (Resight history Table 3.3 above): Photography of ventral tail fluke, left and right dorsal fin shape and lateral body marks (top to bottom) in 1998, 1999 and 2010. Damage to the primary trailing edge is clearly evident in 2010. This sequence illustrates how close inspection of the high-resolution photography of the undamaged trailing edge together with the primary dorsal fin shape and secondary lateral body marks provides confirmation that the fluke is of the same individual whale. This illustrates how, even though some damage has occurred to the trailing edge of the ventral fluke, the combined use of ventral fluke natural marks and dorsal fin shape and lateral body marks can be utilised to avoid a ‘false negative’. 
Figure 3.4. Whale UID 0715 [Peru] (Resight history Table 3.3 above): Photography of ventral tail fluke, left and right dorsal fin shape and lateral body marks (top to bottom) in 2001, 2004 and 2009. Minor damage is evident to the left side of the trailing edge of the ventral tail fluke in 2009. While changes occurred in the primary ACDC characteristics of the ventral tail fluke the primary dorsal fin shape is constant throughout the years. Changes in tertiary lateral body marks (clearly observable with high-resolution photography) are consistent with the observed changes in horizontal and vertical surface scratch marks observed in 75% of males (Table 3.3). In spite of the changes identification can be maintained over years using the strict ACDC viewing protocols for ventral tail fluke and primary dorsal fin shape and secondary lateral body marks. The changes in tertiary marks do not interfere with individual identification.
<table>
<thead>
<tr>
<th>Mnemonic Name</th>
<th>UID</th>
<th>Gender</th>
<th>Resightings (Number of Years)</th>
<th>Year/Month Resighted (With Calf)</th>
<th>Span of Years</th>
<th>Ventrail Tail Flukes* Array of Coded Discrete Characteristics (ACDC)</th>
<th>Dorsal Fin Shape &amp; Lateral Body Marks</th>
<th>Scratches, Dots, Rings &amp; Rub marks on Lateral Body</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Atoll</td>
<td>0966</td>
<td>Unknown</td>
<td>4</td>
<td>01/09, 02/08, 03/08, 04/08</td>
<td>4</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>2 Ayla</td>
<td>0944</td>
<td>Female</td>
<td>2</td>
<td>02/08, 05/10</td>
<td>4</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>3 Crowe</td>
<td>0723</td>
<td>Unknown</td>
<td>2</td>
<td>00/09, 01/08</td>
<td>2</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>4 Gemini</td>
<td>1063</td>
<td>Unknown</td>
<td>2</td>
<td>02/09, 04/08</td>
<td>3</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>5 Hitch</td>
<td>0767</td>
<td>Unknown</td>
<td>2</td>
<td>01/08, 03/09</td>
<td>3</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>6 Marcus</td>
<td>0536</td>
<td>Inferred M</td>
<td>2</td>
<td>09/09, 04/09</td>
<td>6</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>7 Moon E.T.</td>
<td>0665</td>
<td>Female</td>
<td>3</td>
<td>00/08, 01/08, 04/09</td>
<td>5</td>
<td>C</td>
<td>C</td>
<td>C</td>
</tr>
<tr>
<td>8 Moon Mist</td>
<td>1182</td>
<td>Unknown</td>
<td>2</td>
<td>03/08, 04/08</td>
<td>2</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>9 Ninety Nine*</td>
<td>1046</td>
<td>Inferred M</td>
<td>3</td>
<td>02/09, 04/08, 10/09</td>
<td>9</td>
<td>C</td>
<td>C</td>
<td>C</td>
</tr>
<tr>
<td>10 Santa Maria</td>
<td>1392</td>
<td>Female</td>
<td>3</td>
<td>02/09, 04/08, 06/08</td>
<td>5</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>11 Solstice</td>
<td>0965</td>
<td>Unknown</td>
<td>2</td>
<td>02/08, 03/09</td>
<td>2</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>12 Strike Two</td>
<td>1180</td>
<td>Unknown</td>
<td>2</td>
<td>02/09, 03/08</td>
<td>2</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>13 Tom</td>
<td>0617</td>
<td>Male</td>
<td>3</td>
<td>00/08, 01/08, 02/08</td>
<td>3</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>14 Ustinov</td>
<td>1166</td>
<td>Unknown</td>
<td>3</td>
<td>03/08, 04/08, 05/08</td>
<td>3</td>
<td>NC</td>
<td>NC</td>
<td>NC</td>
</tr>
<tr>
<td>15 Ziggy</td>
<td>0524</td>
<td>Unknown</td>
<td>2</td>
<td>09/09, 00/08</td>
<td>2</td>
<td>C</td>
<td>C</td>
<td>C</td>
</tr>
</tbody>
</table>

* UID = Universal Identification Number in Fluke Catalogue. *NC = No Change observed C = Change observed
* Life-history extended with sightings between 2010 and 2012

Table 3.4. Changes in Characteristics of Ventrail Tail Flukes, Dorsal Fin Shapes and Lateral Body Marks in fifteen immature whales sighted in two to four years.
Changes were observed in the primary and secondary characteristics of the ventral tail flukes of 3 of the 15 (20%) immature whales (Table 3.4) and changes in tertiary marks on the ventral tail fluke were observed in each of the 15 (100%) immature whales (Table 3.4).

No changes were observed in the primary dorsal fin shape or secondary lateral body marks of the 15 immature whales (Table 3.4). However changes in the tertiary marks on the lateral body were observed on 11 of the 15 (73.3%) immature whales (Table 3.4).

Figures 3.5, 3.6 and 3.7 illustrate use of dorsal fin shapes to verify identification with changes in primary and secondary marks on ventral tail fluke and changes in tertiary marks over years.
Figure 3.5. Whale UID 0966 [Atoll] (Resight history Table 3.4 above): Photography of ventral tail fluke, left and right dorsal fin shape and lateral body marks (top to bottom) in 2001, 2002, 2003 and 2004. Increased tertiary dots are evident over the years with no change in the shape of primary trailing edge and a horizontal tertiary scratch mark in the middle of the right side of the ventral fluke over years. Dorsal fin shape is consistent over years.
Figure 3.6. Whale UID 1046 [Ninety Nine]: (Resight history Table 3.4 above): Photography of ventral tail fluke, left and right dorsal fin shape and lateral body marks (top to bottom) in 2002, 2004, 2010. Similar to Ziggy (Figure 3.11 below), the primary black center and the secondary black patch have faded markedly over the early years of this immature whale. Whilst the primary dorsal shape is constant over years there are evident changes in the secondary lateral body marks, especially long scratches consistent with those observed in 75% of males. Note the two raised tertiary peduncle knobs, which can be observed in left and right body photographs over the three years. This illustrates that although some changes occurred in the ventral tail fluke and lateral body the combined use of ventral tail fluke marks together with dorsal fin shape and peduncle knobs aided consistent identification over years.
Figure 3.7. Whale UID 0665 [Moon E.T.] (Resight history Table 3.4 above): Photography of ventral tail fluke, left and right dorsal fin shape and lateral body marks (top to bottom) in 2000, 2001 and 2004. Significant changes are evident in the proportion of secondary white to black pigmentation and in the primary black centre of the ventral fluke. Nevertheless the right hand primary dorsal fin shape is consistent over years allowing confirmation of identity over years in spite of significant changes to the ventral fluke marks. There is a consistent tertiary scratch mark on the left hand side of the ventral fluke, clearly evident in high-resolution photography. A new tertiary rub mark on the rear of the dorsal fin is evident in 2004 when a calf was present.
The number and type of changes observed in natural marks of the 79 individual whales are summarised in Table 3.5.

Table 3.5. Summary of number and type of changes in natural marks of 79 individual females, males and immature humpback whales

<table>
<thead>
<tr>
<th>Whales</th>
<th>Ventral Tail Flukes</th>
<th>Dorsal Fin Shape</th>
<th>Lateral Body Marks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Primary</td>
<td>Secondary</td>
<td>Tertiary#</td>
</tr>
<tr>
<td>Females (44)</td>
<td>0</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Males (20)</td>
<td>3</td>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>Immatures (15)</td>
<td>3</td>
<td>3</td>
<td>15</td>
</tr>
</tbody>
</table>

# Changes in tertiary marks do not affect individual identification

The description of the changes in secondary and primary natural marks on the 8 whales where changes were observed are summarised in Table 3.6.

Figures 3.3, 3.4, 3.6 and 3.7 above and Figures 3.8, 3.9, 3.10 and 3.11 below illustrate the changes in natural marks summarised in Table 3.6.

Of the 79 humpback whales in this study two females (UID 1116, Hodda; UID1017, Klina) and 1 male (UID0161, Floppy; see Figure 3.9 below) were observed from calf to yearling and beyond.
Table 3.6. Description of changes in primary and secondary natural marks of individual whales

<table>
<thead>
<tr>
<th>Whale</th>
<th>UID</th>
<th>Gender</th>
<th>Description of changes</th>
<th>Figure</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Floppy</td>
<td>0161</td>
<td>Male</td>
<td>The secondary lateral body marks evolve in early years</td>
<td>Figure 9</td>
<td>1</td>
</tr>
<tr>
<td>Hockey Stick</td>
<td>0300</td>
<td>Male</td>
<td>Damage evident to approximately 10% of trailing edge</td>
<td>Figure 3</td>
<td>2</td>
</tr>
<tr>
<td>Moon Shark</td>
<td>0586</td>
<td>Male</td>
<td>Damage to dorsal fin in 2007</td>
<td>Figure 8</td>
<td>3</td>
</tr>
<tr>
<td>Peru</td>
<td>0715</td>
<td>Male</td>
<td>Minor damage to trailing edge</td>
<td>Figure 4</td>
<td>4</td>
</tr>
<tr>
<td>Scorpio</td>
<td>0730</td>
<td>Male</td>
<td>Minor changes to primary trailing edge</td>
<td>Figure 10</td>
<td>5</td>
</tr>
<tr>
<td>Moon E.T. (Immature)</td>
<td>0665</td>
<td>Female</td>
<td>Changes in primary and secondary marks on ventral tail fluke</td>
<td>Figure 7</td>
<td>6</td>
</tr>
<tr>
<td>Ninety Nine (Immature)</td>
<td>1046</td>
<td>Inferred Male</td>
<td>Changes in primary and secondary marks on ventral tail fluke</td>
<td>Figure 6</td>
<td>7</td>
</tr>
<tr>
<td>Ziggy (Immature)</td>
<td>0524</td>
<td>Unknown</td>
<td>Changes in primary and secondary marks on ventral tail fluke</td>
<td>Figure 11</td>
<td>8</td>
</tr>
</tbody>
</table>

Notes:
1 No changes in Ventral tail fluke, identification over years not impeded by changes
2 No changes to dorsal fin shape or lateral body marks, identification over years not impeded by changes
3 No changes to primary ventral tail fluke, identification over years was not impeded by changes
4 No changes to dorsal fin shape or lateral body mark, identification over years not impeded over years
5 No changes to dorsal fin shape or lateral body mark, identification over years not impeded over years
6 No changes in dorsal fin shape, changes in tertiary rub marks, Identification over years not impeded by changes.
7 No changes in dorsal shape, changes in tertiary scratch marks. Identification over years not impeded by changes.
8 No changes to primary trailing edge, identification over year not impeded by changes
Figure 3.8. Whale UID 0586 [Moon Shark]: (Resight history Table 3.3 above): Photography of ventral tail fluke, left and right dorsal fin shape and lateral body marks (top to bottom) in 2001, 2007, 2008. Changes in tertiary natural marks on the ventral tail fluke are evident but there was no change to the primary trailing edge and notch, which provided continuity of identification over years. In 2007 there was damage to the top of the dorsal fin and extensive changes in lateral body marks consistent with Moon Shark being a male. The dorsal shape remained consistent over years.
Figure 3.9. Whale UID 0161 [Floppy]: (Resight history Table 3.3 above): Photography of ventral tail fluke, left and right dorsal fin shape and lateral body marks (top to bottom) in 1996 (calf), 1997 (yearling), 2001, 2003, 2006, and 2007. There are no changes to the ventral tail fluke, which is identifiable over years by the trailing edge and notch. The dorsal fin shape is constant but there is a natural evolution of the lateral body marks from a calf to 5 years. The lateral body marks are stable from 5 years onwards.
Figure 3.10. Whale UID 0730 [Scorpio]: (Resight history Table 3.3 above): Photography of ventral tail fluke, left and right dorsal fin shape and lateral body marks (top to bottom) in 2000, 2001, 2002, 2004, 2010. Minor changes were observed in the primary trailing edge of the ventral fluke. The primary dorsal shape and secondary lateral body markings were consistent over years. Note the small white patch just below both sides of the dorsal visible in each year. Sequential photography was used to match the ventral fluke, dorsal shape and lateral body marks as being from the same individual. The two tertiary dots on the mid-right hand side of the ventral fluke are evident in 2000 and 2010. Yearly observations and year-to-year identification was supported by combined fluke, dorsal and lateral body marks.
Figure 3.11. Whale UID 0524 [Ziggy]: (Resight history Table 3.4 above): Photography of ventral tail fluke in 1999 and 2000. There were no changes in the trailing edge providing confirmation of identification between the two years. The primary black center and secondary black stem patch in the center of the ventral tail fluke exhibit marked fading, while two tertiary dots on the upper mid-left of ventral tail fluke are constant. As with all the immature whales in the sample there are several changes evident in tertiary scratch marks and dots on the ventral tail fluke.
3.4 DISCUSSION

In this study the stability of natural marks on humpback whales was examined by analyzing images taken over relatively long timespans of up to 21 years. All natural marks including natural marks on ventral tail flukes as well as dorsal fin shapes and later body natural marks were examined for changes on 79 individual whales. We report low levels of changes in primary and secondary natural marks of ventral tail flukes (Table 3.1 above), (6 of 70, 7.6% and, 4 of 79, 5.1% respectively) and lower levels of change in primary dorsal fin shape and secondary lateral body marks (Table 3.1 above), (0 of 79, 0.0% and 2 of 79, 2.5% respectively). An analysis of a pair-matched sample of the changes in primary and secondary natural marks of ventral tail flukes compared to changes in primary dorsal fin shapes and secondary lateral body marks of 79 individual whales revealed no significant differences in the proportions of changes in ventral tail fluke natural marks compared to changes in dorsal fin shapes and lateral body natural marks (F=0.939, df=1/156, p =0.334).

The use of all available natural marks on a humpback whale, for individual identification, has been consistently recommended over the years by various researchers (Hammond 1986, Carlson et al. 1990, Blackmer 2000, Stevick 2001, Clapham and Mayo 1990, Burns 2010). However most studies of the behaviour, ecology, distribution and migratory interchange of humpback whales have relied on datasets developed from only ventral fluke natural markings (e.g. Katona and Whitehead 1981, Calambokidis et al. 2008, Garrigue et al. 2011). Double tags potentially limit misidentification errors in large natural tags datasets and other types of datasets (Stevick et al. 2001, Yoshizaki 2007, Morrison et al. 2011, Winship et al. 2012). A double tagging experiment confirmed that natural markings are a reliable means of identifying individual humpback whales on a large scale (Stevick et al.
2001). Misidentification of individual whales in a humpback whale dataset can potentially arise from tag loss due to changes in natural marks (Carlson et al. 1990; Blackmer et al. 2000); Evolving natural marks (Yoshizaki 2007), or from the use of poor quality photography (Friday et al. 2000); Non-evolving natural marks (Yoshizaki 2007). This present study suggests that the systematic use of dorsal fin shapes and lateral body marks, in conjunction with ventral tail fluke data, in humpback whale studies provides a reliable mechanism to reduce the potential for misidentification errors in the photo-identification process of large humpback whale datasets.

Two primary sources of misidentification can occur during the visual matching process. Firstly if two matching ventral fluke photographs are declared different individuals when in fact they are of the same individual, this creates a ‘false negative’ as the effective match count will be reduced. Secondly, if two photographs of different individuals are declared to be of the same individual this creates a ‘false positive’ as the effective match count will be increased (Yoshizaki 2007, Burns 2010). If such misidentification errors cannot be identified and/or resolved the capture history of an individual can be split into multiple histories leading to ‘ghost’ histories in tandem with the individuals real history (Yoshizaki 2007, Yoshizaki et al. 2009). Moreover failure to eliminate such misidentification errors can lead to serious overestimation of population size and biases in other parameters using conventional estimators (Yoshizaki et al. 2009, Link et al. 2010, Morrison et al. 2011). This study shows that the systematic use of dorsal fin shapes and lateral body natural marks in conjunction with ventral tail fluke natural marks, can effectively contribute to the minimisation and management of misidentification errors in a large humpback whale dataset.

Male humpback whales tend to have more marks than females on dorsal fins and lateral bodies most likely from intrasexual competition amongst males in competitive
groups (Chu and Nieukirk 1988). In Hervey Bay 6.3% of pods are involved in competitive group behaviour (Franklin 2012). This study found changes were observed in lateral body tertiary marks in 75% (15 of 20) of humpback males observed over timespans of 7 to 16 years, compared to only 22.7% (10 of 44) of changes in lateral body tertiary marks on female humpback whales (see Figures 3.4, 3.8 and 3.9 above).

Substantial change in the tertiary natural marks (scratches, dots and scars), have been reported to occur with immature humpback whales (Carlson et al. 1990, Blackmer et al. 2000). Consistent with these reports this study found substantial changes over time in the tertiary natural marks on ventral tail flukes and lateral bodies of immature humpback whales (0 of 15, 100% and, 11 of 15, 73.3% respectively). Blackmer (2000) suggested that photographs of dorsal fin shape and the caudal peduncle knobs “provide the most consistent way to re-identify humpback whales, particularly calves following weaning”. In this study no changes were observed in dorsal fin shapes of immature whales (0 of 15, 100%) over timespans raging from 2 to 6 years. There were 3 of 79 humpback whales that were observed from calf onwards and dorsal fin shapes and secondary lateral body marks were crucial to re-identifying these whales in conjunction with ventral tail flukes (e.g. see ‘Floppy’, Figure 3.9). Carlson et al. (1990) reported that where changes in natural marks occurred in immature whales that such changes stabilised within the first five years. The results reported in this study are consistent with that report (e.g. see ‘Ninety Nine’ Figure 3.5 and; ‘Floppy’, Figure 3.9). These results substantiate the reliability of primary and secondary natural marks on the ventral tail flukes, used in conjunction with dorsal fin shape and secondary lateral body marks, as a means of maximising observations over time of individual humpback whales and minimising misidentification errors.
3.5 LITERATURE CITED


Kendall, W.L. and Bjorkland, R., 2001. Using open robust design models to estimate


Chapter 4

Population dynamics parameters, abundance and usage of Hervey Bay by Humpback whales

(Megaptera novaeangliae)
4.1 INTRODUCTION

Hervey Bay is located at 25°S, 152°E, which is to the south of the putative overwintering and breeding ground of eastern Australian humpback whales (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999, Franklin et al. 2011, Franklin 2012, Smith et al. 2012, also see Chapter 1.7 and Fig. 1.7.1 above).

Humpback whales bypass Hervey Bay during the northern migration and only begin moving into Hervey Bay in late-July after the commencement of the southern migration from the overwintering and breeding grounds within the inter-reef lagoon of the Great Barrier Reef. They continue to occur in the Bay until mid-October (Corkeron 1993, Corkeron et al. 1994, Franklin et al. 2011, Franklin 2012, Smith et al. 2012). Research in the late 1980s and early 1990s showed that Hervey Bay is a stopover early in the southern migration with humpback whales moving into and out of the Bay from the north, and aggregating in the eastern Bay along the western shore of Fraser Island (Corkeron 1993, Corkeron et al. 1994). Hervey Bay is neither a terminal destination nor a calving area for humpback whales, but an important stopover for particular classes of humpback whales early in the southern migration (Franklin et al. 2011, Franklin 2012). It has been suggested that between 30% and 50% of eastern Australian humpback whales use Hervey Bay during the southern migration (Chaloupka et al. 1999).

The following information on previous research on pod characteristics, behaviour and timing of classes of humpback whales using Hervey Bay is useful in evaluating and setting prior expectations for modeling of long term capture history data (see 4.2.7 below). A long-term study of pod size and pod composition in Hervey Bay was undertaken between 1992 and 2005 (Franklin et al. 2011), and of behaviour of humpback whales in Hervey Bay between 1992 and 2009 (Franklin 2012), to
investigate the importance of Hervey Bay for particular classes of humpback whales (Franklin et al. 2011, Franklin 2012). Between 1992 and 2005 there was no significant variation in the proportion of pods with calves present (approximately 40%, Franklin et al. 2011). Pods with calves present were rarely sighted during the first four weeks of the season, while pods with calves present dominated the last six weeks of the season (increasing steadily from 3.6% in week 4, to 92.8% in week 10, Franklin et al. 2011). Pod associations were also significantly higher during the first four weeks of the season compared to the last 6 weeks of the season (15.0%, 9.8%; Fisher’s exact test, $P < 0.001$), Franklin 2012).

Modelling of the estimated probability of 1, 2, 3+ adults in pods revealed significant differences in pod size and composition in pods with no calves present compared to pods with calves present (see Fig. 4.1.1 from Franklin et al. 2011, below). In pods with no calves present pairs and singletons predominated early in the season, while in pods with calves present mothers alone with their calves predominated later in the season. There was a significant increase over years, of pods with 3+ adults, possibly related to the increase in the size of the population, the skew toward younger whales in the population, and increased aggregation of pods as a result of the density of whales entering and leaving Hervey Bay.
Figure 4.1.1 Estimated probabilities of pods with 1, 2, or 3+ adults: (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. 4.1.1 C the single adult category represents mothers alone with their calves and the 2 and 3+ categories are adults accompanying a calf or calves), (reprinted from Franklin et al. 2011)

Whilst non-agonistic social behaviour and competitive behaviour occurred throughout the season, non-agonistic social behaviour occurred predominantly during the first four weeks of the season and competitive group behaviour increased significantly towards the end of the season (Franklin 2012). Both non-agonistic social behaviour and competitive group behaviour were more common in larger groups and newly associated pods (Franklin 2012). Competitive behaviour did not vary significantly over years and was significantly more frequent in pods with calves present. In contrast, non-agonistic social behaviour did vary significantly over years and was observed significantly more often in pods with no calves present (Franklin et al. 2011). 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. Overall there was a low level of competitive behaviour in Hervey Bay (6.3% of pods, Franklin 2012) and mothers spent most of their time alone with their calves (69.4%, Franklin 2012) involved in maternal activities.

The variations in pod characteristics and pod behaviour over the season when humpback whales occur in Hervey Bay are related to different sexual and maturational classes of humpback whales using Hervey Bay. Predominantly immature males and females occur in early August, mature males and females dominate in late August and mothers with older calves either with or without escorts, dominate during September and October (Franklin et al. 2011, Franklin 2012, Fig. 4.1.2 below).

Dawbin (1966,1977) undertook an extensive study of the timing and temporal segregation of different sex, age, reproductive and maturational classes of humpback whales in the Southern Hemisphere using whaling samples from the early 1930s to the early 1960s. He reported that the first class of humpback whales to travel south were resting and newly pregnant females together with immature males and females. These two classes preceded mature males by about 10 days. The final cohort to move south was lactating-females, and the peak density interval between resting and newly pregnant females, and mothers with calves, was approximately one month.

Franklin (2012) used long-term resighting histories (1992 to 2009) of 361 individually identified humpback whales to investigate temporal segregation of known sex, age, reproductive and maturational classes across the season in Hervey Bay (Fig. 4.1.2 below).
Figure 4.1.2 Observations by day within season, of 361 individually identified whales by sex, age, reproductive and maturational sub-classes, (a) to (h). Note: days 1 to 31 within season occur in August, days 32 to 61 occur in September and days 62 to 80 occur in October (Re-printed from, Franklin 2012).

Mature non-lactating females were observed mainly during August and mature lactating females in September and October (Fig. 4.1.2, (d) and (e) ). There was
some overlap of these classes in September with peak density of the two classes separated by 32 days. Few mature males were observed in August, but overlapped with non-lactating females in September but to a greater extent with lactating females in September and October (Fig. 4.1.2, (a) and (b)). The data show that immature males and females interact with both non-lactating and lactating females to a greater extent than previously reported (Fig. 4.1.2 (c), (g) and (h), Franklin 2012). The data also show that calves travelling to Hervey Bay with their mothers subsequently return to Hervey Bay as immature whales and continue to return as they mature (Fig. 4.1.2, (f), (g) and (h)). The temporal segregation observed in Hervey Bay is consistent with that reported by Dawbin (1966, 1977) 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 (Franklin 2012).

In contrast to the male-biased sex ratio reported in breeding grounds (Herman et al. 2011), using a sample of the individual resighting histories of whales of known sex, Franklin (2012) reported that Hervey Bay has a female-biased sex ratio of 2.94:1 females to males. Franklin (2012) suggested 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.

The research presented in this chapter uses long-term capture histories of individual humpback whales obtained by systematic sampling over thirteen years from 1997 to 2009 (Table 2.6.1 above). The data were analysed with program MARK (White and Burnham 1999) and modeled utilising a robust design model (Pollock 1982; Kendall et al. 1995, 1997; Kendall and Nichols 1995). Estimates were obtained of the probability of capture on each sampling occasion, rates of survival between seasons
and between weeks within season, rates of temporary absence from the cohort visiting Hervey Bay in a season, and rates of entry into the Bay between weeks within season. Estimates of abundance over years and by week within season were also derived. These results are discussed in terms of recent research in Hervey Bay on pod size, pod composition, pod behaviour and temporal segregation and timing of classes of humpback whales using Hervey Bay.

4.2 METHODS

4.2.1 Sampling, capture histories and effort

Sampling for this study was conducted in Hervey Bay (see Study Area, Figure 2.2.1 above) for 10 weeks per year from 1997 to 2009 (Table 2.6.1). Sampling was conducted from Sunday to Friday each week, beginning in early August and continuing to late October in each year. A full description of the study site, survey timing, observations made, photo-identification methodology and extraction of capture histories is provided in Chapter 2 above (also see Franklin et al. 2011 and Franklin 2012).

The daily capture histories were collapsed into weeks for analysis to reduce the complexity of the model used in analysis and to ensure that there was good coverage of the sample area in each weekly sample. This yielded capture histories over 130 weeks (13 years x 10 weeks).

An effort variable was calculated for each week based on the number of full days (0700 till 1700) in each week when surveys occurred between 1997 and 2009, with Sundays counted as 0.75 d due to a later start and Fridays as 0.5 d due to an earlier
stop. Days lost to bad weather or for operational reasons were counted as zero. This calculation yielded a value of 5.25 days for a full sampling week.

The model employed for the analysis is described below in a general, schematic rather than a formal, mathematical form. Formal specification can be found in the references provided (Kendall and Bjorkland 2001, Stauffer et al. 2013).

4.2.2 Robust Design (RD) Models

Sampling of humpback whales from the movement through Hervey Bay each year over a thirteen year period, creates a hierarchical sampling structure in which the intervals between samples occur at two scales:

1. Between years considered as wholes (primary samples)
2. Between samples within years (secondary samples)

Robust design models (Pollock 1982; Kendall et al. 1995, 1997; Kendall and Nichols 1995) were designed to take advantage of hierarchical sampling schemes where, in the classic case, the sets of secondary samples were taken over periods of time short enough for the population to be considered closed within primary samples while being open between them (Kendall et al. 1995, 1997). This allows closed population model structures to be fitted within each primary samples, to correct abundance estimates for biases that may be introduced by variation in capture probabilities between animals which have previously been captured and those which haven’t (behavioural response to first capture – ‘trap happy’ and ‘trap shy’ effects), or by variation among individuals (individual heterogeneity), (Otis et al. 1978).

Only apparent survival was estimated between primary samples in early formulations of the model (Kendall et al. 1995), but subsequent development has also incorporated estimation of temporary emigration; i.e., the proportion of the
population present in one primary sample that is absent from the sampling area and unavailable for capture in the next (Kendall et al. 1997). Temporary emigration may be a random process in which the previous state of an animal (present or absent) does not affect its subsequent state, or a Markovian process in which it does. An example of Markovian temporary emigration is when primary samples of females that breed every second year are taken annually on breeding grounds and the probability of presence varies by reproductive state.

In the case of breeding grounds or migratory stopovers, animals may arrive and leave the sampling area in sequence creating an open population within each of the primary samples. The open robust design model (Schwarz and Stobo 1997, Kendall and Bjorkland 2001) was developed for this situation and, while behavioural response to first capture (first sighting in this study) or individual heterogeneity cannot be accommodated, the rates of entry into the sampling area and probabilities of apparent survival between secondary samples may be estimated along with abundance within primary samples. Consequently, the model provides estimates of apparent survival both between and within primary samples; the between primary sample estimate describes the probability of remaining alive and maintaining fidelity (returning) to the sampling area (biological survival x fidelity) while the within primary sample estimate describes the probability of remaining in the sampling area between secondary samples (related to residency or length of stay, Kendall and Bjorkland 2001).

In the open robust design model, temporary emigration is modeled in terms of state transition probabilities. In the basic model the states are present or ‘observable’ (P) and absent or ‘unobservable’ (A), and the possible transitions are present to absent (PA) and absent to present (AP). Further states in addition to present or absent may be included in the model, such as capture locations (e.g., bay 1, bay 2, bay 3),
maturity (e.g., juvenile, adult), or breeding status (e.g., with, or without neonate) and the transitions among them can be estimated (Stauffer et al. 2013). The capacity to incorporate multiple states in the open robust design has resulted in the model being described as the open robust design multistate (ORDMS) or multistate open robust design (MSORD) model. Analysis of the capture history data was undertaken with program MARK (White and Burnham 1999)

4.2.3 Parameters estimated by the multistate open robust design model (MSORD)

The parameters estimated by the MSORD may be informally presented as:

S Probabilities of apparent survival between primary samples

psi Probabilities of transition between states (PA, AP) between primary samples

pent Probabilities of entry to the sampling area between the secondary samples of each primary sample (proportions of the total number of visitors to the sampling area over the sampling period)

phi Probabilities of apparent survival between the secondary samples of each primary sample

p Probabilities of capture in each secondary sample of each primary sample.

Estimates of the total number of visitors each year are obtained as derived parameters, as are estimates of the mean length of stay each year.

4.2.4 Model reduction – constraints on parameter estimates

The probability of apparent survival between primary samples (S) may be modeled as constant, time varying, or as function of covariates.

The probability of transition from present to absent (PA) may be specified as its complement PP (present to present), and AP (absent to present) may be specified as its complement AA (absent to absent). A model in which the transition probabilities PA and AA are separately estimated is a Markovian temporary emigration model, a
model in which PA is constrained equal to AA is a random temporary emigration model, and a model in which PA is constrained to equal AP is an ‘even flow’ temporary emigration model (Kendall et al. 1995a, 1997). The transition probabilities may be modeled as constant, time-varying or as function of covariates with an additional constraint being necessary for identification of the parameter estimates when both between primary sample apparent survival (S) and the transition probabilities (psi) are estimated as time-varying. Specifically, the last transition probabilities PA and AA must be set equal to the transition probabilities PA and AA from some earlier interval such as the second last interval.

The probabilities of entry, being the proportions of the total number of visitors to the sampling area in a primary sample that are present at the beginning of sampling and enter between the secondary samples, must sum to 1 (the total). The software employed for the analysis, program MARK (White and Burnham 1999), may not explicitly estimate the proportion present at the beginning of sampling (pent0) in which case it may be estimated as 

\[ \text{pent}_0 = 1 - \sum_{i=1}^{i=k-1} \text{pent}_i, \]

where i indexes the secondary samples 1...k within a primary sample.

The probabilities of entry (pent), apparent survival (phi) and capture (p) may be modeled in terms of primary samples (constant, time-varying or as a function of covariates), secondary samples (constant, time-varying or as a function of covariates), or a combination of both.

4.2.5 Model comparisons

The MSORD is a maximum likelihood model and a set of alternative models (i.e., with different structures for, or constraints on, the parameters) may be compared using an information criterion such as Akaike’s Information Criterion (AIC) which is
adjusted for small samples for capture-recapture models (AICc), and may be further adjusted for overdispersion (QAICc, Burnham and Anderson 2002). AIC = -2LL + 2P, where LL is the natural logarithm of the model likelihood and P is the number of parameters. Models with smaller values of AICc are considered better in the sense that they balance the virtue of close fit of the model to data (smaller deviance is better) with the vice of using many parameters to fit it (so models using fewer parameters – parsimony – are better). The ‘balance’ involved arises because similar models with more parameters generally have smaller deviances but may include separate estimates that vary little relative to their precision and be less interpretable in terms of theories about the underlying processes that generated the data (Burnham and Anderson 2002). AICc weights, which describe the relative likelihoods of a set of models, may also be used in model comparison, with larger AICc weights indicating better models.

4.2.6 Data demands of the MSORD

With 5 parameter types and samples at both the primary and secondary sample levels, and the potential for all to be time-varying (with appropriate constraints on transition probabilities when required), a very large number of parameters may theoretically be estimated, in the present study it is possible to estimate 399 parameters with additional parameters, such as abundance, derived from these. The number of parameters it is possible to estimate in any case however, is dependent upon there being sufficient data to support their separate estimation. The number of different models (i.e., with different structures for [constraints on] the various parameters), can be very large indeed. The MSORD is a model for which prior expectations (theories) are very important in guiding specification of constraints on the various parameters of a set of models for comparison that are estimable and
meaningfully interpretable. Formulation of sensible prior expectations is important not only for these reasons but also because how each parameter is estimated is reflected in the estimates obtained for the others, with all being related through the model formulation (its likelihood equation).

4.2.7 Prior expectations for the Hervey Bay data

As described in the introduction (Section 4.1, pages 155 to 161 above), data from previous research on the composition of groups, their behaviour and timing of classes of humpback whales using Hervey Bay (Fig. 4.1.1 and Fig. 4.1.2) has led to conclusions that there is a regular within-year pattern to the humpback whale movements through Hervey Bay, with several classes of whale entering, staying for a period of time, and then leaving the bay in sequence throughout the season (Fig. 4.1.2).

As concluded from previous research, the classes have different ‘reasons’ for visiting the bay which are reflected in the timing of their entry, the duration of their stay and their behaviour while present. The probability of capture by fluke photograph may vary among classes due to their varying propensities to make fluke-up dives. Capture probability is also likely to vary with the number of whales in the bay, being smaller when more whales are present: with more whales in the Bay and a limit to the total number that can be captured in a day, the probability of capturing any one of them is smaller than when there are fewer whales in the Bay. The total number of visitors is very likely to have increased from year to year with growth in the size of the migrating eastern Australian population (see Chapter 5, Figure 5.1 below), while the number of humpback whales in the bay appears to decrease within the year from a maximum early in the season to a minimum at the end.
While the different classes of whales may have different probabilities of capture, the strong correlation of their presence in the bay with week within year means that, if capture probability is modeled as a function of week, the heterogeneity that would otherwise be present due to behavioural differences between classes would be largely stratified out.

These considerations led to expectations that the probability of capture may vary by both year and week within year. The probabilities of entry (pent) and within year apparent survival (phi) are likely to vary by week within year but also by year with the timing of the migration relative to the timing of sampling.

With 13 years by 10 weeks per year of data, there would be 130 p, 117 pent and 117 phi parameters if all were estimated separately (i.e., year*week). It is likely however, given the regularity of the pattern of within year entries and exits, that models which estimate the weekly variation within year with an overall adjustment (offset) for year (i.e., year + week) will provide reasonable estimates of the variation in these parameters and interpretable models. For these ‘additive’ models, there are 23 p, 22 pent and 22 psi parameters. Multiplicative models (year*week) are not included among the models considered here due to their extreme complexity, with 297 fewer parameters for a model with year+week rather than year*week structures for p, pent and phi.

Both the between year apparent survival (S) and transition parameters (psi) may vary by year, and temporary emigration may be Markovian, random, display an even flow pattern or not occur at all.

The most complex model considered has S varying by year, psi displaying a yearly variable Markovian pattern (with constraint on the last psi), and pent and phi varying
additively by year and week (year+week). The effort variable is also included in the model for capture probability (year+week+effort).

As required for the MSORD model, $S$ for the absent state is set equal to $S$ for the present state in each year, and $p$ (absent), $pent$ (absent) and $phi$ (absent) are set to zero (Kendall and Bjorkland 2001).

4.3 RESULTS

4.3.1 Data

There were 130 weeks of sampling from 1997 to 2009. Of the weekly samples there were 113 full weeks (5.25 days, 86.9%), 8 weeks of 4.75 days (6.2%), 4 weeks of 4.5 days (3.1%) and 5 weeks of 4.25 days (3.8%). Two thousand seven hundred and eight (2708) Humpback whales were each captured between 1 and 17 times: 2133 were captured once, 382 twice, 96 three times, 41 four times, 26 five times, 10 six times, 8 seven times, and 5 more than 8 times. There were a total of 3717 captures over the thirteen years from 1997 to 2009. The dates of beginning sampling each year and the number of captures by week within year are summarised in Table 4.3.1.1.
Table 4.3.1.1. Sampling in Hervey Bay for years 1997 to 2009; start date in August and number of captures of individual humpback whales by week

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<td>13</td>
<td>12</td>
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<td>6</td>
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4.3.2 Models

Given the prior expectations for the patterns of visitation of whales to the Bay outlined in 4.2.7 above, The 11 models selected for comparison were extracted as the better fitting models from a larger set of 23 models that explored alternative parameter structures. The initial models included models with capture probability varying as a function only of effort and as a function of year and effort, and a model with the probability of entry varying as a function of week but not by year. None of the excluded models had an AICc weight greater than 0.00005 in the larger set. The model structures, a description of their temporary emigration types, their AICc values, AICc weights, likelihoods, numbers of parameters and deviances are presented in Tables 4.2.2.2A and 4.3.2.2B. Table 4.3.2.2A gives the model structures
and descriptions of the temporary emigration types, and Table 4.3.2.2B gives the statistics for each model.

Table 4.3.2.2A. Model structures and description of temporary emigration type for the 11 selected models

<table>
<thead>
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<th>Model #</th>
<th>Model</th>
<th>Temporary emigration</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>(S,.)psi(PA=AP=.)pent(y+w)phi(y+w)p(y+w+effort))</td>
<td>Even flow - constant</td>
</tr>
<tr>
<td>2</td>
<td>(S,.)psi(ZERO)pent(y+w)phi(y+w)p(y+w+effort))</td>
<td>None</td>
</tr>
<tr>
<td>3</td>
<td>(S,.)psi(PA=AA=.)pent(y+w)phi(y+w)p(y+w+effort))</td>
<td>Random - constant</td>
</tr>
<tr>
<td>4</td>
<td>(S,.)psi(PA=AA=y)pent(y+w)phi(y+w)p(y+w+effort))</td>
<td>Random - year</td>
</tr>
<tr>
<td>5</td>
<td>(S(t)psi(ZERO)pent(y+w)phi(y+w)p(y+w+effort))</td>
<td>None</td>
</tr>
<tr>
<td>6</td>
<td>(S,.)psi(PA=AP=y)pent(y+w)phi(y+w)p(y+w+effort))</td>
<td>Even flow - year</td>
</tr>
<tr>
<td>7</td>
<td>(S(t)psi(PA=AP=.)pent(y+w)phi(y+w)p(y+w+effort))</td>
<td>Even flow - constant</td>
</tr>
<tr>
<td>8</td>
<td>(S,.)psi(PA=AP=.)pent(y+w)phi(y+w)p(effort+w))</td>
<td>Even flow - constant</td>
</tr>
<tr>
<td>9</td>
<td>(S,.)psi(PA=y, AA=y)pent(y+w)phi(y+w)p(y+w+effort))</td>
<td>Markovian - year</td>
</tr>
<tr>
<td>10</td>
<td>(S,.)psi(PA=AP=.)pent(w)phi(y+w)p(y+w+effort))</td>
<td>Even flow - constant</td>
</tr>
<tr>
<td>11</td>
<td>(S,.)psi(PA=AP=.)pent(y+w)phi(w)p(y+w+effort))</td>
<td>Even flow - constant</td>
</tr>
</tbody>
</table>
Table 4.3.2.28. AICc, Delta AICc, AICc Weight, model Likelihood, Number of parameters and Deviance for the 11 selected models (arranged by increasing AICc values)

<table>
<thead>
<tr>
<th>Model #</th>
<th>AICc</th>
<th>Delta AICc</th>
<th>AICc Weight</th>
<th>Model Likelihood</th>
<th>Num. Par.</th>
<th>Deviance</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>23841.844</td>
<td>0.000</td>
<td>0.896</td>
<td>1.000</td>
<td>67</td>
<td>23705.35</td>
</tr>
<tr>
<td>2</td>
<td>23846.816</td>
<td>4.972</td>
<td>0.075</td>
<td>0.083</td>
<td>66</td>
<td>23712.39</td>
</tr>
<tr>
<td>3</td>
<td>23848.793</td>
<td>6.949</td>
<td>0.028</td>
<td>0.031</td>
<td>67</td>
<td>23712.30</td>
</tr>
<tr>
<td>4</td>
<td>23855.639</td>
<td>13.795</td>
<td>0.001</td>
<td>0.001</td>
<td>78</td>
<td>23696.25</td>
</tr>
<tr>
<td>5</td>
<td>23858.587</td>
<td>16.743</td>
<td>0.000</td>
<td>0.000</td>
<td>77</td>
<td>23701.29</td>
</tr>
<tr>
<td>6</td>
<td>23859.536</td>
<td>17.692</td>
<td>0.000</td>
<td>0.000</td>
<td>78</td>
<td>23700.15</td>
</tr>
<tr>
<td>7</td>
<td>23860.673</td>
<td>18.829</td>
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</tr>
<tr>
<td>8</td>
<td>23861.293</td>
<td>19.449</td>
<td>0.000</td>
<td>0.000</td>
<td>54</td>
<td>23751.67</td>
</tr>
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<td>9</td>
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<td>0.000</td>
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</tr>
<tr>
<td>10</td>
<td>23883.571</td>
<td>41.727</td>
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<td>0.000</td>
<td>57</td>
<td>23767.76</td>
</tr>
<tr>
<td>11</td>
<td>23883.896</td>
<td>42.052</td>
<td>0.000</td>
<td>0.000</td>
<td>57</td>
<td>23768.09</td>
</tr>
</tbody>
</table>

The best fitting model considering parsimony (model 1; lowest AICc and 90% of AICc weight) has between year apparent survival constant over years [S(,)], constant even flow temporary emigration [psi(PA=AP=.)], probability of entry and probability of apparent survival within years varying additively by year and week [pent(y+w), phi(y+w)] and probability of capture varying additively by year, week and effort [p(y+w+effort)].

This model was compared to models with the same structures for S, pent, psi and p but different temporary emigration structures: model 2 has no temporary emigration, model 3 has constant random temporary emigration, model 4 has
random temporary emigration varying by year, model 6 has even flow temporary emigration varying by year, and model 9 has Markovian temporary emigration varying by year. A model was fitted with constant Markovian temporary emigration but the between year apparent survival was estimated at the upper boundary (0.999999 with standard error = 0.0004) and was removed from the model set.

Model 1 was also compared to a model with the same structure for pent, psi and p but no temporary emigration and between year survival varying by year (model 5), and a model with constant even flow temporary emigration and between year survival varying by year (model 7).

Models 8, 10 and 11 compare model 1 with models with the same structures for all parameters except that model 8 has no yearly variation on p, model 10 has no yearly variation on pent, and model 11 has no yearly variation on psi.

Only models 1 (constant even flow temporary emigration) and 2 (no temporary emigration) (Table 4.3.2.2A) carry more than 3% of the model weight (see section 4.2.5 above). Model 1 (Table 4.3.2.2A above) with 90% of the AICc weight, was selected for interpretation.

4.3.3 Parameter and derived estimates for model 1

The parameter estimates and derived estimates from model 1 are summarised with SE and 95% CI in Appendix III – Table 4.3.3.1; page 350 below.

4.3.3.1. Capture probabilities [p(y+w+effort)]

Capture probabilities vary additively by year, week and effort. The weekly capture probabilities are presented for 1997 in Figure 4.3.3.1.1 and for 2008 in Figure 4.3.3.1.2.
These years were selected because they consist only of full weeks of survey effort (5.25 days) and because they are at the beginning and near the end of the series. The pattern of capture probabilities is the same over weeks within year and its level decreases over years.

![p-hat ±95% CI by week in 1997](image)

*Figure 4.3.3.1.1. Estimated capture probabilities (p-hat) with 95% confidence intervals by week within year for 1997.*
Figure 4.3.3.1.2. Estimated capture probabilities (\(p\text{-hat}\)) with 95\% confidence intervals by week within year for 2008.
4.3.3.2. Yearly abundance

Yearly abundances (total number of visitors) with 95% confidence intervals are presented in Figure 4.3.3.2.1. A linear trend is fitted to the data.

![Graph showing yearly abundance estimates with 95% confidence intervals and linear trend for thirteen years from 1997 to 2009.](image)

*Figure 4.3.3.2.1. Yearly abundance estimates (total number of visitors) with 95% confidence intervals and linear trend for thirteen years from 1997 to 2009.*

The estimates of yearly abundances in Hervey Bay were compared to estimates of the total eastern Australian migration (Chapter 5, Fig. 5.1, Table 5.2.5 below) and between 23% and 46% (mean = 34%, standard deviation = 5.3%) of the estimated eastern Australian migration were estimated to have visited Hervey Bay each year. The two extremes – a low of 23% in 1997 and a high of 46% in 2000 – were anomalous, with all other estimates falling in the range 30% to 38%.

Reproduction rates and population rates of increase in Hervey Bay relative to the eastern Australian population are investigated and discussed in Chapter 5 below.
4.3.3.3 Between Year Survival \([S(.)]\)

Between year apparent survival was estimated as constant over years with probability (standard error, L95%CI:U95%CI) = 0.947 (0.012, 0.918:0.966).

4.3.3.4 Temporary emigration \([\psi_i(\text{PA}=\text{AP}=.)]\)

Temporary emigration was estimated as even flow (the probability of presence in year \(t\) and absence in year \(t+1\) is equal to the probability of absence in year \(t\) and presence in year \(t+1\)) and constant over years with probability (standard error, L95%CI:U95%CI) = 0.141 (0.038, 0.081:0.234).

4.3.3.5 Between week entry \([p\text{ent}(y+w)]\) and a typical within-year profile

Between week entry probabilities display the same form over weeks with an offset for years which raises or lowers the profile from year to year. One implication of this yearly variation is that the proportion of the yearly visitors that were present at the beginning of sampling (\(\text{pent}_0\)) varies from year to year: the percentages present in each year from 1997 to 2009 were estimated as 25, 15, 15, 19, 26, 15, 16, 15, 7, 9, 28, 10 and 14 (mean = 17%, standard deviation = 6.5%).

The within-year profile of abundances in the Bay follow a very similar form for all years. A typical within-year profile is presented for 2003 (at the middle of the series with 16% present at the beginning of sampling) in Figure 4.3.3.5.1.
Figure 4.3.3.5.1. Probability of entry (pent-hat), with 95% confidence interval between weeks within year for 2003, with 16% present at the beginning of sampling.
4.3.3.6. Between week apparent survival \([\phi(y+w)]\) and a typical within-year profile

Between week apparent survival probabilities display the same form over weeks with an offset for years, which raises or lowers the profile from year to year. A typical within-year profile is presented for 2003 (at the middle of the series) in Figure 4.3.3.6.1.

![Figure 4.3.3.6.1. Probability of apparent survival, with 95% confidence interval between weeks within year for 2003](image)
4.3.3.7. Within-year abundance

The within-year pattern of abundance is also of interest and follows a regular pattern as a consequence of the additive (year+week) structures for pent, psi, and p. Estimated weekly abundances in 2003 with 95% CI’s are presented in Figure 4.3.3.7.1.

![Weekly abundance estimates (n-hat) with 95% confidence intervals for 2003.](image)

*Figure 4.3.3.7.1. Weekly abundance estimates (n-hat) with 95% confidence intervals for 2003.*
4.3.3.8. Estimated mean residency

The estimated mean residency time (mean = 1.6 weeks, standard deviation = 0.34 weeks) with 95% confidence intervals, are presented by year in Figure 4.3.3.8.1.

![Estimated residency time (weeks) with ±95% CI by year, 1997-2009](chart.png)

*Figure 4.3.3.8.1. Estimated mean residency time (weeks) with 95% confidence intervals by year for the thirteen years from 1997 to 2009*
4.4 DISCUSSION

The yearly estimates of the number of humpback whales entering Hervey Bay during the thirteen years from 1997 to 2009 (Fig. 4.3.3.2.1), show a steady, near linear, trajectory of increase and overall a five-fold increase in the annual total of humpback whales visiting Hervey Bay from 1997 to 2009. This result mirrors, but is greater than, the trajectory of increase in the estimates of yearly abundance of eastern Australian humpback whales during the same period (see Chapter 5, Fig. 5.1, Table 5.2.5. below, Noad et al. 2011b), with a four-fold increase in the total number of humpback whales in the eastern Australian population. During the period 1997-2009 a relatively stable proportion of the eastern Australian humpback whales visited Hervey Bay (mean = 34%, SD = ±5.3%) each year.

The estimated between-year apparent survival rate (0.95, 0.92:0.97; see 4.3.3.1 above) is relatively high and close to the estimated biological survival rate for this species (Buckland 1990, 0.951 SE = 0.01; Barlow and Clapham 1997, 0.960, SE = 0.0083). The steady annual increase in the estimates of abundance over the study period (1997-2009, Fig. 4.3.3.2.1), combined with the constant high level of apparent survival between years indicate that most of the humpback whales which visit Hervey Bay do so regularly and that fidelity to Hervey Bay is very high. Taken together the estimates of abundance and between-year apparent survival, suggest that a specific sub-group from the eastern Australian humpback whale migration visits Hervey Bay and that the sub-group is growing at about the same rate as the eastern Australian population. Anderson (2013) identified genetic heterogeneity between the northbound migration off Byron Bay and Ballina and the southbound migration at Hervey Bay. The source of differentiation was between Byron Bay males and Hervey Bay males and the hypothesis, that the heterogeneity detected was due to individuals (mainly males) from South Pacific breeding stocks using the eastern
Australian migratory corridor, was suggested. The results presented in this study suggests an alternative parsimonious hypothesis, that the heterogeneity detected in Anderson (2013) is more likely related to the differences between the sub-group of eastern Australian humpback whales utilising Hervey Bay and the sub-group or sub-groups of migrating eastern Australian humpback whales that do not use Hervey Bay. There were no formal reports of humpback whales in Hervey Bay prior to the late 1980s. In 1987 local fishermen realised that there was a public interest in viewing humpback whales visiting Hervey Bay and commenced commercial whalewatching operations (Vang 2000). It was estimated that approximately 550 humpback whales visited Hervey Bay in 1988 (Chaloupka et al. 1999).

At the cessation of commercial and illegal whaling in the early 1960s it was estimated that fewer than 200 individual eastern Australian humpback whales had survived (Paterson et al. 1994, Jackson et al. 2009). Chittleborough (1955) reported that from his sample of 894 humpback whales collected between 1952 and 1962, he found very low levels of physical maturity, 1.4% of males and 1.8% of females. In contrast for a mature baleen whale stock, the range of physically mature individuals was expected to be between 25% and 35% (Macintosh 1942). Furthermore Clapham et al. (2006) suggested that after the last period of commercial whaling surviving immature whales from Pacific populations may have aggregated with surviving eastern Australian humpback whales. Consequently is likely that the survivors in the eastern Australian population in the early 1960s were heavily skewed towards smaller immature and younger whales with very few mature males and females of breeding age (also see Clapham and Zerbini 2015). This is likely to have contributed to the low trajectory of increase in the number of humpback whales in the eastern Australian population over the next thirty years, and therefore the relatively low number of humpback whales visiting Hervey Bay. By 1992 it was
estimated that the eastern Australian population had increased to about 1900 humpback whales (95% CI 1650-2150, Paterson et al. 1994) and that about 935 humpback whales (95% CI 827-1043, Chaloupka et al. 1999), visited Hervey Bay.

It has been suggested that migratory routes and migratory behaviour of humpback whales are maternally directed (Baker et al. 1990, Martin et al. 1984) while very long-term photo-identification has revealed strong maternally directed fidelity to feeding areas in some regions (Clapham et al. 1993, Clapham and Mayo 1987, Katona and Beard, 1990). The proportion of eastern Australian humpback whales visiting Hervey Bay has remained relatively constant over the years from 1997 to 2009. In the late 1980s and early 1990s population estimates of humpback whales visiting Hervey Bay were highly variable, increasing from 554 (95% CI 329-779) in 1988, to a peak of 1040 (95% CI 783-1297) in 1991 before declining to 921 (95% CI 690-1152) by the mid-1990s (Chaloupka et al. 1999). Between 1992 and 1995, Franklin et al. (2011) also reported a decrease in humpback whales observed in Hervey Bay, and a large decrease in the proportion of pods with calves present from just under 40% in 1992 down to just over 20% in 1994. Using long-term photo-identification resighting histories, Franklin (2012) reported that older male and female calves sighted in Hervey Bay return to Hervey Bay in subsequent seasons as yearlings, during their years of immaturity, and then as early mature whales up to at least 12 years of age (Fig. 4.1.2, F, G and H above). Between 1997 and 2009 there was a significant increase in groups of 3+ adults observed in Hervey Bay (Fig. 4.1.1, a) related to the increasing population and a skew in the population towards immature and younger whales (Franklin et al. 2011). Finally between 1997 and 2009 the annual proportion of pods with calves present in Hervey Bay remained constant at between 40% and 50% (Franklin et al. 2011). Consequently it is suggested that since the mid-1990s, the sub-group of the Eastern Australian humpback whale population visiting Hervey
Bay during the southern migration, is predominantly a consistent cohort of breeding females either with older calves later in the season or involved in accompanying the sub-groups of immature and younger mature males and females early in the season.

The finding of strong evidence for an ‘even flow’ temporary emigration pattern with a constant annual temporary emigration rate (4.3.3.2 above) is consistent with two cohorts of breeding females taking turns to visit Hervey Bay in alternate years depending upon their reproductive status. The typical breeding cycle of the female humpback whale is biennial (Chittleborough 1958). The high portion of pods with calves present in Hervey Bay (40%, Franklin et al. 2011) suggests that females may be more likely to visit Hervey Bay when they have a calf than when they do not have a calf.

The proportion of yearly visitors to Hervey Bay present at the beginning of sampling varies from year to year, ranging from a low of 7% in 2005 to a high of 28% 2007 (mean = 17%, standard deviation = 6.5%, see 4.3.3.3 above). Variations in the timing of the peak of the annual migration of humpback whales, ranging from 3 to 5 weeks, have been reported in both the Northern and Southern Hemisphere (Dawbin 1956, Chittleborough 1965, Baker and Herman 1981). Variations in the proportion of yearly visitors present at the beginning of sampling may be indicative of variations in the peak timing of the migration in any given year.

Within-season weekly abundance is a consequence of the total number of visitors in the year (Fig. 4.3.3.2.1) and the rates of entry (pent, see 4.3.3.3) and rates of exit (phi, see 4.3.3.3). The total number of visitors increased from year to year over the period of the study (Fig. 4.3.3.2.1) but the pattern within years was the same, albeit at higher levels in years with greater total abundance. In a typical within-year pattern
of abundance (Fig. 4.3.3.5.1) the number of visitors to Hervey Bay is skewed towards the first five weeks of the season compared to the last five weeks of the season.

The probability of entry (pent-hat, Fig. 4.3.3.3.1) reveals that 83% of all visitors enter by week 5, with a peak between weeks 2 and 3, and only 17% enter between week 5 and week 10 with a peak between weeks 8 and 9. The first two cohorts to travel south during the first half of the season are immature males and females accompanied by mature newly pregnant or resting females (Dawbin 1966, 1997; Franklin 2012, Fig 4.1.2). Pods with calves are rarely seen early in the season and only a few mature males are present (Franklin 2012, Fig 4.1.2).

During the first five weeks of the season both pod composition (pairs, singletons and groups of 3+ adults), and pod behaviour (predominantly non-agonistic social behaviour, significantly higher rates of pod association and low probability of observing competitive groups), are consistent with the presence of immature males and females, mature females and a few mature males (Franklin et al 2011, Franklin 2012). Franklin (2012) reported that calves first sighted in Hervey Bay return in early August the following season as yearlings (Fig. 4.1.2 g). The proportion of visitors present prior to sampling in week 1 together with the low proportion entering between week 1 and 2 (16.1% and 4.5% (95% CI 02.5-07.9), Fig. 4.3.3.3.1) may be a latent class consisting of the first wave of mature, early pregnant or resting, females and last year’s calves as yearlings (also see Fig 4.1.2 g), with the bulk of the older immatures and mature females (39.1%, Fig. 4.3.3.3.1) entering at the peak between week 2 and week 3.

The lowest level of visitors entering Hervey Bay occurs between week 5 and week 6. This coincides with the departure of the mature female cohort and the immature male and female cohort; and the arrival of the lactating females with older calves and
accompanying mature male escorts (Fig. 4.1.2). The lactating females with calves and accompanying mature males dominate the last five weeks of the season (Fig. 4.1.2), with peak entry of these cohorts occurring between week 7 and week 8 (6.9%, Fig. 4.3.3.3.1).

While between weeks apparent survival was typically around 20% (Fig. 4.3.3.4.1) throughout the season, a high proportion of visitors present in week 2 were likely to still be there in week 3 (73.8%, Fig. 4.3.3.4.1). This coincides with highest level of entry of visitors between week 2 and week 3 (39%, Fig. 4.3.3.3.1) and is likely to be the cohorts of older immature males and females and the resting or newly pregnant mature females.

Towards the end of the season a high proportion of the whales present in week 7 are still present in week 8 (59%, Fig. 4.3.3.4.1), coinciding with the highest probability of entry of the mother-calf and escort cohort (6.9%, Fig. 4.3.3.3.1). The lowest probability of between week apparent survival is between week 5 and week 6 (13.3%, Fig. 4.3.3.4.1), which coincides with the lowest between week probability of entry between week 5 and week 6 (1.2%, Fig. 4.3.3.3.1) and the lowest weekly abundance within season in week 6. These results clearly reflect the transition between the entry and passage of the large numbers of immature males and females during the first five weeks of the season (83% of entries, Fig. 4.3.3.3.1) and the entry and passage of the smaller numbers of lactating females, calves and mature males escorts during the last five weeks of the season (17% of entries, Fig. 4.3.3.3.1). Taken together the above results suggest that the use of the habitat is not random but follows a well-established pattern.

The estimated residency times, although varying from year to year, indicate that in a typical year the residency time of humpback whales in Hervey Bay is about 1.4 – 2.0
weeks (mean=1.6 weeks SD=0.34, Fig 4.3.3.8.1) weeks. Although not analysed here, residency times may vary by class and breeding status, which might be most informatively modelled in terms of breeding status and ‘cohort’ or the week in which a whale arrived in Hervey Bay. There are no recent vessel based data available on aggregations or residency of humpback whales in the breeding grounds north of Hervey Bay (Smith et al. 2012).

Burns et al. (2013) studied intra season movements and migratory timing of individual humpback whales sighted northbound past Byron Bay, NSW and southbound in Hervey Bay and at Ballina, NSW. They reported that eastern Australian Humpback whales spend approximately two months on the northern part of the migratory range north from Byron Bay, NSW and south back to Ballina, NSW. Approximately a month of that time is spent in the breeding grounds, 1.5 weeks of travel time is involved from the southern end of the putative breeding grounds to Hervey Bay, and 2.5 weeks of travel time from the southern end of the putative breeding grounds to Ballina, NSW. The data presented in this study confirms that the sub-group of eastern Australian humpback whales that enter Hervey Bay during the early stage of the southern migration spend an average of 1.6 weeks (SD=0.34) stopping over in the Bay.

Franklin (2012) found that the temporal segregation of age, sex and reproductive classes across the season in Hervey Bay was consistent with the results based on whaling data from the early 1930s to the 1960s reported by Dawbin (1996, 1997). Therefore this segregation appears to be a consistent and coherent feature of the social organisation of humpback whales over many decades (Dawbin 1996, 1997; Franklin 2012). The regular within season patterns over years, of probability of entry, between week apparent survival and within year abundance reported in this study
are also consistent with a regular annual structure to the classes of whales visiting Hervey Bay.

Estimated capture probabilities within year have a regular annual pattern but have decreased over years as the population has grown. There has been a steady near linear trajectory of yearly increase and overall a five-fold increase in the number of whales visiting Hervey Bay (Fig. 4.3.3.2.1) while the annual abundance within season has a regular pattern with 83% of visitors entering during the first five weeks and 17% during the last five weeks (Fig. 4.3.3.3.1). Consequently capture probabilities both over years and within season appear to be related to the number of humpback whales visiting Hervey Bay.

Future modeling should distinguish between females with calves compared with other whales and assess residency time in terms of entry cohort. This could be accommodated in the MSORD model by including female with calf as a state and between-week survival (residency) as a function of entry cohort. A first step in this direction is to conduct a separate analysis for known breeding females only with a focus on the relative probabilities of presence in Hervey Bay as a function of breeding state. Here we might expect a Markovian model in which temporary emigration is lower for females without calf in the previous year, which may be expected to often be with calf in the current year. The entry and exit times and periods of residency are expected to vary with the breeding state of females, and residency times could be estimated separately for these groups in terms of their entry cohorts. This model will, however, be a first step to integrating the entire population in terms of breeding status and entry cohort in a MSORD model with several classes of whales included as states. There are limits to this however, as the sex and age of many whales is unknown and, there were some classes of whales that were present but for which it
was not possible to identify each member (e.g. juveniles). Consequently they will be ‘latent classes’ underlying variation in the model estimates.
4.5 LITERATURE CITED


http://epubs.scu.edu.au/theses/357/


* novaeangliae). Journal of Cetacean Research and Management (Special Issue) 3, 243-252.


Smith, J.N., Grantham, H.S., Gales, N., Double, M.C., Noad, M.J. and Paton, D.


Chapter 5

Reproduction rates and population rate of increase of Humpback whales (*Megaptera novaeangliae*) in Hervey Bay, relative to the eastern Australian population
5.1 INTRODUCTION


Three explanations for the predominance of calf pods in calm, shallow waters have been proposed: a preference for calm, shallow, sheltered waters by breeding female humpback whales (Whitehead and Moore 1982, Smultea 1994, Ersts and Rosenbaum 2003); avoidance of predators, such as killer whales (Orcinus orca) (Corkeron and Conner 1999); and avoidance of male harassment (Smultea 1994, Ersts and Rosenbaum 2003). In a recent study in Hawai'i, Craig et al. (2014) tested the hypothesis that spatial distribution of females is driven primarily by avoidance of males. They rejected the ‘preference of shallow water’ and ‘predator avoidance’ hypotheses based on available evidence. Their test of the ‘male avoidance’ hypothesis showed that pods containing a calf occurred in significantly shallower water than pods that did not contain a calf (median = 53.54 m versus median = 62.51); unescorted maternal females occurred in significantly shallower water than escorted maternal females (median 49.58 versus median = 55.35) and, that the
number of males escorting a female decreased significantly with decreasing water depth (Craig et al. 2014).

Hervey Bay is a large shallow bay, of less than 18 m depth throughout, formed by Fraser Island and mainland Australia (Vang 2002) and is located south of the putative breeding grounds for eastern Australian humpback whales (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999, Smith et al. 2012). Humpback whales enter and leave Hervey Bay from the north during the southern migration and aggregate on the eastern side of Hervey Bay along the western shore of Fraser island, see Figure 1.7.1 in Chapter 1 (Paterson 1991, Corkeron 1993, Corkeron et al. 1994, Franklin et al. 2011, Franklin 2012). In Hawaii the modal size of pods having a calf present is three (Mobley and Herman 1985), in contrast in Hervey Bay the modal size of pods having a calf present is two because of the significantly higher proportion of mothers that are alone with their calf in Hervey Bay, compared to Hawaii (Franklin et al. 2011).

The size of the Group E1 Eastern Australian humpback population prior to the Second World War was estimated at 22,093 whales (95% PPI; 20,062 - 26,673, Jackson et al. 2009). Eastern Australian humpback whales were severely depleted during the last phase of coastal and Antarctic pelagic whaling (Chittleborough 1965, Clapham and Baker 2009), particularly from illegal Soviet whaling (Clapham et al. 2009). Between 1947 and 1973 Soviet whalers took 45,341 humpback whales from Antarctic Areas V and VI (see Figure 1.2.2.1 above) with 25,192 being taken in only two seasons, 1959 to 1961 (Clapham et al. 2009). Overall between 1946 and 1986 the total Soviet catch of humpback whales was 48,721, with only 2,710 being reported to the International Whaling Commission (Ivaschenko et al. 2011). It was estimated that in the early 1960s there may have been fewer than 200 survivors in the eastern Australian population (Patterson et al. 1994, Jackson et al 2009, Table
1.6.1 in Chapter 1) with possibly less than two per cent of that number being mature breeding females and males (Chittleborough 1965).

In the thirty years between 1962 and 1992, eastern Australian humpback whales were estimated to have increased to 1,900 whales (95% CI 1,650–2,150, Paterson et al. 1994) with a further increase to about 3,185 humpback whales by 1996 (Bryden et al. 1996). The eastern Australian humpback whale population has increased rapidly between 1996 and 2009 with an annual growth rate of approximately 10.6% (Noad et al. 2011a and b). Using multi-point sampling and capture-recapture analysis Paton et al. (2011) estimated east coast humpback abundance of 7,041 (95% CI 4,075–10,008) whales.

Estimates of yearly abundance from 1996 to 2009 are presented in Figure 5.1 (courtesy of Dr. M. Noad, University of Queensland).
Figure 5.1. Estimates of yearly abundance of eastern Australia humpback whales (Data summary provided by Dr. M. Noad, University of Queensland: 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. 2011b; 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. 2011a).

Consistent with the above yearly abundance estimates, modelling of the recovery of the east Australian population (Jackson et al. 2009, see Fig. 1.6.1 above) predicts a logistic population recovery curve with low levels of recovery from the early 1960s to the early 1990s, a steady recovery rate (approximately 10.5%) between 1995 and 2015 with the growth rate lessening after 2015, as the eastern Australian humpback whale population returns towards its natural population size (Jackson et al. 2009).
The recovery of a depleted humpback whale population is likely to be constrained by biological parameters such as age at first parturition, birthing rates, and non-calf and calf survival (Zerbini et al. 2010). Zerbini et al. (2010) reviewed available evidence on humpback whale life-history parameters and modelled plausible growth rates for humpback whale populations. They suggested that mean rates of increase for humpback whale populations occur in the range 7.3% per year to 8.6% per year, with a proposed maximum plausible rate of increase of 11.8% per year.

Noad et al. (2011b) reported an annual rate of increase for the eastern Australian humpback population (Breeding Group E1) of 10.6% ±0.5% (95% CI) for the period 1987–2004. In contrast modeling of the Oceania humpback whale populations (Breeding Groups E2, E3 and F) has estimated the annual rate of increase to be about 5.1% (Jackson et al 2009, Table 1.6.1 in Chapter 1). Estimates of rates of annual increase for the Western Australian sub-population (Breeding Group D) have ranged from 10.15% between 1982 to 1994 (Bannister 1994, Bannister and Hedley 2001) and 9.7% between 1999 to 2008 (Hedley et al. 2011). A recent higher estimate of the rate of increase of 13% (Salgado Kent et al. 2012) is considered to be biologically implausible (Zerbini et al. 2010, Clapham and Zerbini 2015).

Two previous studies of abundance in Hervey Bay for the periods 1987 to 1996 and 1987 to 2007 estimated an average annual growth rates of 6.3% and 13.4% respectively with survival estimated at 0.966 and 0.945 respectively (Chaloupka et al. 1999 and Forestell et al. 2011).

In this study observations of the proportion of calves to whales observed in Hervey Bay are used to assess the reproduction rate of the humpback whales utilising Hervey Bay. Available abundance estimates from the robust design model (Chapter 4, section 4.3.3.2 above) are used to investigate trends of abundance in Hervey Bay,
relative to plausible rates of increase in a humpback whale population and estimated rates of increase of the eastern Australian population.
5.2 METHODS

5.2.1 Fieldwork

Fieldwork was conducted in Hervey Bay during the years 1997 to 2009 (see Section 2.2 and Figure 2.2.1 above for a detailed description of the location of Hervey Bay and the study site). Vessel-based surveys were undertaken for 10 weeks each season commencing on the first Sunday after the 5th August until mid-October. The study area (Fig. 2.2.1 above) is approximately 27.6 km from Urangan Boat Harbour, Hervey Bay. Fieldwork was planned for six days each week, leaving Urangan harbour at 0600 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.

5.2.2 Observations

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.
The primary data for this study was the number of unique individual humpback whales sighted in each of the ten weekly sampling periods each year classified as either a ‘humpback whale’ or a ‘humpback whale calf’. The photo-identification data were used to eliminate resights of individual whales or calves within each sampling period.

An individual whale was considered to be a calf if it appeared to be less than half the length of a particular adult and 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 inferred to be the mother. Yearlings were distinguished from calves visually by an experienced observer as being too large to be calves of the year in which they were observed (Clapham et al. 1999, Craig et al. 2003).

5.2.3 Rates of increase

The rate of increase observed in a humpback whale population is a function of life-history parameters including age at first parturition, birth rates and non-calf and calf survival rates (Zerbini et al. 2010). In the case of the eastern Australian humpback whale population there is an available estimate of the rate of increase in the population (10.6% ±0.5% (95% CI) for the period 1987–2004, Noad et al. 2011a and b). The proportion of the eastern Australian population visiting Hervey Bay has been reasonably consistent (mean = 34%, standard deviation = 5.3%, Chapter 4.3.3.2 above) indicating that rates of increase in Hervey Bay are similar to rates of increase in the eastern Australian population. Non-calf survival has been estimated in Hervey Bay at 0.947 (SE = 0.012, 95%CI = 0.918:0.966) (Chapter 4.3.3.3 above), which is close to biological non-calf survival rate of 0.96 reported by Barlow and Clapham (1997).
5.2.4 Estimates of additions needed to achieve rates of increase

Using the non-calf survival rate of 0.96 (Barlow and Clapham 1997), calf survival rates of 0.808 and 0.669 (Zerbini et al. 2010) and the Hervey Bay survival rate = 0.947, from Chap. 4, Sect. 4.3.3.3 above, together with the population rates of increase for eastern Australia (10.6%, Noad et al. 2011), it is possible to derive an estimate of the proportions of calves to whales expected to be observed given these parameters:

\[ N_{t+1} = N_t - L + G, \]

where \( N_{t+1} \) is the population size at time \( t+1 \),
\( N_t \) is the population size at time \( t \),
\( L \) is the number of losses due to deaths or emigration between \( N_t \) and \( N_{t+1} \),
and \( G \) is the number of gains due to births or immigration between \( N_t \) and \( N_{t+1} \).

Dividing through by \( N_t \),
\[ \frac{N_{t+1}}{N_t} = 1 - l + g, \]

where \( l \) is the rate of losses between \( N_t \) and \( N_{t+1} \),
and \( g \) is the rate of gains between \( N_t \) and \( N_{t+1} \).

Substituting \( \frac{N_{t+1}}{N_t} = 1.106 \) from Noad et al. 2011a,
and \( l = 1 - \phi = 1 - 0.96 \) from Barlow and Clapham 1997,
\[ \frac{N_{t+1}}{N_t} = 1 - (1 - 0.96) + g, \]
\[ g = 1.106 - 0.96 = 0.146. \]

The rate of gains \( g \) is due to the survivors of births at \( N_t \) to \( N_{t+1} \).

Taking mean calf survival = 0.808 from Zerbini et al. (2010),
\[ b = \frac{0.146}{0.808} = 0.181, \]
where \( b \) is the rate of births at \( N_t \).

Taking mean calf survival = 0.669 from Zerbini et al. (2010),

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\[ b = \frac{0.146}{0.669} = 0.218, \]
where \( b \) is the rate of births at \( N_t \).

Using the estimated Hervey Bay survival = 0.947, from Chap. 3, Sect. 3.3.3.3 above,

\[ b = \frac{0.146}{0.947} = 0.154, \]
where \( b \) is the rate of births at \( N_t \).

Thus the expected proportion of calves to whales for a population rate of increase of 10.6\% is estimated to be between 18.1\% and 21.8\% relative to calf survival of 0.808 to 0.669.

Assuming calf survival equal to estimated Hervey Bay survival of 0.947, the expected proportion of calves to whales for a population rate of increase of 10.6\% is estimated to be between 15.4\% and 21.8\% relative to calf survival of 0.947 to 0.669.

### 5.2.5 Estimates of abundance in Hervey Bay

Estimates of yearly abundance (\( N\)-hat) were derived from the robust design model:
\[ S(.)psi(PA=AP=.)pent(y+w)phi(y+w)p(y+w+effort). \]
The model selection is fully reported in Chapter 4.2 above and the estimates of yearly abundance (\( N\)-hat) were presented in 4.3.3.2 above and are summarised with \( \ln(N\)-hat); together with estimates for the eastern Australian population in Table 5.2.5.
Table 5.2.5. Estimates of yearly abundance in Hervey Bay 1997-2009 (N-hat) and ln(N-hat), estimates of eastern Australian abundance and the proportion of Hervey Bay (HB) to eastern Australia (EA).

<table>
<thead>
<tr>
<th>Year</th>
<th>N-hat</th>
<th>ln(N-hat)</th>
<th>Eastern Australia^ (See Fig. 5.1 above)</th>
<th>Proportion HB/EA</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>791</td>
<td>6.67</td>
<td>3425</td>
<td>0.23</td>
</tr>
<tr>
<td>1998</td>
<td>1304</td>
<td>7.17</td>
<td>3683</td>
<td>0.35</td>
</tr>
<tr>
<td>1999</td>
<td>1188</td>
<td>7.08</td>
<td>3961</td>
<td>0.30</td>
</tr>
<tr>
<td>2000</td>
<td>1966</td>
<td>7.58</td>
<td><strong>4260</strong></td>
<td>0.46</td>
</tr>
<tr>
<td>2001</td>
<td>1640</td>
<td>7.40</td>
<td>4958</td>
<td>0.33</td>
</tr>
<tr>
<td>2002</td>
<td>2002</td>
<td>7.60</td>
<td>5771</td>
<td>0.35</td>
</tr>
<tr>
<td>2003</td>
<td>2416</td>
<td>7.79</td>
<td>6718</td>
<td>0.36</td>
</tr>
<tr>
<td>2004</td>
<td>2320</td>
<td>7.75</td>
<td><strong>7819</strong></td>
<td>0.30</td>
</tr>
<tr>
<td>2005</td>
<td>3048</td>
<td>8.02</td>
<td>8669</td>
<td>0.35</td>
</tr>
<tr>
<td>2006</td>
<td>3661</td>
<td>8.21</td>
<td>9611</td>
<td>0.38</td>
</tr>
<tr>
<td>2007</td>
<td>3740</td>
<td>8.23</td>
<td>10656</td>
<td>0.35</td>
</tr>
<tr>
<td>2008</td>
<td>4345</td>
<td>8.38</td>
<td>11814</td>
<td>0.37</td>
</tr>
<tr>
<td>2009</td>
<td>4406</td>
<td>8.39</td>
<td>13098</td>
<td>0.34</td>
</tr>
</tbody>
</table>

^ The eastern Australian estimates were provided by Dr Mike Noad, University of Queensland; see Fig. 5.1 above.

* 2000 estimate from an unpublished report by Brown *et al.* 2000 which was partly reported in Brown *et al.* 2003.

# 2004 estimate is an updated but unpublished estimate of the estimate reported in Noad *et al.* 2011b.

^ The other eastern Australian yearly estimates are interpolated, while those post 2004 are based on the relative abundance surveys and the 2004 data published in Noad *et al.* 2011a (see Fig. 5.1).

To examine the trends in abundance over the years 1997 to 2009 in Hervey Bay three models - linear, exponential and logistic - were fitted to the above abundance estimates for Hervey Bay (Table 5.2.5).
5.3 RESULTS

5.3.1 Proportion of calves observed in Hervey Bay 1997-2009

The proportion of calves to whales observed in Hervey Bay for the years 1997 to 2009 are summarised in Table 5.3.1 below.

Table 5.3.1. Number of whales and calves observed in Hervey Bay 1997-2009 by year, proportion of calves to whales (Yearly %*) and weekly average proportion of calves to whales (Weekly Average %*).

<table>
<thead>
<tr>
<th>Year</th>
<th>Whales</th>
<th>Calves</th>
<th>Yearly %*</th>
<th>Weekly Average %*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1997</td>
<td>179</td>
<td>29</td>
<td>16.20</td>
<td>17.59</td>
</tr>
<tr>
<td>1998</td>
<td>254</td>
<td>45</td>
<td>17.72</td>
<td>17.12</td>
</tr>
<tr>
<td>1999</td>
<td>250</td>
<td>32</td>
<td>12.80</td>
<td>12.91</td>
</tr>
<tr>
<td>2000</td>
<td>264</td>
<td>49</td>
<td>18.56</td>
<td>15.59</td>
</tr>
<tr>
<td>2001</td>
<td>317</td>
<td>62</td>
<td>19.56</td>
<td>19.45</td>
</tr>
<tr>
<td>2002</td>
<td>357</td>
<td>67</td>
<td>18.77</td>
<td>19.29</td>
</tr>
<tr>
<td>2003</td>
<td>338</td>
<td>61</td>
<td>18.05</td>
<td>20.28</td>
</tr>
<tr>
<td>2004</td>
<td>409</td>
<td>85</td>
<td>20.78</td>
<td>20.53</td>
</tr>
<tr>
<td>2005</td>
<td>468</td>
<td>77</td>
<td>16.45</td>
<td>16.30</td>
</tr>
<tr>
<td>2006</td>
<td>411</td>
<td>60</td>
<td>14.60</td>
<td>14.91</td>
</tr>
<tr>
<td>2007</td>
<td>381</td>
<td>75</td>
<td>19.69</td>
<td>18.45</td>
</tr>
<tr>
<td>2008</td>
<td>529</td>
<td>110</td>
<td>20.79</td>
<td>19.47</td>
</tr>
<tr>
<td>2009</td>
<td>417</td>
<td>100</td>
<td>23.98</td>
<td>20.86</td>
</tr>
<tr>
<td>Total</td>
<td>4574</td>
<td>852</td>
<td>18.63</td>
<td>17.90</td>
</tr>
</tbody>
</table>

* The ‘Yearly %’ result is likely to be biased by variation in captures and capture probabilities over years and by week within year (see Chapter 4.3.3.1 above). In contrast the ‘Weekly Average %’ does not depend upon the relative number of captures in each week of each year and therefore provides an unbiased measure of the proportion of calves to whales.
There is a slight trend towards increasing weekly average percentage of calves over years (increase = 0.26% pa) but it is not significant (p=0.165) due to the extent of variation from year to year.

5.3.2 Trends in abundance in Hervey Bay 1997-2009

To examine the trends in abundance in Hervey Bay over the thirteen years from 1997 to 2009, three models were fitted to the derived abundance estimates reported in Table 5.2.5. above: linear, exponential and logistic; using the following equations.

Linear \[ N_{\text{hat}} = B_{1996} + B_1 \times (\text{year}-1996) \]

Exponential \[ \ln(N_{\text{hat}}) = B_{1996} + B_1 \times (\text{year}-1996) \]

\[ N_{\text{hat}} = \exp(B_{1996}) \times \exp[B \times (\text{year}-1996)] \]

Logistic

**Note** this function requires an estimate of \( K \), the carrying capacity,

*Jackson et al. 2009 estimated historical \( K \) for eastern Australia at 22093 whales (Table 1.6.1 above),

*The Hervey Bay group appears to be about 34% of eastern Australia,*

\[ K_{\text{HB}} = 7512 \]

\[ Y = 1 / (1/u + (b0 \times (b1**t)) \]

\[ N_{\text{hat}} = 1 / (1 / K_{\text{HB}} + (B_{1996} \times (B_1 \times (\text{year}-1996)))) \]

The model summary and parameter estimates are reported in Table 5.3.2.
Table 5.3.2. Abundance trends in Hervey Bay, 1997 to 2009; model summary and parameter estimates.

<table>
<thead>
<tr>
<th>Equation</th>
<th>Model Summary</th>
<th>Parameter Estimates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>R Square</td>
<td>F</td>
</tr>
<tr>
<td>Linear</td>
<td>.956</td>
<td>236.476</td>
</tr>
<tr>
<td>Exponential</td>
<td>.941</td>
<td>176.531</td>
</tr>
<tr>
<td>Logistic</td>
<td>.961</td>
<td>268.068</td>
</tr>
</tbody>
</table>

The independent variable is year-1996.

The logistic curve was based on an estimate of $K_{HB} = 7512$, which assumes:

a) That the Jackson et al. (2009) estimate of eastern Australian historical $K$ is reasonable and

b) That about 34% of the eastern Australian population is in the Hervey Bay group (Chapter 4.3.3.2 above).

The models’ curves are plotted against observed abundance in Figures 5.3.2, 5.3.3 and 5.3.4 below.
Figure 5.3.2. Abundance in Hervey Bay 1997 to 2009; plot of linear model against observed abundance (year 0=1996, R Square = 0.956)

Figure 5.3.3. Abundance in Hervey Bay 1997 to 2009; plot of exponential model against observed abundance (year 0=1996, R Square = 0.941)

Figure 5.3.4. Abundance in Hervey Bay 1997 to 2009; plot of logistic model against observed abundance (year 0=1996, R Square = 0.961)
Although the exponential model (Fig. 5.3.3 above) was apparently the poorest-fitting of the three alternative growth models for the annual abundance observed in Hervey Bay, an estimate of the exponential growth rate is reported as a simple summary of the average growth rate for descriptive purposes: the average rate of growth of humpback whales utilising Hervey Bay between 1997 and 2009 was estimated to have been 14.2% (95%CI, 11.1% to 15.5%).

The estimates of yearly abundances in Hervey Bay were compared to estimates of the total eastern Australian migration (Table 5.2.5. above) and between 23% and 46% (mean = 34%, standard deviation = 5.3%) of the estimated eastern Australian migration were estimated to have visited Hervey Bay each year. The two extremes – a low of 23% in 1997 and a high of 46% in 2000 – were anomalous, with all other estimates falling in the range 30% to 38.
5.4 DISCUSSION

5.4.1 Rate of reproduction of Humpback whales utilising Hervey Bay

The rate of reproduction of the humpback whales observed in Hervey Bay in terms of
the proportion of calves to whales (weekly average 1997-2009 - 17.9%, Table 5.3.1
above) is fully consistent with the proportion of calves to whales that would be
expected to be observed in the eastern Australian humpback whale population
(18.1%, 5.2.4 above), given an estimated rate of increase in the population of 10.6%
per annum (Noad et al. 2011a). The result is also consistent with a high rate of calf
survival in Hervey Bay (0.947 from Chap. 4, Sect. 4.3.3.3 above) and is consistent
with the estimated rate of population increase in Hervey Bay (14.2%; 95%CI, 11.1%
to 15.5%).

The birth and early development of calves in warm, sheltered, tropical or sub-tropical
coastal waters may be conducive to an overall higher rate of reproductive success
(Brodie 1975; Whitehead and Moore 1982; Clapham 1996, 2001). Hervey Bay is
neither a terminal destination nor a calving or breeding area. It is a stopover early in
the southern migration for particular classes of humpback whales (Franklin et al.
2011, Franklin 2012). Mature females accompanying immature males and females
predominate early in the season, while females with new calves dominate during the
latter part of the season (Dawbin 1966, 1997; Franklin et al. 2011). There are few
escorts associated with females with new calves (10.8% of mother-calf pods); low
levels of competitive activity (6.3% of all pods), occurring mainly late in the season,
and higher levels of non-agonistic social behaviour (11.8% of all pods), occurring
mainly early in the season (Franklin et al. 2011). Mothers with calves in Hervey Bay
spend 69.4% of their time alone involved in maternal activities (Franklin et al. 2011).
Mean residency of humpback whales in Hervey Bay is estimated at 1.6 weeks
(SD=0.34, this study 4.3.3.8 above). The extended stopover in Hervey Bay and the
dense aggregations of mature humpback whale females and immature males and females early in the season and, mother-calf pods later in the season provides increased opportunities for social interactions and social development. This may contribute to the high levels of reproductive success and calf survival of the humpback whales utilising Hervey Bay.

5.4.2 Trends in rates of population increase in Hervey Bay

The differences in R Square values between the linear, exponential and logistic models fitted to the Hervey Bay abundance data (Table 5.2.3) are not substantial. However it is interesting to note that the logistic curve has the best fit and the exponential curve the least good fit to the data (Fig. 5.3.4 and Fig. 5.3.3). This indicates that the growth curve of the population has gone past the initial rapid expansion phase and is starting to decline after the near-linear increase evident in the middle area of the graph (Fig. 5.3.4). These results indicate that an exponential function with a constant annual growth rate is not a good fit to the observed trends, with the annual rate of increase decreasing over years. Although caution is needed in interpreting the subtle differences in R Square values between the linear, exponential and logistic functions, it should be noted that the exponential function had the lowest R Square value (R Square = .941, Table 5.3.2 of the three models and the logistic the highest R Square value (R Square = .961, Table 5.3.2).

At the cessation of commercial whaling in the early 1960s the east Australian humpback whale population is estimated to have numbered fewer than 200 individual whales (Patterson et al. 1991, Jackson et al. 2009) and owing to the very small proportion of whales of mature breeding age (Chittleborough 1955), population increase was initially very slow, after commercial whaling ceased. The eastern Australian population was estimated to have increased to only to about 1900 humpback whales by 1992 (Patterson et al. 1991). However from the mid-1990s and
during the 2000s the rate of increase in the population of the eastern Australian humpback whales increased and approached the upper limit of plausible biological growth for a humpback whale population, with no indication of a slowing of the rate of increase during that period (Jackson et al. 2009, Noad et al. 2011a and b). The upward trend in the logistic curve in the early-1990s (Figure 5.3.4) and the near linear growth from the mid-1990s to the mid-2000s observed in Hervey Bay (Figure 5.3.4) are consistent with the growth patterns reported for the eastern Australian humpback whale population.

Analysis of further future data points beyond 2010 for the estimation of eastern Australian abundance will be required to detect a significant slowing in the rate of increase of the eastern Australian humpback whale population. The population trajectory for the eastern Australian humpback whale population presented in the Jackson et al. (2009) suggests that a slowdown in the present high rates of increase may not occur until 2015 or beyond (Figure 1.6.1 above, Jackson et al. 2009). However, the logistic model fitted to the Hervey Bay abundance data indicates a slight slowdown in the rate of increase in the Hervey Bay population is evident by 2009. Franklin et al. (2011) reported a significant increase in groups of 3 or more humpback whales in Hervey Bay between 1992 and 2009. With the rapid rate of increase in the population that has occurred in Hervey Bay between 1997 and 2009, the slowing of the rate of increase of humpback whales utilising Hervey Bay evident in the logistic growth curve (Figure 5.3.4), may be a density dependent effect from the rate of increase of humpback whales using Hervey Bay.

5.4.3 Comparison of population size and growth in Hervey Bay compared with eastern Australia

The available estimates of the size of the eastern Australian population are those summarised in Noad et al. (2011 a and b) and a multi-point sampling capture-
recapture estimate for 2007 of 7,041 whales (95% CI 4,075–10,008, Paton et al. 2011). The Noad et al. (2011 a and b) estimates were based on data collected by Bryden et al. 1996 for the year 1996 (Fig. 5.1 above), by Brown et al. 2000 (partly reported in Brown et al. 2003) for the year 2000 and by Noad et al. (2011a and b) for 2004 (Fig. 4.4.3 below) with estimates for other years interpolated (see Fig. 5.1 above). There were both survey and methodological differences in the primary surveys in 1996, 2000 and 2004 and these are presented and discussed in detail in Noad et al. (2011a). The eastern Australian growth rate estimates provided for this study by Dr Noad were based on the three estimates for 1996, 2000 and 2004 (see Fig. 5.4.3 below) and assumed interpolated exponential growth rates between those years (see Fig. 5.1; Table 5.2.5).

The Noad et al. (2011 a and b) abundance estimates and the abundance estimates provided by Dr Noad (Fig. 5.1.1; Table 5.2.5) do not provide a sound basis for an analytical comparison of the form or size of the population growth in Hervey Bay and eastern Australia, although they were used here to estimate the approximate proportion of the eastern Australian population that visit Hervey Bay (Fig. 5.1; Table 5.2.5 and Fig. 5.4.3 below).
Figure 5.4.3. Data points used in the estimates of abundance for the eastern Australian population (Circles; see Table 5.2.5 above) and for the humpback whales using Hervey Bay in this study (Squares; from Table 5.2.5 above).

Note: The 2004 estimate is an updated but unpublished estimate of the estimate reported in Noad et al. (2011b).

Although the proportion of the eastern Australian population that visited Hervey Bay was estimated as an approximately constant 34% (Fig. 5.1, Table 5.2.5 above), it was observed to have been increasing over time but not significantly so (p=0.380).

The average rate of population growth in Hervey Bay between 1997 and 2009 from the exponential model (Fig. 5.3.3) was estimated to have been 14.2% (95%CI
11.1% to 15.5%). This is not only greater than the Noad et al. (2011b) estimate of 10.6% ±0.5% (95% CI) for the period 1987–2004 but also greater than the theoretical biological plausible maximum for the humpback whale species estimated by Zerbini et al. (2010) at 11.8%. While it is possible that the Zerbini et al. (2010) theoretical biological plausible maximum and the Noad et al. (2011b) empirical estimates may be underestimates, it is also possible that the population rate of growth in Hervey Bay has been growing at a faster rate than that of the eastern Australian population as a whole. Moreover is it possible that the extended residency in Hervey Bay, of mature females and their calves late in the season and mature females, yearlings and the younger cohort early in the season, may contribute to a higher than typical humpback whale calf survival in Hervey Bay and to a higher population growth rate than eastern Australia as a whole.

Although the proportion of the eastern Australian population utilising Hervey Bay was relatively constant at 34%, it was observed to have been increasing over time (although not significantly: p=0.380). Consequently proportionally more humpback whales may be entering Hervey Bay contributing the higher rates of increase being observed in Hervey Bay.

5.4.4 Comparison of rates of increase in Hervey Bay with other humpback whale populations

The estimated population rate of increase (ROI) in Hervey Bay for the period 1997 to 2009 (14.2%; 95%CI, 11.1% to 15.5%) reported in this study, is greater that the proposed maximum biologically plausible ROI of 11.8% per year reported in Zerbini et al. (2010). In the North Pacific ROI have been reported ranging from 6.6% per year to 10% per year: 6.6% per year in the Northern Gulf of Alaska for the period 1987 to 2003 (Zerbini et al. 2006); 6.8% per year in the North Pacific Ocean for the
period 1966 to 2005 (Calambokidis \textit{et al.} 2008) and 8.0\% per year for the West Coast of the USA for the period 1990 to 2008 (Calambokidis 2009). In the North Atlantic ROI have been reported ranging from 3.1\% per year to 14.8\% per year: in the North Atlantic Ocean, 3.1\% per year for the period 1997 to 2003 (Stevick \textit{et al.} 2004); in the Gulf of Maine, 4.0\% per year for the period 1992 to 2000 (Clapham \textit{et al.} 2003); 6.5\% per year in the Gulf of Maine fort the period 1997 to 1991 (Barlow and Clapham 1997) and 14.8\% per year for Iceland for the period 1968 to 1988 (Sigurjonsson & Gunnaugsson 1990). In the Southern Hemisphere ROI reported for breeding populations have ranged from 7.4\% per year to 30.6\% per year: Western South Atlantic, 7.4\% for the period 1995 to 1998 (Ward \textit{et al.} 2011); Western Indian Ocean, 7.9\% per year for the period 1991 to 2003 (Findlay \textit{et al.} 2004) and Western Australia, 10.1\% per year for the period 1977 to 1991 (Bannister and Hedley 2001) and Western Australia, 13.0\% per year for the period 2000 to 2008 (Salgado Kent \textit{et al.} 2012). Zerbini \textit{et al.} (2010) in a comprehensive review of the above reported ROI suggested that many of these estimates are inflated as a result of undetected survey bias, population sub-structuring and immigration from other populations. The sampling protocols adopted and the use of the multi-state robust design modelling in analysis avoids the issues raised by Zerbini \textit{et al.} (2010) for the ROI results reported for Hervey Bay in this study.

5.4.5 \textit{Is Hervey Bay unique? – Future research}

The rate of reproduction and the population rate of increase of humpback whales utilising Hervey Bay presented in this study are fully consistent with, and may be greater than the rate of increase of the eastern Australian humpback whale population. They are also consistent with earlier Hervey Bay estimates of rates of increase and survival reported in Chaloupka \textit{et al.} 1999 and Forestell \textit{et al.} (2011). The near maximum biological level of between year survival of humpback whales in
Hervey Bay (Chapter 4.3.3.3; 0.947, 95% CI 0.918:0.966) and the apparently consistent proportion of the eastern Australian population using Hervey Bay (Chapter 4.3.3.2; Mean = 34%, SE = 5.3%) suggest that the humpback whales utilising Hervey Bay are a sub-group of the eastern Australian population. The bi-annual pattern of temporary immigration (Chapter 4.3.3.4; 0.141, 95% CI 0.081:0.234) and the female biased sex ratio in Hervey Bay (Franklin 2012) are consistent with a cohort of mature females accompanying immature males and females early in the season, and mother-calf pods during the latter part of the season (Chapter 4, Figure 4.1.2), utilising Hervey Bay. However as only about 34% of eastern Australian humpback whales utilise Hervey Bay this raises the question: Are there other site-specific sub-groups within the eastern Australian population?

Only broad-scale information is available on the movements and locations of humpback whales within the putative breeding areas to the north of Hervey Bay between 16° and 23° (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999, Smith et al. 2012 and Chapter 2. Figure 2.2.1). Consequently there are presently insufficient data to address a number of important management questions: Does the breeding cohort using Hervey Bay exhibit natal philopatry to site-specific birthing locations prior to visiting Hervey Bay? If other sub-groups exist do they share site-specific birthing locations with the Hervey Bay cohort or occupy different site specific birthing locations? The availability of a large long-term photo-identification dataset from Hervey Bay (1992-2009, n = 2821 unique fluke identifications) and a large number of genetic samples (1992-2009, n = 1471 samples) provides the opportunity for collaborative analysis, between site-specific data obtained within the putative breeding grounds or from other locations along the eastern coastline of Queensland and New South Wales, to address the above questions.
5.5 LITERATURE CITED


105-138.


Noad, M. J., R. A. Dunlop, D. Paton, and H. Kniest. 2011b. Abundance estimates of


302-305.


Chapter 6

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.

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Conception of the study: WF (80%), TF (10%), PB (10%)

Data analysis: WF (70%), TF (20%), LB (10%)

Statistical analysis: WF (60%), LB (40%)

Interpretation of data: WF (60%), TF (10%), LB (10%), PB (10%), PH (10%)

Writing of manuscript: WF (70%), TF (10%), LB (10%), Other Authors (10%)
6.1 INTRODUCTION

A comprehensive investigation of humpback whales (*Megaptera novaeangliae*) migrating through New Zealand waters was undertaken during the 1950s (Dawbin and Falla, 1949; Dawbin, 1956; Dawbin, 1966). After reviewing a range of factors that might influence the migratory routes taken by humpbacks past New Zealand including ocean currents, bottom topography and geography of land masses encountered, Dawbin (1956) concluded that the primary factors determining the migratory route of humpbacks past New Zealand were feeding behaviour in Antarctic waters and the location of breeding grounds in eastern Australia and the islands of the western Pacific further to the east (Dawbin and Falla, 1949; Dawbin, 1956; Dawbin, 1964; Dawbin, 1966).

Initially, Dawbin considered the breeding ground destinations of humpback whales migrating from Antarctic feeding areas through New Zealand waters, and up along the eastern coast of Australia, were the eastern Coral Sea including the Chesterfields and New Caledonia, with the Tongan Group of islands being the northern limit of north bound humpbacks passing New Zealand (Dawbin and Falla, 1949). However, Dawbin subsequently noted that the ‘great length of the eastern Australian coastline situated in the tropics should however provide a much more extended area of coastal conditions suitable for breeding than is available at near Pacific Islands’ (Dawbin, 1956).

Geographic separation and isolation of discrete breeding groups was considered to occur and to influence breeding ground destinations of migrating humpback whales (Mackintosh, 1942; Chittleborough, 1965; Dawbin, 1964; Dawbin, 1966). The Discovery marking programs provided the first direct evidence of linkages between polar feeding areas and temperate breeding grounds and intermingling among discrete breeding groups (Rayner, 1940; Mackintosh, 1942; Dawbin, 1959; Dawbin,
1964; Dawbin, 1966; Chittleborough, 1965). This evidence supported the hypothesis that western Australia, eastern Australia and Oceania were discrete breeding grounds with little interchange among individuals and no evidence for permanent exchange of individuals (Dawbin, 1964; Chittleborough, 1965). Dawbin reported links between eastern Australia and Antarctic Area V with occasional interchange between eastern Australia and New Zealand and significant segregation between eastern Australia and the New Zealand/Oceania region (Dawbin, 1959; Dawbin, 1964; Dawbin, 1966).

Members of the South Pacific Whale Research Consortium and the Southern Cross University Whale Research Centre have been undertaking long-term photo-identification, genetic and satellite tagging studies on humpback whales in the Pacific basin and eastern Australia. The studies have substantiated that western Australia (breeding area D) and eastern Australia (breeding area E (i)) are discrete breeding populations (Olavarría et al. 2006A; Olavarría et al. 2006B; Anderson and Brasseur, 2007; Anderson et al. 2010). The data also substantiated that the IWC breeding area E, which included eastern Australia, New Caledonia and Tonga, should be considered to be three discrete breeding sub-populations; eastern Australia (E (i)), New Caledonia (E (ii)) and Tonga (E (iii)) (Garrigue et al. 2006; Olavarría et al. 2007). The observed limited movements of individual humpback whales between eastern Australia and Oceania (Garrigue et al. 2000; Garrigue et al. (2011b) and within Oceania (Garrigue et al. 2002; Garrigue et al. (2011a); Garrigue et al. 2010; Hauser et al. 2010) are consistent with the reported levels of genetic differentiation between breeding areas E (i), E (ii) and E (iii). Similarly acoustic evidence substantiates low levels of intermingling between breeding area D and E (i) (Noad et al. 2000). Only six movements of humpback whales have been documented, by photo-identification, between Antarctic Area V feeding grounds and eastern Australia
(Kaufman et al. 1990; Rock et al. 2006; Franklin et al. 2007). Satellite tagging has documented a movement from the Cook Islands to Antarctic Area VI (Hauser et al. 2010). One recent genotype match was reported between New Caledonia and the Antarctic Area V feeding area, and also a small number of genotype matches have been reported between Oceania breeding grounds and Antarctic Area V, VI and I feeding areas (Steel et al. 2008).

Genetic evidence in a recent study suggested that the humpback whales passing New Zealand may be closely related to the New Caledonia (E (i) ) population (Olavarría et al. 2006B) and a recent photo-identification matching of the New Zealand Catalogue with the Oceania catalogues produced only 3 matches: two matches with New Caledonia and one with Vava’u, Tonga (Constantine et al. 2007). These studies have demonstrated links between New Zealand and tropical breeding grounds in Oceania but the relationship between New Zealand and Australia has yet to be investigated. Therefore, there remains considerable uncertainty about the destination of humpback whales migrating past New Zealand from Antarctic Area V feeding areas.

Here we use photo-identification data collected from 1999 to 2004 to investigate movements of individual humpback whales between eastern Australia and Oceania and within Oceania and discuss the breeding ground migratory interchange and migratory destinations of humpback whales travelling through New Zealand waters.
6.2 METHODS

6.2.1 Photo-identification

Vessel-based photo-identification of humpback whale pods in Hervey Bay, Queensland (25°S, 153°E) was undertaken between 1992 and 2005 as part of a long-term study of social behaviour. Photo-identification was also utilised in a study of Humpback whales on the northern migration at Byron Bay (26°36′S, 153°36′E) and on the southern migration at Ballina (26°52′S, 153°36′E) between 2003 and 2004. The combined reconciled eastern Australian fluke catalogue for the years 1999-2004, after reconciliation within and between the catalogues and rejection of photographs of unsuitable quality, consists of 1315 individuals.

Dedicated surveys of humpback whales in Oceania were conducted between 1999-2004 during the austral winter in four primary sampling sites: New Caledonia; Tonga; the Cook Islands and French Polynesia. Surveys were conducted in only one or two seasons in other adjacent sampling sites: Vanuatu, Fiji, Samoa, and Niue. Sampling at American Samoa began in 2003. The combined Oceania fluke catalogue for 1999-2004, after reconciliation within and between the catalogues and rejection of photographs of unsuitable quality, consists of 692 individuals.

A comprehensive description of site sampling effort and the method used to compare the Oceania and eastern Australian catalogues, within and between regions, are fully reported in Garrigue et al. (2011a) and Garrigue et al. (2011b). Although some site samples are small the reported effort is consistent with the site samples being considered random samples from the populations for the purposes of these analyses.

The eastern Australian and Oceania catalogues selected for inclusion in this study are the most recent, fully reconciled, photo-identification catalogues from each of the
sample sites and are summarised in Table 6.2.1.1 Photo-identification survey work is still underway in most sites. Sampling site locations are shown in Fig 6.2.1.1.

Table 6.2.1.1 Summary of eastern Australian and Oceania reconciled catalogues 1999-2004 by population catalogues (POP) \(^1\) and sampling sites (SITE) \(^2\)

<table>
<thead>
<tr>
<th>(A) eastern Australia (EA)</th>
<th>(B) Oceania west (OW)</th>
<th>(C) Oceania east (OE)</th>
<th>(D) New Zealand(^1)</th>
</tr>
</thead>
<tbody>
<tr>
<td>SITE</td>
<td>Flukes (n)</td>
<td>SITE</td>
<td>Flukes (n)</td>
</tr>
<tr>
<td>New</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hervey Bay</td>
<td>871</td>
<td>Caledonia</td>
<td>160</td>
</tr>
<tr>
<td>Byron Bay</td>
<td>415</td>
<td>Vanuatu</td>
<td>6</td>
</tr>
<tr>
<td>Ballina</td>
<td>29</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
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<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total EA</td>
<td>1315</td>
<td>Total OW</td>
<td>166</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^1\) The pooling of sample site catalogues into the population catalogue groupings of EA, OW, and OE population is based on: Olavarría \(et al\). (2006A); Olavarría \(et al\). (2006B); Anderson and Brasseur, (2007) and Anderson \(et al\.). (2010).

\(^2\) Although the sample size at some sites is small the combined site effort and samples are consistent with these being random samples from the populations and are considered such for this analysis.

\(^3\) New Zealand is not considered a discrete population, however for the purposes of this analysis it was treated as such.
Figure 6.2.1.1 Locations of the New Zealand (NZ), Eastern Australian (EA), Balleny Islands and Oceania photo-identification survey sites; Eastern Australia and Oceania breeding grounds (E (i), E (ii), E (iii), F); and Antarctic feeding areas IV, V and VI (IWC, 2006) and the photo-id matches reported between NZ/EA, EA/OW and OW/OE.

The circle symbols (a), (b) and (c) show the location of humpback whales reported in Rock et al. (2006); whale (a) was sighted in Point Lookout and Eden, (b) in the Whitsundays, Hervey Bay and Eden and (c) in Hervey Bay and Eden. The triangle symbols (e), (f) and (d) show the Balleny Island/EAs matches reported in Franklin et al. (2007); whale (d) was sighted in Ballina and (e) and (f) were sighted in Byron Bay and Hervey Bay but in different years. The square symbol marked (g), (h), (i) shows the NZ/EAs matches reported in Garrigue et al. (2011a); all three were resighted in Hervey Bay, two within the same season; June in NZ and September in Hervey Bay. The square symbol marked (j), (k), (l) and (m) shows the four New Caledonia/Hervey Bay matches reported in Garrigue et al. (2011a).
6.2.2 Statistical analysis

For the analyses, fluke data from New Caledonia and Vanuatu were combined into an Oceania west (OW) catalogue (166) while Tonga, Fiji, American Samoa, Samoa, Niue, Cook Islands and French Polynesia were combined into an Oceania east (OE) catalogue (513). The eastern Australian (EA) catalogue (1315) and New Zealand (NZ) catalogue (13) were treated as separate population catalogues (Table 6.2.1.1).

Several analyses were conducted investigating the number of matches found between sample site (SITE) and population catalogues (POP), \( m_{SITE,POP} \): NZ-EA, OW-EA, OE-EA, OW-OE, NZ-OW, NZ-OE. In each case, if the whales sighted at the sample site (SITE) were all members of the population catalogues (POP); then the proportion of the SITE catalogue we would expect to be matched to the POP catalogue, would be equal to the proportion of the estimated population that was in the POP catalogue. Alternatively, if the whales sighted at the sample site (SITE) were not all members of the population, the proportion of the SITE catalogue we would expect to be matched to the POP catalogue would be lower than the proportion of the estimated population in the POP catalogue.

This rationale provides a means of estimating the expected number of matches under a null hypothesis that the whales identified at the sample site were all members of the population catalogue for testing against the alternative hypothesis that they were not. The analysis is based on a test of association in a 2x2 cross-table of frequencies constructed as ‘not seen’ or ‘seen’ at the sample site by ‘not seen’ or ‘seen’ in the proposed population (Table 6.2.2.1).
Table 6.2.2.1. Scheme for the cross-tables.

<table>
<thead>
<tr>
<th>Sample site (SITE)</th>
<th>Hypothesised population (POP)</th>
<th>Not seen</th>
<th>Seen</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not seen</td>
<td>$N_{\text{POP}} - n_{\text{SITE}} - n_{\text{POP}} + m_{\text{POP-SITE}}$</td>
<td>$n_{\text{POP}} - m_{\text{POP-SITE}}$</td>
<td>$N_{\text{POP}} - n_{\text{SITE}}$</td>
<td></td>
</tr>
<tr>
<td>Seen</td>
<td>$n_{\text{SITE}} - m_{\text{POP-SITE}}$</td>
<td>$m_{\text{POP-SITE}}$</td>
<td>$n_{\text{SITE}}$</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>$N_{\text{POP}} - n_{\text{POP}}$</td>
<td>$n_{\text{POP}}$</td>
<td>$N_{\text{POP}}$</td>
<td></td>
</tr>
</tbody>
</table>

- $N_{\text{POP}} =$ Estimated 2004 population size
- $n_{\text{POP}} =$ Size of the population catalogue
- $n_{\text{SITE}} =$ Size of the sample site catalogue
- $m_{\text{POP-SITE}} =$ Number of whales matched between the population and sample site catalogues

Given these data and estimates, the expected numbers of matches, $m_{\text{POP-SITE}}$, may be derived from expected equality of proportions, $m_{\text{POP-SITE}}/n_{\text{SITE}} = n_{\text{POP}}/N_{\text{POP}}$, and calculated as $m_{\text{POP-SITE}} = (n_{\text{POP}} * n_{\text{SITE}})/N_{\text{POP}}$. This is both the standard way of calculating the expected frequencies under a null hypothesis of independence in a cross-table (row total by column total over grand total) and a simple transformation of the estimator, $N = (n_{1} * n_{2})/m_{2}$. The expected frequencies for each of the other cells were obtained in the standard way.

A one-tailed test of association is appropriate because the alternative hypothesis is that the observed frequency of whales seen at both locations will be lower than the expected frequency under the null hypothesis. We used one-tailed p-values from Fisher’s Exact Test. This test is preferred over the asymptotic Pearson Chi-Square test when expected frequencies are small.

The sizes of sampling site catalogues ($n_{\text{SITE}}$), the sizes of populationcatalogues ($n_{\text{POP}}$), the estimated 2004 population sizes ($N_{\text{POP}}$) and the numbers of matches between the sampling site catalogues and the population catalogues ($m_{\text{POP-SITE}}$), except for the Ballina catalogue (Dan Burns, unpublished data), were derived from Garrigue et al. (2011), Baker et al. (2006) and Paton et al. (2011), and are reported in Table 6.3.2.2.
Table 6.2.2.2. Data summary: Sizes of sampling site catalogues, sizes of population catalogues, the estimated 2004 population sizes and the numbers of matches between the sampling site catalogues and the population catalogues.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Sample site catalogue ($n_{SITE}$)</td>
<td>13</td>
<td>166</td>
<td>513</td>
<td>166</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>Population catalogue ($n_{POP}$)</td>
<td>1,315</td>
<td>1,315</td>
<td>1,315</td>
<td>513</td>
<td>166</td>
<td>513</td>
</tr>
<tr>
<td>Estimated population size ($N_{POP}$)</td>
<td>7,090</td>
<td>7,090</td>
<td>7,090</td>
<td>3,366</td>
<td>472</td>
<td>3,366</td>
</tr>
<tr>
<td>Site-population matches ($m_{POP,SITE}$)</td>
<td>3</td>
<td>4</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

1 Estimated population sizes ($n_{POP}$) are based on comparable abundance estimates utilising photo-identification data: Baker et al. 2006 and Paton et al. (2011).

6.3 RESULTS

Matching between the eastern Australian and the Oceania catalogues, after reconciliation within and between the catalogues and rejection of photographs of unsuitable quality, resulted in 3 matches between eastern Australia and New Zealand; 4 matches between eastern Australia and Oceania west (New Caledonia, Vanuatu) and 5 matches between Oceania west and Oceania east (Tonga, Fiji, American Samoa, Samoa, Niue, Cook Islands and French Polynesia). No matches were found between New Zealand and any other of the Oceania catalogues in this comparison (but see Constantine et al. 2007).

The frequencies of whales in sampling sites by whales in proposed populations with the expected frequencies for site to population matches and Fisher’s one-tailed p-values are reported in Table 6.3.1.
Table 6.3.1. Frequencies of whales not seen and seen in sampling sites by whales not seen and seen in proposed populations with expected frequencies for site to population matches and Fisher’s one-tailed p-values.

<table>
<thead>
<tr>
<th>SITE - POP</th>
<th>NZ-EA</th>
<th>OW-EA</th>
<th>OE-EA</th>
<th>OW-OE</th>
<th>NZ-OW</th>
<th>NZ-OE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not seen - Not seen</td>
<td>5,765</td>
<td>5,613</td>
<td>5,262</td>
<td>2,692</td>
<td>293</td>
<td>2,640</td>
</tr>
<tr>
<td>Not seen - Seen</td>
<td>1,312</td>
<td>1,311</td>
<td>1,315</td>
<td>506</td>
<td>166</td>
<td>513</td>
</tr>
<tr>
<td>Seen - Not seen</td>
<td>10</td>
<td>162</td>
<td>513</td>
<td>161</td>
<td>13</td>
<td>13</td>
</tr>
<tr>
<td>Seen - Seen</td>
<td>3</td>
<td>4</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Expected matches</td>
<td>2.4</td>
<td>30.6</td>
<td>95.1</td>
<td>25.3</td>
<td>4.6</td>
<td>2.0</td>
</tr>
<tr>
<td>Fisher’s one-tailed p-value</td>
<td>N/A</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.003</td>
<td>0.166</td>
</tr>
</tbody>
</table>

Of the 13 whales sighted in New Zealand, 3 were matched to the eastern Australian catalogue. This is consistent with the 2.4 expected if the New Zealand whales were all members of the eastern Australian population. With the data falling in the wrong tail of the test distribution this result is entirely consistent with that hypothesis. Of the 166 whales sighted in Oceania west, 4 were matched to the eastern Australian catalogue. This is considerably and significantly fewer than the 30.6 expected if they were all members of the eastern Australian population. Of the 513 whales sighted in Oceania east, none were matched to the eastern Australian catalogue. This is significantly fewer than the 95.1 expected if they were all members of the eastern Australian population. Of the 166 whales sighted in Oceania west, 5 were matched to the Oceania east catalogue. This is significantly fewer than the 25.3 expected if they were members of the Oceania east population.

Of the 13 whales sighted in New Zealand, none were matched to the Oceania west catalogue. Although these catalogues were relatively small, this is significantly fewer
than the 4.6 expected if they were members of the Oceania west population. However, if we assume that the New Zealand population is in fact the eastern Australian population, we would expect approximately the same proportion, $p_{NZ,OW}$, of the whales sighted in New Zealand to have been seen in Oceania west as the proportion of the Oceania west whales that were seen in eastern Australia; i.e. $p_{NZ,OW} = 4/166 = m_{POP,SITE}/13$. On this basis 0.3 matches would be expected between the NZ and OW catalogues. That no matches were found is consistent with this.

Of the 13 whales sighted in New Zealand, none were matched to the Oceania east catalogue. This is fewer but not significantly fewer than the 2 expected if they were members of the Oceania east population.

6.4 DISCUSSION

The result of the comparison between the New Zealand and eastern Australian populations, is entirely consistent with the hypothesis that the whales observed in New Zealand are from the eastern Australian population.

While there is evidently appreciable interchange between the eastern Australian and the Oceania west populations and between the Oceania east and Oceania west populations, the results presented herein support the view that these are discrete populations. There may be some interchange between the eastern Australian and the Oceania east populations however, there is no evidence of that from these data, and the result provides further evidence for that these populations are discrete.

While there may be some interchange between the Oceania west and New Zealand populations there is no evidence of interchange from these data, and the result supports the hypothesis that these populations are discrete. The failure to find significance in the comparison between New Zealand and Oceania east (Table 6.3.1), may be largely due to the small size of the New Zealand catalogue and the
relative small proportion of the Oceania east population in the Oceania east catalogue. However, there is weak evidence in these data supporting the hypothesis that New Zealand and Oceania east are discrete populations.

6.4.1 Movements of humpback whales through New Zealand waters

Dawbin (1956) reported that northbound humpback whales travelling from Antarctic feeding areas approached New Zealand from various directions suggesting widespread lateral dispersion whilst in the Antarctic waters. The northward migration followed three main pathways through New Zealand waters. One stream moved along the eastern coastline and was deflected to the northeast, before rounding the northeastern tip and resuming their northerly migration. Another stream passed to the southwest of the South Island through Foveaux Strait and a separate but significant stream passed through Cook Strait between the North and South Island (Dawbin, 1956; Dawbin, 1966, and see Figure 6.4.1.1).
Figure 6.4.1.1. The square symbol marked (g), (h) and (i) are the Cook Straits samples reported in Garrigue et al. (2011a). The migratory pathways and migratory destinations described in Dawbin (1956) and the hypothesised migratory pathways and migratory destinations described in this study are shown in solid and broken lines respectively. The additional proposed photo-id sampling sites are shown as diamond shapes.
We speculate that humpbacks travelling from the eastern region of the Antarctic Area V feeding areas, with site fidelity to the eastern Australian (E (i) ) breeding grounds, are likely to pass to the south of the South Island of New Zealand and/or through the Foveaux and Cook Strait from east to west, rather than travel up along the north eastern coastline of New Zealand (see Figure 6.4.1.1).

In contrast humpback whales with site-fidelity to the New Caledonia (E (ii) ) and Tonga (E (iii) ) breeding grounds are likely to pass northwards along the eastern coastline of the North Island of New Zealand and after clearing the northern tip of New Zealand, they would then resume their migration to New Caledonia (E (ii) ) on a northwesterly track, or to the Tongan Islands (E (iii) ) on a northeasterly track along the Tongan trench. Two humpbacks sighted off Kaikoura during the northward migration, were also photographed in New Caledonia and Tonga, which suggests this may be the case (Constantine et al. 2007, see Figure 6.4.1.1).

Dawbin (1956) reported that humpback whales migrating southbound, from tropical breeding grounds, approached New Zealand from the north in narrowly focused pathways. The major proportion of the migration arrived along the western coastline of the North and South Islands; were deflected to the southwest, until they rounded the southern tip of the South Island and continued their southern migration to Antarctic waters. Some southbound Humpback whales passed around the northeastern tip of the North Island (Dawbin, 1956; Dawbin, 1966). This was the case with a humpback whale sighted in New Caledonia, which was also sighted in New Zealand at the Bay of Islands (NE of North Island) during the southern migration (Constantine et al. 2007). Similarly whales off New Caledonia satellite-radio tagged in 2007 during the southern migration, travelled southeast towards the north of the north island of New Zealand (Garrigue et al. 2010). An even smaller
proportion of the migration, move from west to east through the Cook Strait and Foveaux Strait (Dawbin 1956, see Figure 6.4.1.1).

Humpback whales travelling directly from eastern Australia are likely to approach the western coastline of New Zealand from the east, whereas those migrating from New Caledonia and Tonga would be travelling from the north. Consequently humpback whales from eastern Australia would more likely arrive at, or towards the southern end of, the western coastline of the South Island of New Zealand (see Figure 6.4.1.1).

Photo-identification sampling on the southeastern coast of New Zealand and in Cook Strait may therefore represent a sampling bias. Selecting at least three additional sampling sites for systematic photo-identification of humpback whales in New Zealand waters could provide data to determine the destinations of humpbacks passing through the northern waters of New Zealand. These sampling sites could include a site within the Foveaux Strait, a site on the northeastern coast of the North Island, a site on the northwestern coast of the North Island, and a site on the southeastern coast of the South Island, while continuing concurrent sampling in the Cook Strait.

6.4.2 Migration to breeding grounds north of New Zealand

Dawbin (1964) found Discovery mark matches between eastern Australia and Foveaux Strait, at the southern tip of New Zealand and Cook Strait located between the North and South Islands of New Zealand. The recapture rates of humpbacks marked off eastern Australia and in waters near New Zealand and Norfolk Island indicated that there was ‘very highly significant’ segregation between groups that
migrated along the eastern coast of Australia and those that migrate past islands further east (Dawbin, 1964).

Differentiation between the eastern Australian (E (i) ) breeding grounds, New Caledonia (E (ii) ) and Tonga (E (iii) ) has been substantiated by recent genetic and photo-identification studies (Garrigue et al. 2006; Olavarría et al. 2006A; Olavarría et al. 2006B; Olavarría et al. 2007; Garrigue et al. (2011a); Garrigue et al. (2011b); Anderson and Brasseur, 2007 and Anderson et al. 2010). Over 600 sightings of humpback whales have been reported in New Zealand waters between 1970 and 2007 (Nadine Gibbs, Pers. Comm.). The majority of sightings were made on the southeast coast of New Zealand off Kaikoura and during systematic surveys conducted in Cook Strait (Gibbs and Childerhouse 2000; Constantine et al. 2007).

Comparisons of the New Zealand and eastern Australian catalogues for the synoptic period 1999-2004, reported herein, resulted in 3 matches with eastern Australia. All three matches were sighted in the Cook Strait during the early northbound migration and in Hervey Bay during the late southbound migration, two of the matches occurred within the same season (Garrigue et al. (2011b). Previous matches between New Caledonia, eastern Australia and New Zealand have been reported (Garrigue et al. 2000; Garrigue et al. 2002) and more recent comparisons of the New Zealand and Oceania catalogues have reported matches between New Caledonia, Tonga and New Zealand (Constantine et al. 2007).

The results reported in this paper confirm that humpback whales are migrating from Antarctic feeding areas through New Zealand waters to the eastern Australian (E (i) ) breeding grounds (see Figure 6.4.1.1). Whilst there is some photo-identification and genetic evidence of humpback whales travelling through New Zealand waters to the New Caledonia (E (ii) ) breeding grounds to the northwest, and the Tongan (E (iii) )
breeding grounds to the northeast of New Zealand further systematic sampling, at
different locations around the northern coastline of New Zealand, is required to fully
substantiate the destinations of humpbacks whales travelling through New Zealand
waters.

6.4.3 Effect of exploitation and recovery on Pacific migratory destinations

Commercial and illegal Soviet post-war whaling reduced the Area V humpback whale
population to 500 individuals or less by the early sixties (Chittleborough 1965:
Clapham et al. 2005). Dawbin (1964) noted that the great decline in humpback
numbers between 1959 and 1962 paralleled simultaneous decreases of humpbacks
observed in many other South Pacific localities, such as the Chesterfields, Vanuatu
and Fiji. Recent modeling estimated that the humpback pre-exploitation population
for eastern Australia and Oceania ranged from 26,363-31,400 and 16,022-22,957
respectively (Jackson et al. 2006).

The humpback population from the eastern Australian (E (i) ) breeding grounds has
increased over the last fifty years was independently estimated to be around 7,000 to
6,000 in 2004 (Noad et al. 2005, Paton et al. 2011). In contrast population levels in
Oceania are relatively low. An overall estimate of the humpback population in
Oceania by 2004 was 3,627 (CV, 0.12) individuals, with 472 in New Caledonia (E (ii)
) and 2,311 in Tonga (E (iii) ) (Baker et al. 2006). There is little evidence of
humpback whale population recovery in Vanuatu, Fiji and Norfolk Island, and no
evidence of recovery at the Chesterfields in the Coral Sea (Baker et al. 2006, Jackson
et al. 2006). Whilst numbers of humpback whales have been observed in New
Zealand waters in recent years, no abundance estimate is available for the humpback
whales migrating past New Zealand (Gibbs and Childerhouse, 2000; Constantine et
al. 2007).
Clapham and Zerbini (2015) have suggested that social aggregation among the surviving Oceania humpback whales (i.e. that whales that once went to now-depleted breeding grounds changed their migratory destination to eastern Australia) may provide an explanation of why the eastern Australian (E (i)) group has recorded relatively earlier and stronger population increase than has been seen in New Caledonia (E (ii)) and Tonga (E (iii)), and why little recovery has been observed in Fiji and no recovery observed in the Chesterfields (see Clapham et al. 2006 and Clapham and Zerbini (2015), for a discussion of the humpback Social Aggregation Hypothesis).

6.4.4 Further research

Accumulation and comparison of photo-identification data, together with genetic and satellite tagging data obtained across the breadth of the Antarctic Area V feeding areas (130°E to 170°W), would greatly improve our understanding of the level and rate of intermingling among humpback whales from different breeding groups while in Antarctic waters. Data on individual humpback whales, passing through New Zealand waters to breeding grounds in eastern Australia and the western Pacific, offers the opportunity to document and quantify temporary and/or permanent immigration between existing breeding grounds and to monitor and assess recovery of humpback whales in formerly occupied breeding grounds in Oceania.

6.4.5 Conclusion

The data herein supports earlier research that, although low levels of intermingling occur between eastern Australia (E (i)) and Oceania west (E (ii)) breeding ground populations and, Oceania west (E (ii)) and Oceania east (E (iii) and F) breeding ground populations, these populations are discrete breeding populations.
Although based on a small sample size from New Zealand, the results presented here confirm that eastern Australian humpback whales are travelling through southern New Zealand waters en-route from Antarctic feeding areas (see Figure 6.2.1.1. and Figure 6.4.1.1).

A comprehensive understanding of intermingling amongst populations and the migratory pathways utilised between low latitude breeding grounds and high latitude feeding areas contributes to the delineation of stocks and informs likely areas where further stock mixing may occur during the migratory cycle.
6.5 ACKNOWLEDGEMENTS

All authors acknowledge the remarkable contribution of Dr Bill Dawbin and Dr Graham Chittleborough to our understanding of humpback Whales. We acknowledge Fond Pacifique for funding through Opération Cétacés and the South Pacific Whale Research Consortium for the project of matching the catalogues of east Australia and Oceania. The study of humpbacks undertaken in Oceania by the SPWRC is partly supported by the International Fund for Animal Welfare (IFAW). The long-term study of humpbacks in Hervey Bay being conducted by Trish and Wally Franklin is supported by The Oceania Project and in part by an Australian Research Council Linkage grant with the International Fund for Animal Welfare (IFAW) and the Southern Cross University Whale Research Centre (SCUWRC). We also thank participants in The Oceania Project’s Internship program for their financial contribution and assistance to the Hervey Bay study. Research undertaken in Hervey Bay was conducted under research permits issued by the Queensland Parks and Wildlife Service (permit numbers MP2006/020 and WISP03749606). The research undertaken off Ballina and Byron Bay was funded by the Southern Cross University Whale Research Centre and conducted under Scientific Research Permits issued by the Department of the Environment, Water, Arts and Heritage under the EPBC Act 1999 (permit number E2001/0005) and the New South Whales National Parks and Wildlife Service (permit number S10403). We thank Greg Luker of Southern Cross University for providing assistance with figures. The Cook Strait Project acknowledges the Department of Conservation, Dolphin Watch Ecotours, Picton and WWF for their support. We thank John Calambokidis and two anonymous reviewers for their comments, which contributed to the manuscript.


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feeding and breeding areas based on photo-identification. *J Cetacean Res Manage* 6:301–305

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Constantine, R., Caballero, S., Thiele, D., Paton, D., Clapham, P., Donoghue, 
from South Pacific breeding grounds and Antarctic feeding areas demonstrated 
by genotype matching. Paper SC/60/SH13 presented to the IWC Scientific 
Chapter 7

Humpback whales from Hervey Bay: Migratory linkages with Antarctic feeding areas
Sub-Chapter 7.1

Antarctic waters (Area V) near the Balleny Islands are a summer feeding area for some eastern Australian Breeding Stock E(i) Humpback Whales (*Megaptera novaeangliae*)

This chapter was published in the Journal of Cetacean Research and Management. It was submitted in November 2010 and accepted in December 2010.

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Conception of the study: WF (80%), TF (10%), PB (10%)

Data analysis: WF (70%), TF (20%), LB (10%)

Statistical analysis: WF (60%), LB (40%)

Interpretation of data: WF (60%), TF (10%), LB (10%), PB (10%), PH (10%)

Writing of manuscript: WF (70%), TF (10%), LB (10%), Other Authors (10%)
7.1.1 INTRODUCTION

‘Discovery’ mark tagging provided the first evidence of migratory interchange of humpback whales between the breeding grounds of eastern Australia and Oceania, and also linkages between the feeding and breeding areas within the IWC Areas IV, V and VI (Chittleborough, 1959; Dawbin, 1964, Brown, 1977, Paton and Clapham, 2006; International Whaling Commission, 2011). Investigation of migratory movement of humpback whales in the Western Pacific led Dawbin (1949, 1956) to consider that the Balleny Islands and the Ross Sea were the summer destination for humpback whales that travel along the coasts of eastern Australia and other parts of the Pacific and through New Zealand waters.

Further evidence of the complexity of migratory interactions amongst Oceania breeding grounds (including New Caledonia, Vanuatu, Tonga, Samoa, American Samoa, Cook Islands, Fiji, Niue and French Polynesia) and the New Zealand and Norfolk Island migratory corridors has been obtained from long term photo-identification (hereafter photo-ID) studies of humpback whales undertaken by members of the South Pacific Whale Research Consortium (SPWRC) and the Southern Cross University Whale Research Centre (Abernethy et al., 1992; Donoghue, 2006; Franklin et al., 2006; Garrigue et al., 2002; Garrigue et al., 2007; Gibbs and Childerhouse, 2004; Hauser et al., 2000; Poole, 2002; 2006).

Recent photo-ID matching between eastern Australian fluke catalogues (i.e. Hervey Bay and Byron Bay) and ten regional Oceania fluke catalogues for the period 1999 to 2004 (Garrigue et al., 2011) provides further evidence of the low levels of migratory interchange and illustrates the complexity of linkages between eastern Australia and Oceania (Donoghue, 2006; Franklin et al., 2006).
To date, only three individual photo-ID matches (Fig. 1) have been reported between humpback whales that migrate along the eastern Australian coast (E (i) Breeding Stock) and Antarctic Area V feeding areas in the vicinity of the Balleny Islands and the Ross Sea (Kaufman et al., 1990; Rock et al., 2006). No photo-ID matches have been reported between any of the Oceania breeding grounds and Area V or Area VI Antarctic feeding areas. However, one recent genotype match was reported between New Caledonia and the Antarctic Area V feeding area, and a small number of genotype matches have been reported between Oceania breeding grounds and Antarctic Area I and VI feeding areas (Steel et al., 2008, Schmitt et al. 2014).

The Balleny Islands are located in the Ross Sea at 67°S, 163°E, and are included within the Southern Ocean Whale Sanctuary that was declared at the 46th meeting of the International Whaling Commission (IWC) in 1994 (Fig. 7.1.2.1.1 below).

In this study, photo-ID matches are used to document the migratory movements of individual humpback whales between the Balleny Islands (Antarctic Area V feeding area) and Hervey Bay, Byron Bay and Ballina on the eastern coast of Australia (Breeding Stock (E (i) ). The data are used to investigate whether Antarctic waters near the Balleny Islands are a summer feeding area for some eastern Australian humpback whales and/or Oceania humpback whales.
7.1.2 METHODS

7.1.2.1 Photo-identification data

Observations of humpback whales were undertaken in close proximity to the Balleny Islands (67°S, 163°E), from the 14 to the 25 February 2006 during a marine biodiversity research cruise organised by the New Zealand Ministry of Fisheries. Sightings of humpback whales ranged between latitudes 66°10′260″S and 67°34′771″S and longitudes 162°20′005″E and 164°49′663″E. The Balleny Islands (BI) humpback fluke catalogue consists of \( n = 11 \) individuals. Vessel-based photo-ID of humpback whales in Hervey Bay, Queensland (25°S, 153°E) was undertaken between 1999 and 2005 as part of a long-term study of the behaviour and ecology of humpback whales. Photo-ID studies of humpback whales were undertaken on their northern migration at Byron Bay (BB) (26°36′S, 153°36′E) between 1999 and 2005; and during the southern migration at Ballina (BA) (26°52′S, 153°36′E) between 2003 and 2005. The combined and reconciled eastern Australian fluke catalogues consists of \( n = 3,120 \). Dedicated surveys of humpback whales in Oceania were conducted between 1999 and 2004 during the austral winter in four primary sites: New Caledonia; Tonga; the Cook Islands; and French Polynesia. Surveys were conducted in only one or two seasons in other South Pacific sites: Vanuatu, Fiji, Samoa, and Niue. Surveys at American Samoa began in 2003; New Zealand surveys began in 2004 and surveys at Norfolk Island began in 2003. The reconciled and combined Oceania fluke catalogue consists of \( n = 735 \). The site sampling effort and methods used to compare the Oceania and eastern Australian catalogues, both within and between regions, is fully reported in SPWRC et al. (2007) and Garrigue et al. (2011). Comparisons of each of the 11 individual flukes from the Balleny Islands were made to each of the 3120 individuals in the eastern Australian Fluke Catalogues, and to each of the 725 individuals in the Oceania Fluke Catalogues. The
population and site catalogues used in this analysis are summarised in Table 7.1.2.1.1 and site locations are shown in Fig. 7.1.2.1.1
**Table 7.1.2.1.1** Eastern Australia (EA), Oceania (OC) and Balleny Islands (BI) population and site Fluke catalogues

<table>
<thead>
<tr>
<th>Site</th>
<th>Flukes (n)</th>
<th>Site</th>
<th>Flukes (n)</th>
<th>Site</th>
<th>Flukes (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hervey Bay</td>
<td>1556</td>
<td>New Caledonia</td>
<td>160</td>
<td>Balleny Islands</td>
<td>11</td>
</tr>
<tr>
<td>Byron Bay</td>
<td>916</td>
<td>Vanuatu</td>
<td>6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ballina</td>
<td>648</td>
<td>Norfolk Island</td>
<td>5</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>New Zealand</td>
<td>41</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fiji</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Tonga</td>
<td>282</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Samoa</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>American Samoa</td>
<td>31</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Niue</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Cook Islands</td>
<td>36</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>French Polynesia</td>
<td>159</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Total EA</strong></td>
<td><strong>3120</strong></td>
<td><strong>Total OC</strong></td>
<td><strong>725</strong></td>
<td><strong>Total BI</strong></td>
<td><strong>11</strong></td>
</tr>
</tbody>
</table>
Figure. 7.1.2.1.1 Locations of the Balleny Islands; the Eastern Australian and Oceania photo-ID survey sites; Eastern Australia and Oceania Breeding Stocks E (i), (ii), (iii); Antarctic feeding areas IV, V, VI and I (International Whaling Commission, 2011). The symbols marked (a), (b) and (c) show the location of individual whales reported in Rock et al. (2006) and the symbols marked (d), (e) and (f) show the location of the matches reported herein. Whale (a) was sighted at Point Lookout and Eden; whale (b) was sighted in the Whitsundays, Hervey Bay and Eden; whale (c) in Hervey Bay and Eden (Rock et al., 2006). Whale (d) was sighted in Ballina; whales (e) and (f) were sighted in both Byron Bay and Hervey Bay but in different years (see photo-ID details in Fig. 7.1.3.2 below)
7.1.2.2  *Statistical analysis*

Two separate analyses were conducted, one investigating the matches found between the Balleny Islands (BI) and eastern Australian (EA) catalogues, and one investigating the lack of matches between the Balleny Islands and Oceania (OC) catalogues.

Each tested the question: are these data consistent with the hypothesis that the whales sighted in the vicinity of the Balleny Islands are from a single population? (Single population hypotheses).

The following rationale was used to design the analysis.

(a) If the whales sighted near the Balleny Islands were members of the eastern Australian population, the proportion of the BI catalogue expected to be matched to the EA catalogue would be equal to the proportion of the eastern Australian population that were in the EA catalogue and alive and available for capture near the Balleny Islands. For example, if one third of the eastern Australian population were in the EA catalogue and alive at the time the Balleny Islands was sampled, a third of the BI catalogue would be expected to be matched to the EA catalogue (single population hypothesis).

(b) Alternatively, if the whales sighted near the Balleny Islands were not members of the eastern Australian population, the proportion of the BI catalogue expected to be matched to the EA catalogue would be less than the proportion of the eastern Australian population alive and in the EA catalogue (separate population hypothesis).

The same rationale can be applied in the Oceania – Balleny Islands case.
Given the above rationale and the estimates described below, each of the analyses may be based on a test of association in a 2 x 2 cross-table of frequencies constructed as ‘not seen’ or ‘seen’ near the Balleny Islands by ‘not seen’ or ‘seen’ in eastern Australia/Oceania (Table 7.1.2.2.1).

Table 7.1.2.2.1 Scheme for the cross-tables:

<table>
<thead>
<tr>
<th>Eastern Australia/Oceania</th>
<th>Balleny Islands</th>
<th>Not seen</th>
<th>Seen</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not seen</td>
<td>$N_{EA/OC} - n_{BI}$</td>
<td>$n_{EA/OC} - m_{EA/OC-BI}$</td>
<td>$m_{EA/OC-BI}$</td>
<td>$n_{BI}$</td>
</tr>
</tbody>
</table>

$N_{EA/OC}$ = Population estimate at 2006 for Eastern Australian (EA)/Oceania (OC)  
$n_{EA/OC}$ = Estimate of number of living whales in 2006 from the EA/OC catalogues  
$m_{EA/OC-BI} = Number of whales matched between EA/OC and Balleny Islands  
$n_{BI} = Number of whales identified at Balleny Islands$

Given these data and estimates, the expected numbers of matches in the case of eastern Australia and the Balleny Islands, $m^{-}_{EA-BI}$ and $m^{-}_{OC-BI}$ may be derived from the equal proportions rationale presented above, $m_{EA-BI}/n_{BI} = n_{EA}/N_{EA}$ and $m_{OC-BI}/n_{BI} = n_{OC}/N_{OC}$, and calculated as $m^{-}_{EA-BI} = (n_{EA} \times n_{BI})/N_{EA}$ and $m^{-}_{OC-BI} = (n_{OC} \times n_{BI})/N_{OC}$ respectively. This is both the standard way of calculating the expected frequencies under a null hypothesis of independence in a cross-table (row total by column total over grand total) and a simple transformation of the Lincoln-Peterson estimator, $N^{-} = (n_{1} \times n_{2})/m_{2}$. The expected frequencies for each of the other cells were obtained in the standard way. Note that the null hypothesis of independence in the table corresponds to the single population hypothesis described above.
A one-tailed test of association is appropriate because the alternative hypothesis is that the observed frequency of whales seen at both locations will be fewer (and never more) than the expected frequency under the null hypothesis. A one-tailed \( p \)-values from Fisher’s Exact Test were used. This test is preferred over the asymptotic Pearson Chi-Square test when expected frequencies are small.

The analysis required estimates of the eastern Australian and Oceania populations \((N_{EA}, N_{OC})\) for 2006 and estimates of the number of individuals in the EA and OC catalogues that were alive in 2006 and potentially available for capture near the Balleny Islands \((n_{EA}, n_{OC})\). The estimate of the eastern Australian population in 2006 was based on the Noad et al. (2011) estimate of 7,090 in 2004 with an expected rate of increase of 10.6\% (Noad et al., 2011). The estimate of the number of individuals in the EA catalogue that were alive in 2006 and potentially available for capture near the Balleny Islands was based on the number of individuals catalogued between 1999 and 2005, with an expected mortality rate of 4\% per annum (Clapham et al., 2003; 2001; Zerbini et al., 2010). The estimate of the Oceania population in 2006 was based on the Baker et al. (2006) estimate of 3,627 between 1999 and 2004. The estimate of the number of individuals in the OC catalogue that were alive in 2006 and potentially available for capture near the Balleny Islands was based on the number of individuals catalogued between 1999 and 2004 with an assumed mortality rate (= birth rate) of 4\% per annum (Baker et al., 2006).

As the population size and mortality data are estimates, \( p \)-values were calculated for variation of ±10\% in the estimated numbers of whales in the EA and OC catalogues that were alive and available for capture near the Balleny Islands.
7.1.3 RESULTS

Comparison of the Balleny Islands Catalogue to the Eastern Australian Catalogue found three matches of individual whales, whereas no matches were found from a comparison of the Balleny Islands Catalogue to the Oceania Catalogues. One of the individual whales sighted in the Balleny Islands was sighted in Ballina three years earlier and two of the individual whales sighted in the Balleny Islands were sighted in both Byron Bay and Hervey Bay but in different years (Fig 7.1.3.2)

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>BI-0601-14/Feb/2006</td>
<td>BI-0606-14/Feb/2006</td>
<td></td>
</tr>
</tbody>
</table>

Photo-identification data:
Hervey Bay (HB), Trish Franklin;
Balleny Island (BI), Franz Smith;
Byron Bay (BB), Dave Paton & Daniel Burns;
Ballina (BA), Daniel Burns.

Figure 7.1.3.2. Photographs and dates of the confirmed individual photo-ID matches between the Balleny Islands (BI), Hervey Bay (HB), Byron Bay (BB) and Ballina (BA). Left column: Individual e in Fig. 7.1.3.2; seen in BB, HB and BI. Central column: Individual f in Fig. 7.1.3.2; seen in BB, HB and BI. Right column: Individual d in Fig. 7.1.3.2; seen in BA and BI.
7.1.3.1 Eastern Australia – Balleny Islands matches

Assuming a 10.6% annual increase from 7,090 in 2004 yielded an estimated Eastern Australian population in 2006 of 8,673 whales.

The 3,120 individuals recorded in the EA catalogue between 1999 and 2005 were assumed to have been captured at a constant rate of 446 whales per annum. Application of an estimated mortality rate of 4% per annum yielded an estimated 2,772 whales in the catalogue that were alive and available for capture near the Balleny islands in early 2006.

Table 7.1.3.1.3 reports the frequencies of whales ‘not seen’ and ‘seen’ near the Balleny Islands by ‘not seen’ and ‘seen’ in Eastern Australia based on these estimates together with the size of the Balleny Islands catalogue (n = 11) and the number of Balleny Islands to Eastern Australia matches (n = 3). The expected frequencies shown there were derived on the assumption of independence corresponding to the hypothesis that the whales seen in both places were members of the same population.

*Table 7.1.3.1.3* Observed and expected frequencies of whales *not seen* and *seen* near the Balleny Islands by *not seen* and *seen* in Eastern Australia.

<table>
<thead>
<tr>
<th></th>
<th>Eastern Australia</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Balleny Islands</td>
</tr>
<tr>
<td>Not seen</td>
<td>Observed</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
</tr>
<tr>
<td>Seen</td>
<td>Observed</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
</tr>
<tr>
<td>Total</td>
<td></td>
</tr>
</tbody>
</table>
The one-tailed p-value from Fisher’s exact test for the data in Table 7.1.3.1.3 was 0.512 indicating no evidence of dependency. Indeed, the observed and expected frequencies could not have been closer with 3 (or 4) whales seen at both sites. Thus there was no evidence to reject the null hypothesis that the whales seen near the Balleny Islands were from the Eastern Australian population.

By way of context for this result, the null hypothesis (at p < 0.05) would have been rejected were no matches to have been found (p = 0.014), but not if as few as one match had been found (p = 0.089). Alternatively, if 3 matches were to have been found then the number of Balleny Islands flukes would have had to exceed 21 for the null hypothesis to have been rejected (for 22 Balleny Islands flukes, p = 0.046).

With a 10% lower estimate of the number of whales alive and in the EA catalogue, the expected number of matches was 3.1 and the p-value was 0.614; with 10% higher estimate, the expected number of matches was 3.8 and the p-value was 0.431.

7.1.3.2 Oceania – Balleny Islands comparisons

It was assumed that there was no increase in the Oceania population from the 2004 estimate of 3,827 whales (Baker et al. 2006).

The 735 individuals recorded in the Oceania catalogue between 1999 and 2004, were assumed to have been captured at a constant rate of 122.5 whales per annum. Application of an estimated mortality rate of 4% per annum yielded an estimated 639 whales in the Oceania catalogue that were alive and available for capture near the Balleny islands in early 2006.

Table 7.1.3.2.4 reports the frequencies of whales ‘not seen’ and ‘seen’ near the Balleny Islands by ‘not seen’ and ‘seen’ in Oceania based on these estimates together
with the size of the Balleny Islands catalogue \((n = 11)\) and the number of Balleny Islands to Pacific matches \((n = 0)\). The expected frequencies shown there were derived on the assumption of independence corresponding to the hypothesis that the whales seen in both places were members of the same population.

*Table 7.1.3.2.4* Observed and expected frequencies of whales *not seen* and *seen* near the Balleny Islands by *not seen* and *seen* in Oceania.

<table>
<thead>
<tr>
<th>Balleny Islands</th>
<th>Frequency</th>
<th>Not seen</th>
<th>Seen</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not seen</td>
<td>Observed</td>
<td>3177</td>
<td>639</td>
<td>3816</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>3178.8</td>
<td>637.2</td>
<td>3816</td>
</tr>
<tr>
<td>Seen</td>
<td>Observed</td>
<td>11</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>9.2</td>
<td>1.8</td>
<td>11</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>3188</td>
<td>639</td>
<td>3827</td>
</tr>
</tbody>
</table>

The one-tailed \(p\)-value from Fisher’s exact test for the data in Table 7.1.3.2.4 was 0.134.

Thus, although the data provide weak evidence to reject the null hypothesis that the whales seen near the Balleny Islands were members of the Oceania population, the samples were not large enough to provide a level of significance sufficient to conclude that they were not.

With no matches being found, the null hypothesis (at \(p < 0.05\)) would have been rejected and the alternative hypothesis of two separate populations accepted only if
there were at least 900 whales in the OC catalogue that were alive and available for capture near the Balleny islands in early 2006.

With a 10\% lower estimate of the number of whales alive and in the OC catalogue, the expected number of matches was 1.7 and the p-value was 0.166; with 10\% higher estimate, the expected number of matches was 2.0 and the p-value was 0.107.
7.1.4 DISCUSSION

Only six photo-ID matches have been reported between the eastern Australia (E(i) breeding stock) and Southern Ocean Antarctic Area V feeding areas. These comprise of the three matches reported here, between the Balleny Islands and Hervey Bay, Byron Bay and Ballina, and the three previously reported matches in Rock et al. (2006). All six individual humpbacks photographed in the Area V feeding area and/or around the Balleny Islands show long-term site-fidelity to either the eastern Australian migratory corridor utilised by the E(i) breeding stock or to locations within or near the putative terminus of the E(i) breeding stock within the Great Barrier Reef lagoon (Kaufman et al., 1990; Trish Franklin unpublished data; Rock et al., 2006) (Fig. 7.1.2.1.1 and Fig. 7.1.3.2).

While based on limited data from the Balleny Islands, these results are consistent with the hypothesis that the whales seen near the Balleny Islands were members of the population that migrates up the east coast of Australia. It would have been necessary, given the present sizes of the catalogues, to have found no matches between the Balleny Islands and the eastern Australian catalogues, or given the three matches that were found, for the Balleny Islands catalogue to have exceeded 21 individuals to reject this hypothesis.

While weak evidence was found against the hypothesis that the whales seen near the Balleny Islands were members of the population that migrates into Oceania, there were insufficient data to confidently conclude that they were not members of that population. Given that no matches were found between the Balleny Islands and Oceania catalogues, the null hypothesis (at $p < 0.05$) would have been rejected in favour of the two separate populations hypothesis only if there had been at least 900
whales in the Oceania catalogue that were alive and available for capture near the Balleny Islands in early 2006.

Sampling in the Balleny Islands for this study was only conducted for a short period in February 2006 within a specified area. If whales that migrate from eastern Australia or Oceania arrive within the area around the Balleny Islands at different times during the season, or if the movements of humpbacks whales within and around the Balleny Islands area vary from year to year due to prey availability or other factors, a short sampling period within a specific area may result in a sampling bias. Although a small sample of humpback whale flukes obtained in the vicinity of the Balleny Islands was used in this study the data have provided evidence that some humpback whales from eastern Australia feed in the vicinity of these islands. Expanded temporal and spatial sampling of humpback whale flukes in the area of the Balleny Islands may yield further evidence of whether humpbacks from other populations feed in the vicinity of the Balleny Islands. Previous research (Olavarria et al., 2007) has concluded that, although some migratory interchange has been observed, the eastern Australian and Oceania humpback whales are discrete populations, (Franklin et al., 2007; Garrigue et al., 2007). Franklin et al. (2007) suggested that humpback whales with site-fidelity to eastern Australia may use the New Zealand migratory corridor to the south of the South Island and/or pass through the Foveaux Straits or Cook Straits when travelling to and from the Antarctic Area V feeding areas in the vicinity of the Balleny Islands or the Ross Sea.

If it is assumed that the data presented here indicate that the whales seen both in eastern Australia and near the Balleny Islands were very likely to have been members of the same population, then the whales observed near the Balleny Islands were unlikely to also be members of the Oceania population. While the finding of no matches between the Oceania and Balleny Islands catalogues is consistent with this
argument, the small size of the Balleny Islands catalogue and the location, duration and timing of sampling make it difficult to completely rule out some potential interaction with Oceania.

Given that eastern Australian and Oceania populations are discrete breeding stocks, the most parsimonious explanation is that the individuals at the Balleny Islands are likely to be part of the eastern Australian population based on the limited data available from the Balleny Islands.

Consequently further collection of humpback whale photo-ID fluke data together with genetic data, either in the vicinity of the Balleny Islands, the Ross Sea and/or from across the Area V feeding areas, will be important in clarifying the migratory linkages between Antarctic feeding areas and Oceania and eastern Australian breeding grounds.
7.1.5 ACKNOWLEDGEMENTS

We acknowledge Fond Pacifique for funding through Opération Cétacés and the South Pacific Whale Research Consortium the project of matching the catalogues of East Australia and Oceania. The study of humpbacks undertaken in Oceania by the SPWRC is partly supported by the International Fund for Animal Welfare (IFAW). The long-term study of humpbacks in Hervey Bay being conducted by Trish and Wally Franklin is supported by The Oceania Project and in part by an Australian Research Council Linkage grant with the International Fund for Animal Welfare (IFAW). Research undertaken in Hervey Bay was conducted under research permits issued by the Queensland Parks and Wildlife Service (permit numbers MP2006/020 and WISP03749606). The research undertaken off Ballina and Byron Bay was funded by the Southern Cross University Whale Research Centre and conducted under Scientific Research Permits issued by the Department of the Environment, Water, Arts and Heritage under the EPBC Act 1999 (permit number E2001/0005) and the New South Whales National Parks and Wildlife Service (permit number S10403). We thank the New Zealand Ministry of Fisheries for providing access to the Balleny Islands data. The Department of Conservation, Dolphin Watch Ecotours and WWF provided support for the New Zealand project. We thank Greg Luker of Southern Cross University for providing Figure 1. The authors also thank Emeritus Professor Peter Baverstock for his valued comments. We also thank two anonymous reviewers for their comments, which contributed to the final manuscript.
7.1.6 LITERATURE CITED


Sub-Chapter 7.2

Photo-identification comparison of Humpback whale (*Megaptera novaeangliae*) flukes from Antarctic Area IV with East African, Western Australian and Eastern Australian fluke catalogues
7.2.1 INTRODUCTION

‘Discovery’ tagging marks from the 1930s to the 1950s revealed linkages between humpback whales from East Africa (C) breeding grounds and Antarctic Area III feeding areas (0°E - 70°E), between humpback whales from the Western Australian breeding grounds (D) and Antarctic Area IV feeding areas (70°E - 130°E), and humpback whales from the Eastern Australian breeding grounds (E1) and Antarctic Area V feeding areas (130°E - 170°W). Discovery tag data also revealed low levels of intermingling of individual humpback whales from breeding grounds D and E1 with Antarctic feeding areas IV and V (Rayner 1940, Dawbin 1966, Chittleborough 1965, IWC 2006, Figure 7.2.2.1.1 below).

No recent evidence has been presented of linkages between humpback whales migrating along the East African (C) coast and Antarctic feeding Area III. One photo-identification match supports the linkage between Western Australian breeding grounds (C) and Antarctic feeding Area IV (Gill & Burton 1995). The lateral body of a humpback whale was photographed on the 3rd September 1989 at 32°S, 116°E near Perth on the southwest coast of Western Australia during the southern migration and, was subsequently matched to a photograph of the lateral body of the same individual humpback whale sighted and photographed on the 14th February 1993 at 64°S, 101°E, in the Antarctic Area IV feeding area (Gill & Burton 1995, Figure 7.2.2.1.1). Similarly, only one individual humpback whale satellite-radio tag track supports intermingling between Eastern Australian whales and whales in Antarctic IV feeding area (Gales et al. 2009, also see Appendix II, page 335 below). The whale was tagged off Eden on the 28th October 2008 at 37°S, 150°E. The tag remained
active for 98 days providing 1160 position reports with the final report on 3rd February 2009. The whale tracked to the west around the coast of Victoria, across Bass Strait towards the northwest of Tasmania and then southwest to approximately 64°S, 120°E near the seasonal Antarctic ice-edge. The whale continued moving westward to approximately 61°S, 101°E. (Gales et al. 2009, also see Appendix II, page 335 below). A recent photo-identification match supports intermingling, between humpback whales from Eastern Australia (E1) and Western Australia (D). A humpback whale fluke photograph obtained off North Stradbroke Island (28°S, 154°E) on the 15th September 1987 was matched to a fluke photograph obtained off Perth (32°S, 116°E) on the 10th October 1995 (Kaufman et al. 2011, Figure 7.2.2.1.1). Finally, acoustic evidence also supports low levels of intermingling between humpback whales from breeding Area D and E1 (Noad et al. 2000).

This study utilises the first large photo-identification dataset to investigate linkages and intermingling between breeding areas C off East Africa, D off Western Australia and E1 off Eastern Australia and Antarctic Area IV feeding areas. This paper reports on the outcome of and discusses, a photo-identification comparison between a catalogue of individual humpback whales photographed in the Antarctic Area IV feeding area (2008, n = 30), and three large existing fluke catalogues from East Africa (2000-2006, n = 842), Western Australia (1990-2007, n = 1558) and Eastern Australia (1992-2005, n = 1964).
7.2.2 METHODS

7.2.2.1 Photo-identification and fluke catalogues

The Greenpeace International vessel *Esperanza* undertook a non-lethal research program in Antarctica from November 7\textsuperscript{th} 2007 to February 8\textsuperscript{th} 2008. As part of this program the research team aboard *Esperanza* conducted photo-identification of humpback whales in the Antarctic Area IV feeding area (70°e - 130°e) from 2\textsuperscript{nd} to 9\textsuperscript{th} of January 2008. The locations where the photography of humpback pods and individuals were undertaken ranged between 62° 47'S and 64° 14'S latitude, 112° 57'E and 80° 00'E longitude. The reconciled Greenpeace Antarctic Area IV (ANT) fluke catalogue of ventral underside humpback whale fluke photographs used in this study consists of \( n = 30 \) individual humpback whales. The date and location of individual whales photographed are summarized in Table 7.2.2.1.1 and the Greenpeace Antarctic locations are shown in Figure 7.2.2.1.1.
Table 7.2.2.1.1. Date and location of humpback whales photographed by Greenpeace in Antarctic Area IV feeding area

<table>
<thead>
<tr>
<th>Whale</th>
<th>Date</th>
<th>Latitude Deg.mins (S)</th>
<th>Longitude Deg.mins (E)</th>
</tr>
</thead>
<tbody>
<tr>
<td>001</td>
<td>02-Jan-08</td>
<td>63.34</td>
<td>112.57</td>
</tr>
<tr>
<td>002</td>
<td>02-Jan-08</td>
<td>63.33</td>
<td>112.54</td>
</tr>
<tr>
<td>003</td>
<td>02-Jan-08</td>
<td>63.34</td>
<td>112.57</td>
</tr>
<tr>
<td>004</td>
<td>02-Jan-08</td>
<td>63.34</td>
<td>112.57</td>
</tr>
<tr>
<td>005</td>
<td>02-Jan-08</td>
<td>63.34</td>
<td>112.57</td>
</tr>
<tr>
<td>006</td>
<td>02-Jan-08</td>
<td>63.48</td>
<td>111.47</td>
</tr>
<tr>
<td>007</td>
<td>03-Jan-08</td>
<td>63.25</td>
<td>105.39</td>
</tr>
<tr>
<td>008</td>
<td>03-Jan-08</td>
<td>63.27</td>
<td>104.52</td>
</tr>
<tr>
<td>009</td>
<td>03-Jan-08</td>
<td>63.27</td>
<td>104.52</td>
</tr>
<tr>
<td>010</td>
<td>03-Jan-08</td>
<td>63.25</td>
<td>105.39</td>
</tr>
<tr>
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<td>04-Jan-08</td>
<td>63.02</td>
<td>102.08</td>
</tr>
<tr>
<td>012</td>
<td>07-Jan-08</td>
<td>62.47</td>
<td>87.04</td>
</tr>
<tr>
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<td>07-Jan-08</td>
<td>62.47</td>
<td>87.04</td>
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<td>07-Jan-08</td>
<td>62.47</td>
<td>87.04</td>
</tr>
<tr>
<td>015</td>
<td>07-Jan-08</td>
<td>62.47</td>
<td>87.04</td>
</tr>
<tr>
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<td>07-Jan-08</td>
<td>62.47</td>
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<td>87.04</td>
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<tr>
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<td>07-Jan-08</td>
<td>62.47</td>
<td>87.04</td>
</tr>
<tr>
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<td>07-Jan-08</td>
<td>62.47</td>
<td>87.04</td>
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<tr>
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<td>07-Jan-08</td>
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<td>07-Jan-08</td>
<td>62.47</td>
<td>87.04</td>
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<tr>
<td>023</td>
<td>07-Jan-08</td>
<td>62.47</td>
<td>87.04</td>
</tr>
<tr>
<td>024</td>
<td>07-Jan-08</td>
<td>62.47</td>
<td>87.04</td>
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<td>87.04</td>
</tr>
<tr>
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<td>62.47</td>
<td>87.04</td>
</tr>
<tr>
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<td>07-Jan-08</td>
<td>62.47</td>
<td>87.04</td>
</tr>
<tr>
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<td>09-Jan-08</td>
<td>64.14</td>
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</tr>
<tr>
<td>030</td>
<td>09-Jan-08</td>
<td>64.14</td>
<td>80.01</td>
</tr>
</tbody>
</table>
The Wildlife Conservation Society and American Museum of Natural History Cetacean Conservation and Research Program have conducted photo-identification studies of humpback whales off East Africa since 2000, Figure 7.2.2.1.1 (Cerchio et al. 2008a, 2008b). The focus of the research is abundance of the C3 Madagascar population and migratory interchange between sub-populations C1 and C3. Only the Madagascar catalogue was used for this study. Photography of humpback whale pods was conducted off Madagascar (C3, 16°S, 50°E) between 2000 and 2006. The reconciled East African (EAF) fluke catalogue for the period 2000-2006 consists of \( n = 842 \) unique individuals.

The Centre for Whale Research Western Australia has conducted photo-identification studies of humpback whales off Western Australia since 1990, Figure 7.2.2.1.1 (Jenner et al. 2001). The focus of the research is the migratory pathways and calving grounds of humpback whales along the Western Australian coastline. Photography of humpback whale pods was conducted at Exmouth Gulf (21°40'S, 114°10'E), Dampier (20°20'S, 116°45'E) and the Kimberley region (15°50'S, 123°30'E) between 1990 and 2007, Figure 7.2.2.1.1. The reconciled Western Australian (WA) fluke catalogue for the period 1990-2007 consists of \( n = 1558 \) unique individuals.

The Oceania Project has conducted vessel-based photo-identification of humpback whale pods and individual whales in Hervey Bay, Queensland (25°S, 153°E) between 1992 and 2005, as part of a long-term study of the social behaviour and ecology of humpback whales, Figure 1 (Franklin et al. 2011). The reconciled Eastern Australian (EA) fluke catalogue for the period 1992-2005 consists of \( n = 1964 \) unique individuals.
The sampling sites and the reconciled fluke catalogues are summarised in Table 7.2.2.1.2 and the relative locations of the photo-identification sampling sites and IWC breeding grounds and feeding areas are shown in Figure 7.2.2.1.1.

Table 7.2.2.1.2. Summary of East African, Western Australian and Eastern Australian site (SITE) and population (POP) fluke catalogues

<table>
<thead>
<tr>
<th>East Africa (EAF)</th>
<th>SITE</th>
<th>Flukes (n)</th>
<th>Western Australia (WA)</th>
<th>SITE</th>
<th>Flukes (n)</th>
<th>Eastern Australia (EA)</th>
<th>SITE</th>
<th>Flukes (n)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Madagascar (C3)</td>
<td>Exmouth,</td>
<td>842</td>
<td>Kimberley</td>
<td>1558</td>
<td>Hervey Bay</td>
<td>1964</td>
<td>1964</td>
<td></td>
</tr>
<tr>
<td>Total (POP)</td>
<td></td>
<td>842</td>
<td></td>
<td>1558</td>
<td></td>
<td>1964</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 7.2.2.1.1. Photo-identification sampling sites, other photo-identification locations mentioned in text and IWC breeding grounds and feeding areas.

Photo-identification sampling sites for this study: Madagascar (16°S, 50°E) on the east coast of Africa; Exmouth Gulf (21°40'S, 114°10'E), Dampier (20°20'S, 116°45'E) and Kimberley (15°50'S, 123°30'E) on the west coast of Australia; Hervey Bay (25°S, 153°E) on the east coast of Australia. Antarctic Area IV sampling sites for this study (shown as circles): (g) 2-Jan-08, (60°S, 112°E), 6 flukes; (h) 3-Jan-08, (63°S, 105°E), 4 flukes; (i) 4-Jan-08, (63°S, 102°E), 1 fluke; (j) 7-Jan-08, (63°S, 87°E), 17 flukes; (k) 9-Jan-08, (64°S, 80°E), 2 flukes.

Other photo-identification and satellite-tag locations mentioned in text: (a▲) 3-Sep-89, (32°S, 116°E) one lateral body photo; (b▲) 14-Feb-93, (64°S, 101°E), one lateral body photo (Gill & Burton 1995); (c☆) 10-Oct-08, (37°S, 150°E), sat-tag commenced (d★) 3-Feb -09, (61°S, 101°E), sat-tag ceased (Gales et al. 2009); (e♦) 15-Sep-87 (28°S, 154°E) one fluke, (f♦) 10-Oct-95 (32°S, 116°E) one fluke (Kaufman
et al. 2011). IWC breeding grounds C1, C3, D and E1; IWC feeding area III (0°-70°E), IV (70°E-130°E), V (130°E-170°W) (IWC 2006, SC/58/Rep5).

7.2.2.2 Statistical analysis

Three analyses were conducted to investigate any matches between the Antarctic Area IV (ANT) fluke catalogue and the East African (EAF), Western Australian (WA) or Eastern Australian (EA) fluke catalogues.

Each analysis tested the question: are these data consistent with the hypothesis that the whales sighted in the vicinity of the Antarctic Area IV are from a single population? (single population hypotheses).

The following rationale was used to design the analysis:

(a) If the whales sighted in Antarctic Area IV were members of the East African population, the proportion of the ANT catalogue expected to be matched to the EAF catalogue would be equal to the proportion of the East African population that were in the EAF catalogue and alive and available for capture in Antarctic Area IV. For example, if one third of the East African population were in the EAF catalogue and alive at the time Antarctic Area IV was sampled, a third of the ANT catalogue could be expected to be matched to the EAF catalogue (single population hypotheses).

(b) Alternatively, if the whales sighted in Antarctic Area IV were not members of the East African population, the proportion of the ANT catalogue expected to be matched to the EAF catalogue would be less than the proportion of the East African population alive and in the EAF catalogue (separate population hypothesis).

The same rationale was applied in the Western Australian – Antarctic area IV and Eastern Australian – Antarctic Area IV cases.
Given the above rationale and the estimates described below, each of the analyses may be based on a test of association in a 2 x 2 cross-table of frequencies constructed as ‘not seen’ or ‘seen’ in Antarctic Area IV by ‘not seen’ or ‘seen’ in East Africa / Western Australia / Eastern Australia (Table 7.2.2.2.1).

Table 7.2.2.2.1. Scheme for cross-tables: East Africa, Western Australia/ Eastern Australia (POP) – Antarctic Area IV (ANT)

<table>
<thead>
<tr>
<th>Antarctic Area IV (ANT)</th>
<th>Not seen</th>
<th>Seen</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not seen</td>
<td>$N_{POP} - n_{ANT}$ - $n_{POP} + m_{POP-ANT}$</td>
<td>$n_{POP} - m_{POP-ANT}$</td>
<td>$N_{POP} - n_{ANT}$</td>
</tr>
<tr>
<td>Seen</td>
<td>$n_{ANT} - m_{POP-ANT}$</td>
<td>$m_{POP-ANT}$</td>
<td>$n_{ANT}$</td>
</tr>
<tr>
<td>Total</td>
<td>$N_{POP} - n_{POP}$</td>
<td>$n_{POP}$</td>
<td>$N_{POP}$</td>
</tr>
</tbody>
</table>

$N_{POP}$ = Population estimate at 2008 for East Africa, Western Australia and Eastern Australia.

$n_{POP}$ = Estimate of number of living whales in 2008 from the East African/Western Australian/Eastern Australian catalogues.

$m_{POP-ANT}$ = Number of whales matched between East Africa, Western Australia, Eastern Australia and Antarctic Area IV.

$n_{ANT}$ = Number of whales identified in Antarctic Area IV.
Given these data and estimates, the expected numbers of matches, $m_{\text{POP-ANT}}^*$, may be derived from the equal proportions rationale presented above, $m_{\text{POP-ANT}} \approx n_{\text{POP}}/N_{\text{POP}}$, and calculated as $m_{\text{POP-ANT}}^* = (n_{\text{POP}} \cdot n_{\text{ANT}})/N_{\text{POP}}$. This is both the standard way of calculating the expected frequencies under a null hypothesis of independence in a cross-table (row total by column total over grand total) and a simple transformation of the Lincoln-Petersen Estimator, $N^* = (n_1 \cdot n_2)/m_2$. The expected frequencies for each of the other cells were obtained in the standard way. Note that the null hypothesis of independence in the Table 7.2.2.2.1 corresponds to the single population hypothesis described above.

A one-tailed test of association is appropriate because the alternative hypothesis is that the observed frequency of whales seen at both locations was fewer (and never more) than the expected frequency under the null hypothesis. A one-tailed $p$-value from Fisher’s Exact Test was used. This test is preferred over the asymptotic Pearson Chi-square test when expected frequencies are small.

The analysis required estimates of the East African, Western Australian and Eastern Australian populations ($n_{\text{POP}}$) for 2008 and estimates of the number of individuals in the POP catalogues that were alive in early 2008 and potentially available for capture in Antarctic Area IV ($n_{\text{POP}}$). As the population size and mortality data are estimates, $p$-values were calculated for variation of ±10% in the estimated numbers of whales in the POP catalogues that were alive and available for capture in Antarctica Area IV.
7.2.3 RESULTS

Comparison of the Antarctic Area IV catalogue \((n = 30)\) to the East African \((n = 842)\), Western Australian \((n = 1,558)\) and Eastern Australian \((n = 1,964)\) catalogues found no matches (locations are shown in Figure 7.2.2.1.1 above).

7.2.3.1. **Antarctic Area IV - East Africa analysis**

An estimated population of 7715 was obtained for East Africa. This was based on the estimate of the East African C3 population in 2006 at 6,737, \(CV=0.31\) (Cerchio et al. 2008a). However to allow for growth between 2006 and 2007 and to take into account that the 2006 estimate may only be an estimate of a sub-region of the C population, as suggested by Cerchio et al. (2008a), the upper bound estimate of 7,715, \(CV=0.24\) was used as a minimum estimate for the East African (C) population in early 2008.

The 842 individuals recorded in the EAF catalogue between 2000 and 2006, were assumed to have been captured at a constant rate of 120.3 whales per annum. Application of an estimated mortality rate of 4% per annum (Clapham et al. 2001, Clapham et al. 2006_SC/58/SH4), yielded an estimated 813 whales in the catalogue that were alive and available for capture in Antarctic Area IV in early 2008.

Table 7.2.3.1.1 reports the frequencies of whales ‘not seen’ and ‘seen’ near the Antarctic Area IV by ‘not seen’ and ‘seen’ in East Africa based on the above estimates together with the size of the Antarctic Area IV catalogue \((n = 30)\) and the number of Antarctic Area IV to East Africa matches \((n = 0)\). The expected frequencies shown were derived on the assumption of independence corresponding to an hypothesis that the whales seen in both places were members of the same population.
<table>
<thead>
<tr>
<th>Antarctic Area IV</th>
<th>Frequency</th>
<th>Not seen</th>
<th>Seen</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not seen</td>
<td>Observed</td>
<td>6,872</td>
<td>813</td>
<td>7,685</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>6,875.2</td>
<td>809.8</td>
<td>7685</td>
</tr>
<tr>
<td>Seen</td>
<td>Observed</td>
<td>30</td>
<td>0</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>26.8</td>
<td>3.2</td>
<td>30</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>6,902</td>
<td>813</td>
<td>7,715</td>
</tr>
</tbody>
</table>

The one-tailed p-value from Fisher’s exact test for the data in Table 7.2.3.1.1 was \( p = 0.035 \), indicating that the Antarctic and East Africa data were likely to be from separate populations. With 3.2 matches expected under the single population null hypothesis, it is highly unlikely that no matches would be found unless the data were on whales from separate populations. The null hypothesis would not have been rejected if 1 match had been found (\( p = 0.160 \)).

### 7.2.3.2. **Antarctic Area IV - Western Australia analysis**

The estimated Western Australian population in early 2008 was based on the 2007 estimate of Salgado Kent et al. (2012) of 26,100 (95% CI=20,152–33,272).

The 1,558 individuals recorded in the WA catalogue between 1990 and 2007 were assumed to have been captured at a constant rate of 86.6 whales per annum. Application of an estimated mortality rate of 4% per annum (Clapham et al. 2001,
Clapham et al. 2006_SC/58/SH4), yielded an estimated 1,499 whales in the catalogue that were alive and available for capture in Antarctic Area IV in early 2008.

Table 7.2.3.2.1 reports the frequencies of whales ‘not seen’ and ‘seen’ near the Antarctic Area IV by ‘not seen’ and ‘seen’ in Western Australia based on the above estimates together with the size of the Antarctic Area IV catalogue \((n = 30)\) and the number of Antarctic Area IV to Western Australia matches \((n = 0)\). The expected frequencies shown were derived on the assumption of independence corresponding to an hypothesis that the whales seen in both places were members of the same population.

Table 7.2.3.2.1. Estimated numbers and expected frequencies of whales ‘not seen’ and ‘seen’ in Antarctica Area IV by ‘not seen’ and ‘seen’ in Western Australia

<table>
<thead>
<tr>
<th>Antarctic Area IV</th>
<th>Frequency</th>
<th>Western Australia</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Not seen</td>
</tr>
<tr>
<td>Not seen</td>
<td>Observed</td>
<td>24,571</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>24,572.7</td>
</tr>
<tr>
<td>Seen</td>
<td>Observed</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>28.3</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>24,601</td>
</tr>
</tbody>
</table>

The one-tailed p-value from Fisher’s exact test for the data in Table 7.2.3.2.1 was 0.169, indicating insufficient evidence (i.e., \(P > 0.05\)) to reject the null hypothesis that the Antarctic and WA data were from the same population. However, the finding of no matches weakens the argument that the Antarctic data were from the WA population: even a single match (\(p = 0.479\)) would have strengthened the case
for a single population. The relatively small Antarctic catalogue and the relatively small proportion of the estimated WA population expected to be alive and in the WA catalogue (5.7%) makes for an indefinite conclusion.

7.2.3.3. Antarctic Area IV- Eastern Australia analysis

The Eastern Australian population in early 2008 was estimated at 9,592 whales based on the Noad et al. (2011) estimate of 7,090 in 2004 with an assumed rate of increase of 10.6% per annum.

The 1,964 individuals recorded in the EA catalogue between 1992 and 2005, were assumed to have been captured at a constant rate of 140.3 whales per annum. Application of an estimated mortality rate of 4% per annum (Clapham et al. 2001, Clapham et al. 2006_SC/58/SH4), yielded an estimated 1,891 whales in the catalogue that were alive and available for capture in Antarctic Area IV in early 2008.

Table 7.2.3.3.1 reports the frequencies of whales ‘not seen’ and ‘seen’ near the Antarctic Area IV by ‘not seen’ and ‘seen’ in Western Australia based on the above estimates together with the size of the Antarctic Area IV catalogue ($n = 30$) and the number of Antarctic Area IV to Western Australia matches ($n = 0$). The expected frequencies shown were derived on the assumption of independence corresponding to an hypothesis that the whales seen in both places were members of the same population.
Table 7.2.3.3.1. Estimated numbers and expected frequencies of whales ‘not seen’ and ‘seen’ in Antarctica Area IV by ‘not seen’ and ‘seen’ in Eastern Australia

<table>
<thead>
<tr>
<th>Antarctic Area IV</th>
<th>Frequency</th>
<th>Not seen</th>
<th>Seen</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Not seen</td>
<td>Observed</td>
<td>7,671</td>
<td>1,891</td>
<td>9,562</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>7,676.9</td>
<td>1,885.1</td>
<td>9,562</td>
</tr>
<tr>
<td>Seen</td>
<td>Observed</td>
<td>30</td>
<td>0</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>Expected</td>
<td>24.1</td>
<td>5.9</td>
<td>30</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>7.701</td>
<td>1,891</td>
<td>9,592</td>
</tr>
</tbody>
</table>

The one-tailed p-value from Fisher’s exact test for the data in Table 7.2.3.3.1 was 0.001, indicating that the Antarctic and EA data were from separate populations. With 5.9 matches expected under the single population null hypothesis, it is highly unlikely that no matches would be found unless the data were on whales from separate populations. The null hypothesis would not have been rejected had even 1 match had been found (p = 0.011).
7.2.4 DISCUSSION

This study is the first to utilise large humpback whale photo-identification datasets for comparison against a small catalogue from the Antarctic Area IV feeding grounds to investigate linkages between Area IV feeding grounds and East Africa, Western Australia and Eastern Australia. The data supports the hypotheses that humpback whales feeding in Antarctic Area IV are a separate population from East Africa and Eastern Australia. However as the African and Eastern Australian data used in this study are each from one sampling site, there is a possibility that comparison of the Antarctic flukes with other African and East Australian catalogues may yield matches. Consequently, we cannot discount the likelihood that some East African and Eastern Australian humpbacks may feed in the Antarctic Area IV feeding grounds. There is recent evidence that some Eastern Australian humpbacks feed in Antarctic Area V in and around the Balleny Islands (Franklin et al. 2012, Sub-chapter 7.1 above).

The limited data from Western Australia and the small Antarctic Area IV catalogue used in this study provided weak evidence to reject the null hypothesis that humpback whales feeding in Antarctic Area IV are from the Western Australian population. Both early ‘Discovery’ mark data and recent photo-identification data support the hypothesis that Western Australian humpback whales feed in Antarctic Area IV (Rayner 1940, Dawbin 1966, Chittleborough 1965, Gill and Burton 1995). Consequently the most parsimonious interpretation of available data is that it is likely that the humpback whales feeding in Antarctic Area IV may be from the Western Australian population.

Both early Discovery tag data, recent photo-identification, satellite-tag and acoustic data support the hypothesis of low levels of intermingling between Eastern Australian humpback whales and Western Australian humpback whales (Rayner 1940, Dawbin

The timing and location of sampling in Antarctic Area IV feeding grounds is likely an important factor in determining the linkages between nearby feeding grounds and Antarctic Area IV feeding grounds. The humpback whale satellite-radio tagged off Eden in October 2008 (Appendix II, page 335 below) travelled around the coastline of Victoria and then past Northwest Tasmania and then southwest directly down into Antarctic Area IV feeding grounds. The whale was recorded at 60°S, 121°E on the 4th December 2008, and stayed below 60°S and was moving eastward until 3rd February 2009 when the satellite-radio tag stopped transmitting. Consequently sampling in the Antarctic Area IV feeding grounds throughout December, January and December may yield more useful results for comparison with coastal whale fluke catalogues.

Collection of further photo-identification data of humpback whales in Antarctic feeding areas III, IV and V with sampling across the season will assist in further investigating of the linkages between Antarctic feeding areas and tropical breeding grounds of humpback whales in both the Indian and Pacific Ocean basins, as well as rates of intermingling between these different breeding populations during their period in feeding areas. The Greenpeace Antarctic Area IV catalogue should also be compared to any other existing East African, Indian Ocean, Australian and/or Antarctic catalogue as this is likely to provide further data on the migratory destination of these humpback whales and add to our limited knowledge of the extent of population intermingling within the Antarctic Area III, IV and V feeding areas. In general the availability of existing humpback whale fluke identification catalogues in a databases such as Fluke Matcher (Kniest et al. 2010) could facilitate and expedite the comparison amongst regional catalogues.
7.2.5 LITERATURE CITED


Chapter 8

Thesis Synthesis, General Discussion and Conclusions

8.1 THESIS SYNTHESIS

The focus of this study is to investigate abundance, site-fidelity, residency, reproduction and temporary immigration of humpback whales in Hervey Bay and to address the larger questions of migratory interchange of humpback whales using Hervey Bay with the eastern Australian population, nearby breeding ground populations and the migratory pathways and linkages between breeding grounds and Antarctic feeding areas.

Research in the late 1980s and early 1990s established that humpback whales occur in large numbers in Hervey Bay, travel into/out of the Bay from/to the north, that different classes of humpback whales visit across the season and are resident in the Bay for several days or longer (Chaloupka et al. 1999, Corkeron et al. 1994). Recent research has established that there are significant changes in pod sizes, pod composition and pod behaviour of humpback whales in Hervey Bay within season; that Hervey Bay is important for non-lactating females, immature males and females early in the season, younger mature males and females mid-season and lactating females with older calves and a few mature male escorts later in the season, and that there is a consistent within season temporal structure to the age, sex, maturational and reproductive classes of humpback whales travelling through Hervey Bay (Franklin et al. 2011, Franklin 2012).
However the above research did not provide for Hervey Bay recent long-term estimates of humpback whale abundance over years and within season, investigate long-term survivorship and site-fidelity, provide an unbiased estimate of residency in Hervey Bay, or address the question of the relationship between eastern Australian humpback whales and humpback whales using Hervey Bay (Chapter 5). The previous research did not investigate migratory exchange with nearby breeding populations (Chapter 6, 7.1, 7.2 and Appendix II. Page 335 below), migratory pathways between Hervey Bay and Antarctic feeding areas (Chapter 7.1 and 7.2) and migratory destinations in Antarctic feeding areas (Chapter 7.1, 7.2 and Appendix II, page 335 below). Nor did previous research investigate rates of reproduction or trends in the rate of population increase (Chapter 5). These are the primary questions addressed in this thesis.
8.2 GENERAL DISCUSSION, CONCLUSIONS AND FINAL SYNTHESIS

8.2.1 How many humpback whales visit Hervey Bay?

Results from this study have provided a thirteen-year estimate of yearly abundance of humpback whales visiting Hervey Bay increasing from 791 (95% CI, 407-1106) in 1997 to 4406 (95% CI, 3343-5470) in 2009. The trajectory of increase was near linear and consistent with the trajectory of increase in the estimates of abundance of the eastern Australian humpback whale population over the same thirteen years (Fig 5.1). Chaloupka et al. (1999) using two different years of data estimated that between 30% and 50% of the eastern Australian population visit Hervey Bay. The results of this study found two anomalously extremes in the annual proportion of visitors to Hervey Bay compared to the eastern Australian population - a low of 23% in 1997 and a high of 46% in 2000 – with all other estimates falling in the range 30% to 38% (mean = 34%, standard deviation = 5.3%) (Fig. 5.1 and Fig. 4.3.3.2.1).

During the late 1980s and early 1990s Chaloupka et al. (1999) reported variability in the estimates of annual visitors to Hervey Bay, increasing from 554 (95% CI 329-779) in 1988, to a peak of 1040 (95% CI 783-1297) in 1991 before declining to 921 (95% CI 690-1152) by the mid-1990s. In contrast, this study shows a steady increase in the population visiting Hervey Bay from 1997 to 2009. Franklin et al. (2011) reported a significant increase in larger pods of 3+ adults over year (Fig 4.1.2) and suggested that it may be related to the increase in population. This study confirms the steady increase in the number of humpback whales visiting Hervey Bay and supports the contention that the increase in larger pods over years is likely a density dependent effect from the aggregations of humpback whales occurring on the eastern side of the Bay.
8.2.2 Is there a within season pattern to the timing of visits to Hervey Bay?

The results of this study reveal that there is a regular bi-modal pattern over years of within season visits of humpback whales to Hervey Bay with 83% of all visitors entering the Bay during the first 5 weeks of the season and 17% entering the Bay during the last 5 weeks of the season (Fig. 4.3.3.3.1). This is consistent with the findings of Franklin et al. (2011) and Franklin (2012) who reported significant differences in pod size and composition and pod behaviour during the early part of the season compared to the last part of the season (Fig. 4.1.1), related to the presence of different classes of humpback whales. The latter-half of the season is dominated by mother-calf pods accompanied by a few mature male escorts (Franklin 2012, Fig 4.1.2), with peak entry of this cohort occurring between week 7 and week 8 (6.9%, Fig. 4.3.3.3.1). In contrast the early part of the season consists of mature non-lactating early pregnant or resting females, together with immature males and females and few mature males (Franklin 2012, Fig 4.1.2) with the peak of this cohort occurring between weeks 2 and 3 (39%, Fig. 4.3.3.3.1).

Franklin (2012) reported that pod characteristics and pod behaviour during early August in Hervey Bay were consistent with the presence of immature males and females humpback whales travelling in company with mature non-lactating females. In this study the proportion of humpback whales present prior to sampling in week 1 together with the low proportion entering between week 1 and 2 (16.1% and 4.5% (95% CI 02.5-07.9), Fig. 4.3.3.3.1) may be indicative of a latent class within the first half of the season, which is likely to consist of the first wave of mature non-lactating early pregnant or resting females, together with last year’s calves as yearlings. Franklin (2012) reported that immature whales were amongst the first class sampled in Hervey Bay (Fig 4.1.2 g).
Between week apparent survival during the first 5 weeks of the season was high between weeks 2 and 3 (73.8%, Fig. 4.3.3.4.1), coinciding with the peak entry of visitors between weeks 2 and 3 (39%, Fig. 4.3.3.3.1) and consistent with the presence of mature non-lactating females and the main flow of the immature males and females cohort (Fig. 4.1.2, Franklin 2012). Between week apparent survival was highest between weeks 7 and 8 (59%, Fig. 4.3.3.4.1) during the last 5 weeks of the season, coinciding with the highest probability of entry of the mother-calf and escort cohort accompanied by a few mature males (6.9%, Fig. 4.3.3.3.1, Fig. 4.1.1, Franklin 2012).

The lowest probability of between week apparent survival is between week 5 and week 6 (13.3%, Fig. 4.3.3.4.1), which coincides with the lowest between week probability of entry between week 5 and week 6 (1.2%, Fig. 4.3.3.3.1) and the lowest weekly abundance within season in week 6 (Fig. 4.3.3.7.1). These results clearly reflect the transition between the entry and passage of the very large numbers of immature males and females together with non-lactating females during the first five weeks of the season (83% of entries, Fig. 4.3.3.3.1) and the entry and passage of the smaller numbers of lactating females, calves and mature males escorts during the last five weeks of the season (17% of entries, Fig. 4.3.3.3.1).

The proportion of yearly visitors to Hervey Bay present at the beginning of sampling varies from year to year, ranging from a low of 7% in 2005 to a high of 28% 2007 (mean = 17%, standard deviation = 6.5%, see 4.3.3.3 above). Variations in the proportion of yearly visitors present at the beginning of sampling may be indicative of variations in the peak timing of the migration in any given year.

The regular pattern within season over years, of abundance, apparent survival and probability of entry are fully consistent with the temporal segregation of sex, age,
reproductive and maturational classes reported by Dawbin (1996, 1997) and more recently by Franklin (2012).

Finally the results reported above highlights the importance of long-term monitoring and long-term collection of fluke and body marking data, as short-term collection of such data may give rise to short-term biases in parameter estimates and other estimates derived from the data.

8.2.3 How long do humpback whales stopover in Hervey Bay?

Earlier studies obtained insufficient data to provide an unbiased estimate of humpback whale residency in Hervey Bay (Corkeron et al. 1994). The results of this study provide the first unbiased estimate of residency of humpback whales visiting Hervey Bay from 1.4 to 2.0 weeks (mean=1.6 weeks SD=0.34, Fig 4.3.3.8.1) and provides further evidence of the importance of Hervey Bay as a stop-over early in the southern migration of some humpback whales from the overwintering and breeding grounds to the north. Hervey Bay is neither a terminal destination nor a calving ground (Franklin 2012). The putative breeding and overwintering grounds for eastern Australian humpback whales are considered to be between 16°S and 23°S (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999, Smith et al. 2012) while Hervey Bay is located at 25°S. Eastern Australian humpback whales spend approximately two months on the northern part of the migratory range north from Byron Bay, NSW and south back to Ballina, NSW. Approximately a month of that time is spent in the breeding grounds, 1.5 weeks of travel time is involved from the southern end of the putative breeding grounds to Hervey Bay, and 2.5 weeks of travel time from the southern end of the putative breeding grounds to Ballina, NSW (Burns et al. 2013). Consequently those humpback whales utilising Hervey Bay are spending a significant proportion (about 25%) of the overall time spent on average
in the putative breeding area. Two of the primary breeding grounds in the Northern Hemisphere, Hawaii and the Caribbean, are located between 16ºN and 23ºN (Calambokidis et al. 2008, Stevick et al. 1998) and there is no comparable stopover for humpback whales, travelling to feeding areas from those breeding grounds. Consequently Hervey Bay provides important opportunities to study classes of whales and social organisation during the migration after leaving the breeding grounds, and before departure for the Antarctic feeding areas.

8.2.4 What is the relationship of humpback whales using Hervey Bay with the eastern Australian population?

The results of this study show that the estimated between year apparent survival rate of humpback whales visiting Hervey Bay is very high at 0.95% (95% CI, 0.92:0.97); see section 4.3.3.1), and near the upper limits of the biological survival rate of the species (Zerbini et al. 2010). The relatively stable proportion of eastern Australian humpback whales visiting Hervey Bay and the steady increase in the abundance of whales over years, together with very high site-fidelity to Hervey Bay reported in this study, provides the first evidence that the humpback whales visiting Hervey Bay may be a specific sub-group of the eastern Australian population and that the sub-group is growing at least the same rate, and possibly a higher rate, than the eastern Australian population.

8.2.5 Does maternal fidelity influence site-fidelity to Hervey Bay?

This study provides the first unbiased estimate of the temporary immigration of humpback whales visiting Hervey Bay as even flow and constant over years at 14.1% (SD = 0.038, 95% CI, 0.081:0.234). The result is consistent with two cohorts of breeding females taking turns to visit Hervey Bay in alternate years depending upon reproductive status (Chapter 4). Franklin (2012) reported an overall indicative female
sex-bias in pods visiting Hervey Bay and, for a selected sample of long-term sighting histories of individually identified whales, a female to male sex-bias of 2.94:1. This is in contrast to the male-biased sex ratio reported in breeding grounds and along the coastal migratory corridor off eastern Australia (Herman et al. 2011, Brown and Corkeron 1995). Franklin (2012) suggested that the shallow waters of Hervey Bay may be a deterrent to mature males and that deeper waters in the breeding grounds and along the migratory corridor may offer better mating opportunities.

A study of the temporal segregation of sex, age, reproductive and maturational classes of whales in Hervey Bay (Franklin 2012) showed that non-lactating females are at the vanguard of the southern migration travelling in company with immature males (Fig. 4.1.2 h, g) while lactating females with older calves are at the rearguard of the migration accompanied by a few mature males (Fig. 4.1.2 a, b and d). It was suggested that temporal segregation was a consistent and coherent feature of the social organisation of humpback whales (Franklin 2012). The results from this study of the regular within-season pattern over years, of abundance, survivorship and probability of entry are consistent with those results.

There was considerable variability in estimates of abundance of humpback whales visiting Hervey Bay during the late 1980s and early 1990s (Chaloupka et al. 1999), and a significant fall in the proportion of pods with calves visiting Hervey Bay in the early 1990s (Franklin et al. 2011). However from the mid-1990s the proportion of pods with calves has remained constant at above 40% and there has been a steady near-linear rate of increase in the estimates of abundance in visitors to Hervey Bay, together with very high levels of survivorship and site-fidelity (see Chapter 5, 5.2.5 above).
It is suggested that the sub-group from the east Australian population visiting Hervey Bay from the mid-1990s has been a cohort of breeding females exhibiting very strong site-fidelity to Hervey Bay, together with the accompanying cohort of immature males and females, younger mature males and females and some mature males.

8.2.6 Do Hervey Bay humpback whales mingle with nearby populations?

The results in this study provide the first photo-identification evidence that there are low levels of intermingling by humpback whales from Hervey Bay with the New Caledonia population, and furthermore the results are consistent with the view that New Caledonia is a separate breeding population, and consistent with genetic evidence below, that there is further sub-structuring between western and eastern Oceania breeding aggregations (Chapter 6). Previous studies have reported ‘Discovery’ tag matches and photo-identification matches between New Caledonia and eastern Australia (Chittleborough 1965, Dawbin 1966, Garrigue et al. 2000, 2007, 2011) and genetic studies have indicated that eastern Australia, New Caledonia and Tonga are separate breeding stocks (Olarvaria et al. 2006, 2007).

This study provides the first evidence that some Hervey Bay humpback whales travel east from the Australian coast and through the southern waters of New Zealand including Cook Strait en-route to, and from, feeding Antarctic Area V feeding areas (Chapter 6, Fig. 6.4.1.1; Franklin et al. 2008). Dawbin (1956) showed that humpback whales from New Caledonia and Tonga also travel through the southern waters of New Zealand and consequently it is highly likely that whales from Hervey Bay, New Caledonia and Tonga are intermingling in southern New Zealand waters (see Fig. 6.4.1.1)
Photo-identification matches between Hervey Bay and humpback whales satellite-radio tagged of Eden on the south coast of NSW, Australia (Appendix !!, page 335 below) confirmed that some humpback whales from Hervey Bay travel south past Eden and east from Eden towards the southern waters of New Zealand and suggest that Eden may be a migratory hub for eastern Australian humpback whales.

The photo-identification matches between large catalogues from Hervey Bay and western Australia, east Africa and Antarctic Area IV found no matches (Sub-chapter 7.2), however one of the humpback whales satellite-radio tagged off Eden, NSW traveled south to Bass Strait, westward through Bass Strait and down into the Antarctic Area IV feeding area (Appendix II, page 335 below). This result was consistent with early ‘Discovery’ mark tags (Chittleborough 1965, Dawbin 1966), one photo-identification match with western Australia (Kaufman et al. 2011) and acoustic data (Noad 2002), which revealed low levels of mixing between the eastern Australian and western Australian populations consistent with eastern and western Australia being separate breeding populations (Olavarria et al. 2006).

8.2.7 Where do Hervey Bay humpback whales feed?

The results in this study provided the first photo-identification evidence that the waters near and around the Balleny Islands in Antarctica Area V are a summer feeding area for some east Australian humpback whales. However there was insufficient evidence to determine whether humpback whales from Oceania breeding populations feed near the Balleny Islands (Sub-chapter 7.1). Based on whaling catches in the 1930s to 1960s and ‘Discovery’ mark tag data it had been suggested that the Balleny Islands may be a feeding area for humpback whales from both eastern Australia and New Caledonia (Dawbin 1956, 1966, 1997; Chittleborough 1965; Clapham et al. 2009). Prior to this study only three previous photo-
identification matches between eastern Australia and Antarctica Area V had been reported (Kaufman et al. 1990, Rock et al. 2006).

The longitude of the most westerly of the photo-identification sightings in Antarctica Area V was 155°55′E, and the most easterly was at 170°52′W, while the Balleny Islands sightings were obtained around 163°E (Fig. 7.1.2.1.1). The distance between these two sightings was approximately 817 nautical miles (Rock et al. 2006, see Fig. 7.1.2.1.1). Dawbin (1956) suggested that humpback whales leaving New Zealand Waters for Antarctic Area V feeding areas disperse widely as they travel south. The satellite-linked radio tag data from 16 humpback whales tagged off Eden (Gales et al. 2009) supports the Dawbin hypothesis and results presented in this study (Sub-chapter 7.2, Appendix II, page 335 below) shows that one of those tagged whales travelled towards southern New Zealand en-route to Antarctica Area V (Sub-chapter 7.2 and Appendix II, page 335 below, Fig. 1, Fig. 3). It is likely that humpback whales from Hervey Bay disperse widely across Antarctica Area V for feeding, with a possible larger feeding concentration occurring in and around the Balleny Islands (Sub-chapter 7.1, 7.2 and Appendix II, page 335 below).

The photo-identification matching between the Antarctica Area IV catalogue and larger catalogues from eastern Australia, western Australia and east Africa found no matches (Sub-chapter 7.2, Fig. 7.2.2.1.1). However it provided sufficient evidence to indicate that the humpback whales feeding in Antarctica Area IV were a separate population from the east African or eastern Australian populations, and weak evidence to reject the hypothesis that humpback whales feeding in Area IV are from the western Australian population. Early whaling data, some recent photo-identification data and genetic data support the hypothesis that western Australian humpback whales feed in Antarctic Area IV and that there may be low levels of intermingling between eastern Australian humpback whales, western Australian

The photo-identification match between the 16 humpback whales satellite-linked radio tagged off Eden and the Hervey Bay catalogue reported in this study (Appendix II, page 335 below) provided the first evidence that a humpback whale sighted regularly in Hervey Bay travelled south past Eden, onto and through Bass Strait to the west and then down to the Antarctic Area IV feeding area (Appendix II, page 335 below, Fig.3). The humpback whale was likely to be a female accompanied by a calf, which had previously exhibited strong site-fidelity to Hervey Bay during the breeding season (Appendix II, page 335 below, Fig. 2). This result shows that females from eastern Australia do not always travel to Antarctic Area V to feed; hence these whales exhibit a diverse range of feeding destinations in Antarctica after leaving Australian coastal waters.

8.2.8 Reproduction rates and trends in abundance of humpback whales

in Hervey Bay

The observed proportion of calves to whales in Hervey Bay (weekly average 1997 to 2009 = 17.9%) is consistent with the estimated growth rate of the eastern Australian population and calf survival may be higher than for the eastern Australian population as a whole. Modelling of the population trajectory of humpback whales utilising Hervey Bay reveals that observed abundance estimates exhibit a logistic trend with a slower growth rate in the mid-1970s, near linear growth during the early and mid-2000s and a decreasing growth rate by 2009. The exponential average rate of growth of humpback whales utilising Hervey Bay between 1997 and 2009 was estimated at 14.2% (95%CI 11.1% to 15.9%). The extended residency of mature
females, yearlings, younger males and females and calves together with a limited
presence of mature male whales provides opportunities for social interactions and
social development that may be contributing to high rates of reproduction and high
populations rates of increase for the sub-group of eastern Australian humpback
whales utilising Hervey Bay.

8.2.9 The fit and function of Hervey Bay in the migration of eastern Australian
humpback whales – A Final Synthesis

The focus of this thesis is to improve the understanding of the importance of Hervey
Bay for the migration of eastern Australian humpback whales by investigating the fit
and function of Hervey Bay in the migration. Data from capture-recapture modelling
of long-term individual capture histories presented in Chapter 4 provided
information on population parameters of the humpback whales utilising Hervey Bay
and provided an answer to one of the fundamental questions about Hervey Bay:
whether or not the humpback whales in Hervey Bay are a random sample of the
eastern Australian population or a sub-group of the eastern Australian population?
The high rate of site fidelity combined with near constant proportion of eastern
Australian whales visiting Hervey Bay (8.2.4 above) strongly support the hypothesis
that the humpback whales utilising Hervey Bay are a sub-group of the eastern
Australian population. This of course raises a question as to whether or not those
eastern Australian humpback whales that do not use Hervey Bay are a sub-groups or
possibly further sub-groups.

Another fundamental question answered in Chapter 4 was: what is the average
duration of residency of the humpback whales visiting Hervey Bay relative the overall
average time spent in the putative breeding grounds (8.2.3 above). The residency of
humpback using Hervey Bay relative to the overall average time spent within the

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putative breeding grounds supports the hypothesis that Hervey Bay is an important stopover early in the southern migration of eastern Australian humpback whales (8.2.3 above). Previous research had established that Hervey Bay is neither a calving area, a breeding ground or a terminal destination but rather a stopover early in the southern migration for particular classes of humpback whales. Mature females accompanying yearlings and immature males and females early in the season and mother with older calves and few mature males later in the season. The evidence presented in Chapter 4 on temporary immigration, within season patterns of abundance, survivorship and probability of entry (8.2.2 and 8.2.5 above) are fully consistent with the presence, seasonal timing and temporal segregation of the above classes of humpback whales in Hervey Bay.

The fit of Hervey Bay in the migration of eastern Australian whales was in part addressed by the estimate of average residency (8.2.3 above) and that that a sub-group of eastern Australian humpbacks is stopping over in Hervey Bay (8.2.4 above). The data presented in Chapter 6, Sub-chapters 7.1 7.2 and Appendix II, page 335 below (8.2.6 above) provided additional evidence of how humpback whales stopping over in Hervey Bay fit into the migration of eastern Australian humpback whales. Chapter 6 revealed for the first time that some eastern Australian humpback whales travel through the southern waters of New Zealand when travelling to and from Antarctic feeding areas. It also confirmed low levels of mingling with the New Caledonia population consistent with New Caledonia being a separate population and, consistent with genetic evidence, confirmed the hypothesis that the E1, E2 and F breeding aggregations are separate populations (8.2.6 above). The data presented in sub-chapter 7.1 provided the first post commercial whaling evidence that some Hervey Bay and eastern Australian humpback whales feed in the waters near to and around the Balleny Islands in Antarctica (8.2.7 above). Moreover Appendix II, page
below provided evidence that some Hervey Bay humpback whales travel past Eden during the southern migration and a Hervey Bay humpback female and calf travelled westward through Bass straight to feed in Antarctic Area IV suggesting that Hervey Bay humpback whales may disperse more widely than previously thought to antarctic Area V and IV feeding areas (8.2.7 above). Finally sub-chapter 7.2 provided evidence that humpback whales feeding in Antarctic Area IV are not likely to be from either east Africa or eastern Australia but could not discount the probability that humpback whales feeding in Antarctic Area IV are from the western Australian breeding aggregation.

The thesis addressed the importance and function of Hervey Bay in the eastern Australian migration in Chapter 5. This chapter provided evidence that the humpback whales utilising Hervey Bay are exhibiting a rate of reproduction which is likely greater than the eastern Australian population as a whole but also near to the maximum biologically plausible rate of reproduction (8.2.8 above). This strongly suggests that the stop over in Hervey Bay is providing a reproductive advantage to those classes of humpback whales utilising Hervey Bay. Consistent with this the trajectory of the population rate of increase in Hervey Bay is greater than the estimated rate of increase of the eastern Australian population as a whole reflecting a very high rate of calf survival in Hervey Bay with both calf survival and the population rate of increase of humpback whales in Hervey Bay being at or near to the maximum plausible rate of increase for the species (8.2.8). Additionally the rate of population growth in Hervey Bay exhibits a logistic form with a slower rate of increase early in the study period, a near liner rate of growth during the mid period and a slowing rate of growth towards the end of the study period (8.2.1 and 8.2.8 above). Insufficient data of the estimated growth rate of the eastern Australian population leaves it unclear as to whether the slowing rate of growth in Hervey Bay is a density
dependent effect amongst those whales using Hervey Bay or a reflection of an overall trend in the trajectory of the eastern Australian population.

In summary, the evidence presented in this thesis shows that the humpback whales utilising Hervey Bay as a stop over early in the southern migration are a sub-group of the eastern Australian population and that the stop over appears to provide those whales with an advantage which may offer greater reproductive success than the humpback whales that are not using Hervey Bay. The humpback whales using Hervey Bay are involved in complex mingling and linkages with nearby humpback whale breeding aggregations and Antarctic feeding areas.

8.2.10 Future research

Only broad-scale information is available on the movements and locations of humpback whales within the putative breeding areas to the north of Hervey Bay between 16° and 23° (Simmons and Marsh 1986, Paterson 1991, Chaloupka and Osmond 1999, Smith et al. 2012 and Chapter 2. Figure 2.2.1). Consequently there are presently insufficient data to address a number of important management questions: Does the breeding cohort using Hervey Bay exhibit natal philopatry to site-specific birthing locations prior to visiting Hervey Bay? If other eastern Australian humpback whale sub-groups exist do they share site-specific birthing locations with the Hervey Bay cohort or occupy different site-specific birthing locations? The availability of a large long-term photo-identification dataset from Hervey Bay (1992-2009, n = 2821 unique fluke identifications) and a large number of genetic samples (1992-2009, n = 1471 samples) provides the opportunity for collaborative analysis, between site-specific data obtained within the putative breeding grounds or from other locations along the eastern coastline of Queensland and New South Wales, to address the above questions.
Future capture-recapture modelling of existing Hervey Bay data should distinguish between females with calves compared with other whales and assess residency time in terms of entry cohort. This could be accommodated in the MSORD model by including female with calf as a state and between-week survival (residency) as a function of entry cohort. A first step in this direction is to conduct a separate analysis for known breeding females only with a focus on the relative probabilities of presence in Hervey Bay as a function of breeding state. Here we might expect a Markovian model in which temporary emigration is lower for females without calf in the previous year, which may be expected to often be with calf in the current year. The entry and exit times and periods of residency are expected to vary with the breeding state of females, and residency times could be estimated separately for these groups in terms of their entry cohorts. This model will, however, be a first step to integrating the entire population in terms of breeding status and entry cohort in a MSORD model with several classes of whales included as states. There are limits to this however, as the sex and age of many whales is unknown and, there were some classes of whales that were present but for which it was not possible to identify each member (e.g. juveniles). Consequently they will be ‘latent classes’ underlying variation in the model estimates.

Accumulation and comparison of photo-identification data, together with genetic and satellite tagging data obtained across the breadth of the Antarctic Area V feeding areas (130°E to 170°W), would greatly improve our understanding of the level and rate of intermingling among humpback whales from eastern Australian and Oceania breeding groups while in Antarctic waters. Data on individual humpback whales, passing through New Zealand waters to breeding grounds in eastern Australia and the western Pacific, offers the opportunity to document and quantify temporary and/or permanent immigration between existing breeding grounds and to monitor
and assess recovery of humpback whales in formerly occupied breeding grounds in Oceania.

Also further collection of humpback whale photo-ID fluke data, either in the vicinity of the Balleny Islands, the Ross Sea and/or from across the Area V feeding areas, will be important in clarifying the migratory linkages between Antarctic feeding areas and Oceania and eastern Australian breeding grounds. Collection of further photo-identification data of humpback whales in Antarctic feeding areas III, IV and V with sampling across the season will assist in further investigating of the linkages between Antarctic feeding areas and tropical breeding grounds of humpback whales in both the Indian and Pacific Ocean basins, as well as rates of intermingling between these different breeding populations during their period in feeding areas.

The timing and location of sampling in Antarctic Area IV feeding grounds is likely an important factor in determining the linkages between nearby feeding grounds and Antarctic Area IV feeding grounds. The humpback whale satellite-radio tagged off Eden in October 2008 travelled around the coastline of Victoria and then past Northwest Tasmania and then southwest directly down into Antarctic Area IV feeding grounds. The whale was recorded at 60°S, 121°E on the 4th December 2008, and stayed below 60°S and was moving eastward until 3rd February 2009 when the satellite-radio tag stopped transmitting. Consequently sampling in the Antarctic Area IV feeding grounds throughout December, January and February may yield more useful results for comparison with coastal whale fluke catalogues.

The Greenpeace Antarctic Area IV catalogue should also be compared to any other existing East African, Indian Ocean, Australian and/or Antarctic catalogue as this is likely to provide further data on the migratory destination of these humpback whales
and add to our limited knowledge of the extent of population intermingling within the Antarctic Area III, IV and V feeding areas.
8.3 LITERATURE CITED


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APPENDIX I:

EARLY IMPACTS ON WHALE POPULATIONS IN
THE SOUTH PACIFIC AND EASTERN AUSTRALIA

Humpback whales and other species throughout the South Pacific Ocean were able to evolve and survive over many generations with minimal human impact until the arrival of both British and American sailing whaling ships in the late 18th Century.

The British and American whaling ships sailed into the Pacific from the west, by way of the Cape of Good Hope, across the southern Indian Ocean then onto Australian waters; and from the east around Cape Horn into and across the Pacific Ocean (Stackpole 1953, Dakin 1963). Samuel Enderby Jr., of the London based whaling company Enderby & Sons, in a letter dated 17th January 1789, declared that ‘Lord Hawkesbury took the South Pacific Whale fishery under his wing in 1785... and that the number of vessels that returned to that fishery in 1788 were 45 sail’. He went on to say ‘nothing is wanting to make this Fishery compleat but an unlimited right of fishing in all seas’ ... and that ... ‘the British would soon explore the most distant parts . . . of the South Pacific Fishery . . . and the settlements of New Holland would be often visited, as there are many whales in the sea’ (Stackpole 1953).

Commanded by Captain James Shields with First Mate-Harpooner Archaelus Hammond, both ‘Yankee Whalers’ from Nantucket, the British whale-ship ‘Emelia’ was the first to round Cape Horn from east to west in 1789 and enter the South Pacific Whale Fishery. In November 1791 an American Nantucket Man, Captain Bunker, took the British Whale Fishery across the Pacific to the Australia coast for the
first time via Cape Horn. Twenty-nine or more whale-ships, both British and American, had entered the Pacific via Cape Horn by 1793 (Stackpole 1953).

At least two of the First Fleet ships that arrived in Australia in 1788 had licences to whale in the Southern Ocean fishery (Mawer 1999). Five of the ships of the Third Fleet that arrived in 1791 were whalers, who after the arrival of the Third Fleet were bound, under licence, for the Chile and Peru whaling grounds (Dakin 1963, Gill 1965). Both Governor Phillip and Philip Gidley King reported in late 1791, to the Government in London, that the decision of the five Third Fleet whaling ships to alter their plans and whale along the east coast of Australia, may mean: ‘that a whale fishery on the New South Wales Coast will succeed’ (Gill 1965).

The initial poor results from these early whaling voyages off the east coast of Australia, together with the restrictive monopoly held by the East India Company over trade in the South Pacific, hindered the development of the early Australian Whaling Industry (Dakin 1963, Gill 1965). However this changed with the appointment of Philip Gidley King as the third Governor of NSW in September 1800 and an Act passed by the British Parliament in 1801, which opened all Australian waters to whaling (Dakin 1963, Gill 1965).

Governor King was a strong supporter of the whaling Industry. In a letter to the Duke of Portland dated 28th September 1800 he wrote, ‘merchants in England are now satisfied that spermaceti whales are equally if not more plentiful on this coast than they are on the coast of Peru…. much advantage will arise to this Colony from the frequent intercourse with whalers… and also the advantage of bringing convicts and stores out on lower terms than have hitherto been paid’ (Dakin 1963). By 1803, King was able to write to his friend in London, Joseph Banks that, ‘the spermaceti and common oil fishery goes on very well’ (Gill 1965). King established Hobart as a major
centre for the Southern Ocean whale fishery in 1806 (Dakin 1963, Gill, 1965, Colwell 1977). At the peak of pelagic whaling in 1850, Hobart was considered, ‘the greatest whaling port in the British Empire’ (Gill 1965). Over the first 50 years of the 19th century both pelagic ship and bay-based whaling flourished along the coast of NSW, Tasmania, South Australia and Western Australia (Dakin 1963, Gill 1965, Little 1969).

The 1858 statistical returns of the NSW Government showed that between 1830 and 1850 whaling made a significant contribution to the NSW economy (Little 1969). However whaling production figures reported only sperm and southern right oil, with no mention of humpback whale oil (Little 1969). The primary targets of the pelagic sailing whale-ships were the slow moving whales for their oil, which met a demand for illumination and lubrication during the 18th Century (Gill 1965, Smith et al. 2012). By the peak of sailing ship whaling in the mid-1800s there were 735 vessels in the American whaling fleet in all oceans of the world (Townsend 1935).

Townsend (1935) plotted the location of catches of 53,877 whales, using logbooks from 744 whaling vessels and 1,665 voyages; the main whales reported taken were sperm, bowhead and the northern and southern right whales. Of the total worldwide catch plotted by Townsend (1935) only 2,883 (5.4%) of catches were reported to be humpback whales. In the Pacific the humpback whales were mainly taken around the Islands of Tonga, from the Coral Sea northwest of New Caledonia, some from around New Zealand and Australia as well as Madagascar off the east coast of Africa (Townsend 1935, Smith et al. 2012b).

There were both technical and biological limitations to sailing ship whaling. The major technical limitations were the lack of speed of the sailing whaling ships, and the limited strength of the hand held harpoons and killing lance deployed from rowing boats. The rorqual whales, including the Blue, Fin, Sei, Brydes and Minke are
able to swim at 10 knots or more and were therefore beyond the reach of the sailing ships, their rowing boats and hand-held and thrown harpoons. If, as did occur, a harpoon could be lodged in a rorqual from a rowboat, the boat would likely be either destroyed by the whale or dragged along by the whale out of reach of its mother sailing ship. The other biological factor was that, unlike the slow moving sperm and right whales, rorquals did not float but sunk, after being harpooned (Harrison 1968, Harrison et al. 2009).

Although pelagic sailing ship and bay-based whaling occurred extensively in the Pacific and around Australia from 1790 through to 1890 (Dakin 1963); the primary impact was on slow moving sperm and southern right whales, with only low levels of impact reported on humpback whales (Townsend 1935). This was to change in the Twentieth Century (See Section 1.5 above).
APPENDIX II:

Movement of two Humpback whales 
(Megaptera novaeangliae) satellite-radio tagged 
off Eden, NSW and matched by photo-
identification with the Hervey Bay, Queensland 
fluke catalogue
1 INTRODUCTION

A recent photo-identification study of eastern Australian humpback whales and humpback whales across Oceania (South Pacific), documented four photo-identification matches between the nearby breeding grounds of New Caledonia and eastern Australia and three matches between New Zealand and eastern Australia (Garrigue et al. 2011). Analyses of these matches showed that some eastern Australian whales migrate through Cook Strait and the southern waters of New Zealand while travelling to and from Antarctic feeding areas (Franklin et al. 2008b, Franklin et al. 2014, Chapter 6 above). Two of the New Zealand matches were whales photographed in Cook Strait in June 2004 and subsequently photographed in Hervey Bay in September the same year (Franklin et al. 2014). These photo-identification matches could not provide information about the routes taken by individual humpback whales between New Zealand and eastern Australia.

Dawbin (1949, 1956) noted that the Ross Sea, particularly around the Balleny Islands, “almost certainly represents the summer concentration of humpback whales which pass the coasts of New Zealand, East Australia and other parts of the Pacific”. He developed the hypothesis that dispersal across the Antarctic Area V feeding grounds is a primary determinant of the routes taken by humpbacks as they approach New Zealand on their return to winter breeding areas. Recent photo-identification evidence supports this view. Six photo-identification matches have been reported between the Antarctic Area V feeding areas and breeding grounds to the north (Kaufman et al. 1990, Rock et al. 2006, Franklin et al. 2008b, Franklin et al. 2012, Sub-chapter 7.1 above). Five of these sightings were in close vicinity to the Balleny Islands (67° S, 163°E) (Rock et al. 2006, Franklin et al. 2008b, Franklin et al. 2012, Sub-chapter 7.1 above).
2012, Chapter 7.1 above), and one was near to the eastern border of the Area V feeding area (69°S, 171°W) (Rock et al. 2006). The longitude of the most westerly sighting was 155° 55′E, and the most easterly was at 170° 52′W. The distance between these two sightings was approximately 817 nautical miles (Rock et al. 2006, Franklin et al. 2008b). All of these individuals are reported as having strong site fidelity to eastern Australian breeding grounds (Kaufman et al. 1990, Rock et al. 2006, Franklin et al. 2008b, Franklin et al. 2012, Sub-chapter 7.1 above). Franklin et al. (2012) concluded that some eastern Australian whales feed in and around the Balleny Islands in Antarctica Area V. Rock et al. (2006) also reported two individual humpback that have been sighted in both Hervey Bay and Eden.

During late October 2008, 16 satellite-linked radio tags were attached to southbound humpback whales off Eden, NSW (Gales et al. 2009). The tags remained active from 3 to 156 days providing a full description of the transit tracks of some whales from Eden to Antarctic feeding areas (Figure 1). All but one individual humpback whale travelled southward into the Antarctic Area V (130°E-170°W) feeding area. As predicted by Franklin et al. (2008), several individual humpback whales travelled southeast from Eden passing to the southwest of southern New Zealand and then at least two of these whales continued south, well to the east of the Balleny Islands. Several other individual humpback whales moved down along the Victorian and Tasmanian coast and then migrated towards the Balleny Islands (approximately 67° S, 163°E), with some dispersing well to the west (approximately 148°E) and to the east (approximately 176°W) of the Balleny Islands. A single humpback whale accompanied by a calf at the time of tag deployment, followed the Victorian coast westward, then travelled through Bass Strait to northwest Tasmania and from there southwest to the edge of the Antarctic ice shelf in Area IV (Gales et al. 2009, Figure 1).
Figure 1. Tracks of the 16 individual humpback whales satellite-linked radio tagged off Eden in October 2008 (from Gales et al. 2009).
2 METHODS

Satellite-linked radio tags were deployed on 16 southbound humpbacks whales off the coast of Eden, NSW (37.15°S, 150.07°E) between 24th October and 1st November 2008 (Gales et al. 2009). During deployment of the tags photo-identification images were taken of each of the 16 individual humpback whales. A total of 33 photographs were obtained. Of the 33 photographs, 24 were right lateral body and dorsal photographs, seven were left lateral body and dorsal photographs and two were ventral underside fluke photographs.

Photo-identification of humpback whales in Hervey Bay, Queensland was undertaken for ten weeks each year between 1992 and 2009 as part of a long-term study of the social behaviour and social organization of humpback whales in Hervey Bay. Photography of ventral underside flukes, and related left and right lateral body and dorsal photographs were obtained wherever possible. The Hervey Bay fluke catalogue for the period 1992-2009 consists of $n = 2821$ individual whales. A full description of the Hervey Bay study area, fieldwork, effort and data obtained is provided in Chapter 2 above.

In this study photo-identification images of the whales tagged off Eden in 2008 are compared to the existing humpback whale fluke catalogue and other photo-identification images from Hervey Bay for the period 1992-2009.

To identify any matches between the humpback whales in the 2008 Eden catalogue and the humpback whales in the Hervey Bay catalogue, each fluke and left and right lateral body and dorsal photograph in the Eden catalogue ($n = 16$ whales) was compared to the ventral fluke and left and right lateral body photographs in the Hervey Bay fluke catalogue ($n = 2821$ whales).
3 RESULTS

The comparison of the Eden photographic catalogue with the Hervey Bay photography yielded two matches. Both matches were based on right lateral body and dorsal photographs. The photo-identification images and the details of each individual whale matched are provided in Figure 2 and Figure 3 below.
Figure 2. Photographic match of a humpback whale photographed in Hervey Bay on 21st September 2008 (A, top photograph) and subsequently photographed off Eden on 24th October 2008 (B, bottom photograph) by Gales et al. (2009). The whale was coded as satellite-radio tagged whale 88746 off Eden and was identified in the field as a male. This male whale was only sighted on one occasion in Hervey Bay during 2008, and was not identified in Hervey Bay during other years.
Figure 3. Photographic match of a humpback whale photographed in Hervey Bay on 11th November 2002 (A, top photograph) and then photographed off Eden 29th October 2008 (B, bottom photograph) by Gales et al. (2009). The whale was coded as satellite-radio tagged whale 88729 off Eden and was inferred to be female as a calf accompanied the whale. This whale (mnemonic name ‘Rama’) was photographed in Hervey Bay in the years 1998 from 27th September to 1st October 1999 on the 10th August 2000 from the 6th to 25th September 2001 on the 3rd October, 2002 on the 11th October and in 2005 from the 4th to the 7th September. A calf accompanied the female ‘Rama’ in each year it was sighted in Hervey Bay, except 1999, providing further evidence that this whale is a female.
A satellite-linked radio tag was deployed on the male humpback whale 88746 on the 24th October 2008 (Gales et al. 2009). The whale was in a pod of two adults. The tag remained active for 20 days until 12th November 2008 and provided 138 position locations. The whale moved south from Eden and upon reaching open water in Bass Strait turned eastward and travelled in a steady south-easterly direction towards the southern coast of New Zealand until the tag ceased reporting (Gales et al. 2009). The full track of whale 88746 is shown in Figure 4, below.

A satellite-linked radio tag was deployed on the female humpback whale 88729 on the 29th October 2008 (Gales et al. 2009). A calf accompanied the female at the time the tag was deployed. The tag remained active for 98 days until the 3rd February 2009 and provided 1160 position locations. The female followed the coastline from Eden moving westward around the Victorian coast until Wilsons Promontory. She then travelled southwest passing close to the northwest corner of Tasmania before continuing steadily southwest, moving out of Antarctic Area V (130°E-170°W) and into Antarctic Area IV (70°E-130°E) at approximately 55°S. She continued southwest until reaching approximately 60°S, 121°E on the 4th December 2008. From there, female 88729 moved south towards the Antarctic ice edge and then turned west, tracking along the ice edge and slowly moving northwest until the tag ceased reporting on the 3rd February 2009. The full track of whale 88729 is shown in Figure 4, below.
Figure 4. Satellite-linked radio tag tracks of male whale 88746 and female whale 88729 (Gales et al. 2009). Whale 88746 moved towards New Zealand. Female whale 88729 passed through Bass Strait and down into Antarctic Area IV feeding area.
4 DISCUSSION

The photo-identification matches presented here, of two humpback whales satellite tagged off Eden, NSW and also sighted in Hervey Bay, provides further evidence that some humpback whales that use Hervey Bay as a stopover during the southern migration also migrate to and past Eden, off the southern NSW coast. Some eastern Australian humpback whales travel past southern New Zealand en-route between eastern Australian breeding grounds and Antarctic Area V feeding areas (Franklin et al. 2008, Chapter 6 above), previous photo-identification provides no evidence of the routes taken between eastern Australia and New Zealand. Satellite-radio tagging has shown that some humpback whales passing Eden during the southern migration turn southwest directly towards southern New Zealand (Gales et al. 2009).

It has been suggested that the coast off Eden, NSW is an important feeding area for some humpback whales during the southern migration (Stamation et al. 2007). The availability, early in the southern migration, of an accessible coastal feeding area may provide an incentive for southbound humpbacks, particularly immature males and females and females with new calves, to travel close to the coast until they arrive in the feeding area off Eden. The two matched whales reported herein are likely to have travelled directly along the coast of Queensland and NSW from the Hervey Bay area to Eden off the south coast of NSW. Eden may be an important migratory hub for southbound humpback whales, and possibly northbound humpback whales. Comparison of any existing Eden fluke catalogues with eastern Australian, Victorian, Tasmanian, New Zealand, Oceanian and Antarctic fluke catalogues may provide further insights into the migratory corridors and destinations of humpbacks passing through the waters of Eden, NSW.
Humpback whales leaving Eden travel in three primary migratory corridors prior to moving directly towards and dispersing across the Antarctic Area IV and V feeding areas: southeast towards the southern coast of New Zealand; southward along the New South Wales, Victorian and Tasmanian east coast, and south past New South Wales, west along the Victorian coast then southwest through Bass Strait (Franklin et al. 2008b, Gales et al. 2009, Franklin et al. 2014). This study confirms that some humpback whales using Hervey Bay as a stop over migrate past Eden, NSW before moving into primary migratory corridors towards Antarctic feeding areas.

Mitochondrial segregation of DNA haplotypes in the Northern Hemisphere have been interpreted as maternally directed fidelity to migratory destinations (Baker et al. 1990). Furthermore long-term photo-identification studies of humpback whales in the Northern Hemisphere have 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). Female humpback whales with site-fidelity to eastern Australia, particularly Hervey Bay, have been found to feed in Antarctic Area V near and around the Balleny Islands (Kaufman et al. 1990, Rock et al. 2006, Franklin et al. 2008b, Franklin et al. 2012). The female humpback whale 88729 reported herein had strong site-fidelity to Hervey Bay during previous breeding seasons, but travelled to the Antarctic Area IV feeding area in the 2008-09 feeding season. This result shows that at least one female humpback from eastern Australia does not always travel to Antarctic Area V to feed, and confirms that humpback whales exhibit a diverse range of feeding destinations after leaving Australian coastal waters. The result also indicates that there is intermingling between eastern and western Australian populations and suggests that distinctions between Antarctic feeding areas may not be as clear as previously reported.
5 LITERATURE CITED


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## Appendix III

### TABLE OF PARAMETER ESTIMATES AND DERIVED ESTIMATES FROM THE MULTISTATE OPEN ROBUST DESIGN

#### MODEL 1 (MSORD)

*Table 4.3.3.1  Parameter estimates and derived estimates (with SE, 95%CI)*

from MSORD model 1: $S(.)psi(PA=AP=.)pent(y+w)phi(y+w)p(y+w+effort)$

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<th>Week/ Interval</th>
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Appendix IV:
SUMMARY OF CITATIONS OF RELEVANT AUTHORED, CO-AUTHORED AND RELATED PUBLICATIONS


Mammalogy. DOI: 10.1111/j.1746-7692.2010.00430.x.


and multi-point sampling. IWC Scientific Committee SC/A06/HW32.