

AN ABSTRACT OF THE THESIS OF

Giselle Renee Gibb for the degree of

Master of Science in

Fisheries Science presented

on June 11, 2009

Title: Humpback Whales (*Megaptera novaeangliae*) in the South Pacific Breeding Grounds: An Allocation from Feeding Areas and an Abundance Estimate of Whales Specific to French Polynesia Waters

Abstract approved:

C. Scott Baker

South Pacific humpback whales were devastated by commercial whaling in their Antarctic feeding areas during the 20th century. Understanding migratory connections and current abundance of these isolated breeding stocks is crucial for the allocation of historical Antarctic catches in population dynamic models used to assess current recovery. However, only a small number of migratory connections have been documented between Oceania breeding stocks within the South Pacific and feeding areas in the Antarctic. In addition, little is known about abundance of these stocks which encompass a vast oceanic region. For this thesis I first used mixed-stock analysis (MSA) to allocate migratory connections from four Antarctic feeding areas (n=142) to seven South Pacific breeding stocks (n=1,373), including four in Oceania, based on genetic marker frequencies. The use of this method was justified by the breeding stocks showing genetic differentiation at the haplotype level with an F_{ST} value of 0.027 (p-value <0.001). The results showed a relatively strong connection of Western Australia to Antarctic Area IV, Tonga to the border of Antarctic Area VI/I, Colombia to the Antarctic Peninsula, and a split allocation of Eastern Australia and New Caledonia to Antarctic Area V. This study provides the first population-level information supporting previous individual-based studies that humpback whale migration may not necessarily be direct north south. Next, utilizing capture-recapture methodology of unique humpback whale fluke photographs, I

estimated abundance of one of the least studied Oceania breeding stocks, French Polynesia, a stock which also showed no significant migratory allocation using MSA. Taking into consideration the possible advantages of using Quality Control (QC) photographs to minimize bias in matching, estimates were generated using the complete photo catalogue and also using only photographs adhering to QC criteria. I found that the choice of using QC has an effect on the abundance generated and discuss the implications of this finding. Despite the photo catalogue used, the French Polynesia stock is estimated to number less than 1,900 individuals. Lastly, to provide additional information on the French Polynesia stock I used photo-identification to compare French Polynesia whales to whales in the Antarctic Peninsula and Strait of Magellan (Antarctic Area I), a possible migratory connection suggested by previous microsatellite genotyping. No conclusive matches were found. Although this does not discount the possibility of a few migrants traveling between these regions it does indicate the Antarctic Peninsula and the Strait of Magellan are not primary feeding areas of French Polynesia. This new information regarding abundance and migration of French Polynesia whales is important for the Comprehensive Assessment of Southern Hemisphere humpback whales. This document is currently being completed as the International Whaling Commission considers the next critical steps in recovery for Oceania humpback whales stocks.

©Copyright by Giselle Renee Gibb
June 11, 2009
All Rights Reserved

Humpback Whales (*Megaptera novaeangliae*) in the South Pacific Breeding
Grounds: An Allocation from Feeding Areas and an Abundance Estimate of
Whales Specific to French Polynesia Waters

by
Giselle Renee Gibb

A THESIS

submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented June 11, 2009
Commencement June 2010

Master of Science thesis of Giselle Renee Gibb presented on June 11, 2009

APPROVED:

Major Professor, representing Fisheries Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Giselle Renee Gibb, Author

ACKNOWLEDGEMENTS

First and foremost, I would like to thank my major professor, Dr. Scott Baker, and my co-supervisor Dr. Michael Poole. Scott, I am very grateful for your guidance, patience and loads of editing over the last two years. Even though you were extremely busy, you always took the time to help me continue in the right direction. You are an amazing teacher and I will always be grateful. Michael, your fervor for what you do is infectious. You introduced me to the beauty of French Polynesia and the wonder of the marine mammals that live there. I will never forget your excitement for these amazing creatures, the way you would jump up exclaiming “BREACH!” no matter how many whales we had seen that day or how bad the weather was. Your enthusiasm never wanes which is both admirable and rare. I am very thankful for the opportunity you gave me.

I also greatly appreciate the help of my committee, Michael Banks and Kelly Benoit-Bird, and thank them for their guidance, comments and suggestions. Kelly, thank you for your support, excellent advice and offers of chocolate. Michael, thank you for insisting I do the assignment tests that helped discover the French Polynesia connection. It was a great learning experience for me, and rounded out the project well.

I am grateful for the financial support from the Endowment of the Marine Mammal Institute, the CRSP Aquaculture International Scholarship, Mamie Markham Research Award, and Henry F. Matsen Scholarship.

To Debbie Steel and my lab mates in Newport Alana, Angie, Becca, Claudia and Ursula, it's nice to be part of a lab that supports each other so well. I couldn't ask for better lab mates. Thank you for answering (so many!) questions and your suggestions on manuscripts, posters and presentations. Debbie, you are the heart of this lab, and it shows, your knowledge is exemplary.

To Jennifer Jackson, thank you so much for your endless support, knowledgeable suggestions and unconditional friendship. I am so grateful for everything you have done for me. I'll never forget your excellent teachings (and re-teachings) of Bayesian statistics, MCMC and Arlequin! You are such an amazing person and commendable scientist.

To my Ya-Yas in Portland, thank you for your help and insistence that I stay physically (and mentally) fit. I appreciate the miles we travel pounding the pavement together.

My family has always been very supportive of me with every college degree, travel itinerary and wild idea I have had, and this was no exception. I greatly appreciate your love and support through this and over the years. Mom, thanks especially for your graduate school “advice” and support on those lonely Sunday afternoons after Jason had gone home and I was left with just work in Newport.

Lastly, to my husband Jason who supported me (financially and otherwise) in my crazy decision to leave a perfectly good job to pursue graduate school 3 hours away from our home. Thank you for helping with all the unglamorous jobs like triple-checking data counts and proof-reading papers.

And to my dog Irie, who was patient with my nocturnal writing habits in the last few months of the thesis write-up (my Newport apartment was so small!). She always knew the perfect time to take a break from the writing and just go for a walk.

CONTRIBUTIONS OF AUTHORS

This thesis is made possible by the support and collaboration of the South Pacific Whale Research Consortium, a group of scientists and conservation managers committed to the non-lethal study of whales and dolphins in the vast region of Oceania. The principal investigator of French Polynesia, Dr. Michael Poole, allowed me to use all of his photo-identification data which began in 1990 for the analyses presented in Chapter 3 and 4. He allowed me to work with him in the field and aide in reconciling the photo-identification catalogue in 2005, 2007 and 2008.

The genetic data used in chapter 2 was a collaborative effort from scientists from Oceania, Australia, South America and Antarctica who collected biopsy samples in the field. This included Dr. Michael Poole and Dr. Marc Oremus in French Polynesia, Dr. Claire Garrigue in New Caledonia, Dr. Rochelle Constantine in Tonga, Dr. John Bannister and Dr. Muriel Brasseurs in Western Australia, Nan Hauser in the Cook Islands, Dr. Lilian Flores-Gonzales in Colombia, Megan Andersen in Eastern Australia, the SOWER cruises for the Antarctic samples and Dr. Carlos Olavarria for the Antarctic Peninsula samples. Laboratory analyses were performed primarily by Debbie Steel of the Cetacean Conservation Genetics Laboratory with additional samples analyzed by Carrie Antolik. Dr. Carlos Olavarria identified variable sites in the mitochondrial DNA control region to define 110 haplotypes for South Pacific humpback whales. I used these data in a mixed-stock analysis program to infer migratory destinations of humpback whales using haplotype frequencies of the different breeding and feeding populations. In addition, I used the microsatellites analyzed by Debbie Steel to assign individuals in the feeding area to a breeding region based on their multilocus genotype.

Dr. Rochelle Constantine and Claire Garrigue reviewed all fluke photographs from Oceania and began the Quality Control process discussed in chapter 3.

The photo-identification comparison in chapter 4 was accomplished with help from Dr. Michael Poole in French Polynesia, and Dr. Carlos Olavarria, Jorge Acevedo and Dr. Anelio Aguayo-Lobo in Chile who collect data from the Antarctic Peninsula. This allowed me to compare French Polynesia with the Antarctic Peninsula.

TABLE OF CONTENTS

	<u>Page</u>
CHAPTER 1: INTRODUCTION.....	2
1.1 Overview.....	2
1.2 Taxonomy and morphology.....	3
1.3 The International Whaling Commission.....	4
1.4 Southern hemisphere feeding regions, Antarctic Areas I-VI.....	5
1.5 Exploitation and stock depletion.....	6
1.6 The Comprehensive Assessment and South Pacific stock structure.	8
1.7 Molecular markers – a technique to study whale populations.....	9
1.8 Mixed-stock analysis.....	11
1.9 Photo-identification – a method for the individual identification of cetaceans.....	11
1.10 Capture-recapture analysis.....	11
1.11 French Polynesia humpback whales.....	13
1.12 Scope of this thesis	13
LITERATURE CITED.....	15
CHAPTER 2: Mixed-Stock Analysis of Humpback Whales (<i>Megaptera novaeangliae</i>) from Antarctic Feeding Areas and South Pacific Breeding Grounds	24
ABSTRACT.....	24
2.1 INTRODUCTION.....	25
2.2 METHODS.....	28
2.2.1 Field collection.....	28
2.2.2 MtDNA amplification and sequencing.....	29
2.2.3 Data Analyses.....	29
2.3 RESULTS.....	31
2.3.1 Revised Antarctic Areas.....	31
2.3.2 Population diversity and differentiation.....	31
2.3.3 Migratory apportionments.....	33
2.4 DISCUSSION.....	33

TABLE OF CONTENTS (Continued)

	<u>Page</u>
2.4.1 Area IV.....	34
2.4.2 Area V.....	35
2.4.3 Area VI*.....	35
2.4.4 Area I*.....	36
2.4.5 Implications of this study.....	37
2.4.6 The future of MSA for migratory connections.....	38
LITERATURE CITED.....	39
CHAPTER 3: Capture-recapture estimation of abundance for humpback whales of French Polynesia (Breeding Stock F) using photo-identification.....	49
ABSTRACT.....	50
3.1 INTRODUCTION.....	50
3.2 METHODS.....	51
3.2.1 Field surveys.....	51
3.2.2 Photograph matching procedure	51
3.2.3 Data sets.....	52
3.2.4 Exploration of model selection and assumption violation.....	53
3.2.5 Abundance estimation procedure.....	54
3.2.5.1 Chapman modified Lincoln-Petersen estimate	55
3.2.5.2 Schnabel weighted mean model.....	55
3.2.5.3 Closed population model: Program CAPTURE.....	55
3.2.5.4 Open population model: The Jolly-Seber Model.....	57
3.2.6 Transience.....	57
3.3 RESULTS.....	58
3.3.1 Catalogue results.....	58
3.3.2 Transience.....	59
3.4 DISCUSSION.....	59
3.4.1 Lincoln-Petersen and Schnabel estimate.....	59
3.4.2 Closed population model five year study.....	60
3.4.3 Preferred model in Program CAPTURE.....	60
3.4.4 Limitation of open population model.....	61
3.4.5 Quality Control.....	61
3.4.6 Heterogeneity.....	62
3.4.7 Summary and future direction.....	63
LITERATURE CITED	64
CHAPTER 4: Photo-identification comparison of humpback whales from the Antarctic Peninsula/Strait of Magellan and French Polynesia, (Breeding Stock F).....	71
ABSTRACT.....	71

TABLE OF CONTENTS (Continued)

	<u>Page</u>
4.1 INTRODUCTION.....	72
4.1.1 Previous documentation of connections between Oceania and the Antarctic Peninsula.....	72
4.1.2 Regions used in comparison.....	73
4.2 METHODS.....	75
4.2.1 Samples collection.....	75
4.2.2 Photo-identification catalogues.....	75
4.3 RESULTS.....	76
4.3.1 Photo matching.....	76
4.3.2 Probability of capture.....	76
4.4 DISCUSSION.....	78
LITERATURE CITED.....	79
CHAPTER 5: Summary and Conclusion.....	84
5.1 Mixed-stock analysis of Oceania and West and East Australia.....	85
5.2 French Polynesia abundance estimate.....	85
5.3 Photo comparison of French Polynesia and Antarctic Peninsula/Strait of Magellan.....	86
5.4 Management implications.....	87
LITERATURE CITED.....	88
Bibliography.....	90

APPENDICES

	<u>Page</u>
APPENDIX A: Assignment tests using microsatellite and mtDNA genetic markers to assign South Pacific humpback whales to three Antarctic Areas.....	109
APPENDIX B: Supplementary Material Chapter 2	118
APPENDIX C: Supplementary Material Chapter 3	121
APPENDIX D: Additional Supplementary Material Chapter 3	118

LIST OF FIGURES

<u>Figure</u>	<u>Page</u>
1.1 Morphological characteristics of humpback whales.	18
1.2 Humpback whale southern hemisphere geographic distribution.	19
1.3 Antarctic management areas as currently designated by the IWC....	19
1.4 South Pacific humpback whale breeding stocks and feeding areas..	20
1.5 Population trajectories for Oceania as compared to east Australia showing changes in population abundance (<i>N</i>) over time.	21
1.6 Summary of Photo ID matches 1999-2006 between sites in Eastern Australia (N=1242) and Oceania (n=692).	22
1.7a.b.The use of mitochondrial DNA in cetacean research.	22
2.1 South Pacific humpback whale breeding grounds (Stocks D, E, F, G) and feeding areas (Area IV, V, VI* and I*)	47
2.2 Distribution in the Antarctic feeding grounds of humpback whale samples taken during the IWC-SOWER cruises (1999, 2001, 2005), and INACH Antarctic Peninsula cruises.	48
3.1 French Polynesia including the two locations (circled) humpback whale data has mostly been collected, Moorea in the Society Islands and Rurutu in the Austral Islands (Poole 2006).	69
3.2 Examples of humpback whale fluke photos.....	69
3.3 The number of times individual humpback whales sighted in French Polynesia 1999-2007	70
3.4 Year to year estimates of French Polynesia humpback whale population size using the Chapman modified Lincoln-Petersen Estimate including 95% confidence intervals.	70
4.1 Map of South Pacific humpback whale migratory connections of genotype data (solid line) and Discovery Mark data (dashed line) and photo-identification (dotted line).....	82
4.2 Two humpback whale fluke photos identified as showing many similarities a) INACH 076 Antarctic Peninsula photo and b) French Polynesia photo FP 0014.....	83

LIST OF TABLES

<u>Table</u>	<u>Page</u>
1.1. Known total post-war catches (USSR and other nations) of humpback whales from Areas IV, V and VI, and migratory corridors directly north of these areas (e.g. Australia and New Zealand).	18
2.1.A summary the South Pacific humpback whale samples collected including the number of individuals, the number of haplotypes in each region out of the total 110, and the number of unique haplotypes relative to seasonal habitats.....	44
2.2.Updated South Pacific humpback whale F_{ST} values corrected for replicate samples.	45
2.3.Percent apportionments using SPAM 3.7 of South Pacific humpback whale breeding populations including (standard errors) from the feeding areas IV, V, VI* and I*.....	46
3.1.All photo-identification data representing yearly survey effort for capture-recapture analysis of French Polynesia humpback whales	67
3.2.Abandance estimates of Usable Photos and Quality Control tail fluke photo-identification catalogues for humpback whales found in French Polynesia using the Schnabel estimate, closed models calculated by CAPTURE within Program MARK and an open model calculated by JOLLY.....	68
4.1.Antarctic Peninsula (INACH), and Strait of Magellan (CEQUA) and French Polynesia humpback whale photo-identification catalogues used in the comparison of the Feeding Regions and Breeding Stock.....	82

LIST OF APPENDIX TABLES

<u>Table</u>	<u>Page</u>
A.1.The number of individuals assigned back to each breeding region based on a 15-locus microsatellite analysis using jack-knife iterations in WHICHRUN	116

LIST OF APPENDIX FIGURES

<u>Figure</u>	<u>Page</u>
A.1.South Pacific humpback whales breeding grounds (Stocks D, E, F, G) and feeding areas (Area IV, V, VI* and I*).....	116
A.2.The results from mixed-stock assignment tests in WHICHRUN for Antarctic Area V (n=7), Antarctic Area VI* (n=28) and Antarctic Area I*(n=73) based on 15 microsatellite loci and haplotype data.....	117

Humpback Whales (*Megaptera novaeangliae*) in the South Pacific Breeding
Grounds: An Allocation from Feeding Areas and an Abundance Estimate of
Whales Specific to French Polynesia Waters

Chapter 1 – General Introduction

The highest priority task in international science is to concentrate all efforts on the monitoring of large whale populations, especially in the whaling areas.

-Alfred A. Berzin

The Truth about Soviet Whaling

1.1 Overview

The great whales were hunted intensely in the last two centuries for their oil, meat and baleen (Reeves 2008). Humpback whales were often the first species to be exploited in an area due to their affinity for coastal waters (Clapham *et al.* 1997; Clapham & Mead 1999). The invention of the factory ship in the early 20th century meant whalers were no longer limited to land-based processing stations, and exploitation of the Antarctic waters began (Clapham & Baker 2008). With whaling locations close to shore nearing depletion, Antarctica offered a new frontier of abundant whales. Over the next six decades, more than 2 million whales were killed in the southern hemisphere alone, most of them taken in the Antarctic feeding areas. Of these whales, over 200,000 were humpbacks (Clapham & Baker 2008; Berzin 2008). By 1960 it was apparent that the Antarctic whales were in decline. The number of humpback whales was dangerously low, and the amount of effort put into hunting was increased significantly to maintain a daily catch rate similar to that in previous years (Chittleborough 1965). By 1966 the International Whaling Commission banned the hunting of humpback whales (Reeves 2008). Despite almost 50 years of protection, several humpback populations, or breeding stocks, still remain low in abundance, and recovery throughout the southern hemisphere is variable at best (Garrigue *et al.* 2004). The Eastern Australia humpback whale population appears to have rebounded faster (Paterson *et al.* 2001) than the humpback whale populations that breed around several South Pacific islands (Baker *et al.*

2006), referred to here as Oceania. This thesis investigates humpback whale migratory destinations of the winter breeding grounds of Oceania and summer feeding areas of Antarctica closest to them. In addition, the abundance of the humpback whale population of French Polynesia, an island group in Oceania, is assessed.

1.2 Taxonomy and morphology

Whales are of the order Cetacea encompassing whales, dolphins and porpoises all of which belong to one of two sub-orders, Odontoceti with teeth, or the Mysticeti-the baleen or whalebone whales (Mackintosh 1965). Whales, including dolphins and porpoises, have been defined as a monophyletic group having evolved from a common ancestor in the last 50 million years when whales made the transition from a terrestrial to a fully aquatic medium (Berta *et al.* 2006). Early mysticetes were thought to have had teeth and some modern species include vestigial teeth that are reabsorbed before birth (Fitzgerald 2006). All mysticetes have comb-like baleen plates to filter small crustaceans as well as small fish out of the sea water. The mysticetes are divided into four families including Balaenidae (right and bowhead whales), Neobalaenidae (Pygmy Right whale), Eschrichtiidae (gray whales) and Balaenopteridae (rorquals including humpback, blue, fin, sei, Bryde's and minke). The highly specialized feeding technique of the rorqual whales depends on the unique structure of their skull and grooved ventral pouch (Rice 1984a). The humpback whale, *Megaptera novaeangliae* (Borowski 1781), is the only member of the genus *Megaptera*; "Mega" meaning large, and ptera referring to wing, so named because humpback whales have large pectoral flippers, about a third the length of their body (Clapham 1997). The head of the humpback whale is covered in tubercles, large bumps each containing a sensory hair (Clapham 1997) (Figure 1.1).

Humpback whales are the fifth largest whale and are slightly reverse dimorphic, with the females, averaging 14m, larger than the males (13m-14m) (Evans 1987). Southern hemisphere whales are slightly larger than their northern counterparts (Clapham 2002). Northern hemisphere humpback whales feed on krill and small fish, while southern hemisphere whales feed almost exclusively on the largest species of krill (*Euphasia superba*) endemic to the Antarctic waters (Mackintosh 1965). Although their dorsal side is black, their coloration varies on their ventral side. The northern hemisphere humpback whales have a black ventral side while in certain regions of the southern hemisphere, including Western Australia, Eastern Australia and Oceania, humpbacks show a large extent of white coloration (Rice 1998). These differences in morphology however are not enough to warrant different subspecies status, and throughout the world only one species of humpback whale is recognized (Clapham & Mead 1999).

Humpback whales have one of the longest migrations of any whale and have been known to travel up to 8,000 km between their high-latitude summer feeding areas and their winter breeding grounds in tropical regions; (Clapham 1997) penetrating much farther in tropical waters than other species (Mackintosh 1942) (Figure 1.2). Humpback whales have been downlisted from endangered to least concern by both the US Endangered Species Act and the International Union for the Conservation of Nature with the exception of Oceania (Clapham and Mead 1999; NOAA 2009).

1.3 The International Whaling Commission

The International Whaling Commission (IWC) was established in 1946 to 'provide for conservation of whale stocks and make possible the orderly development of the whaling industry' (Bromley 2006). In principle this was to

investigate sufficiently the life history of great whales to allow the commission to set realistic quotas on whale catches (Clapham & Baker 2008). These quotas in the early years, however, were established without regard to life history parameters of individual species with whale catches being measured in Blue Whale Units (i.e. 1 blue whale is equal to 2.5 humpback whales). This accomplished little to help recovering whale stocks, and several species continued to decline (Clapham & Baker 2008). The Scientific Committee was established to ensure that any amendments to whaling regulations were based on scientific findings. The composition of the IWC began to change in the late 1970's as non-whaling nations joined, concerned about the conservation of great whales. A moratorium on whaling was proposed in 1974, but was rejected by the IWC. In 1982 enough non-whaling nations had joined, providing the necessary votes to pass the moratorium (Clapham & Baker 2008). In 1986 a zero catch quota for whaling went into affect. By this time, however, most great whale stocks were commercially extinct. Although this moratorium is still in effect, Japan engages in a loophole labeled 'scientific whaling', killing a quota of Minke whales annually during the Austral summer months in the Antarctic waters. It has been proposed that 50 humpback whales be taken by Japan as part of this same loophole in the areas where several of these small stocks of Oceania humpback whales are thought to feed in mixed aggregations (Gales *et al.* 2007).

1.4 Southern Hemisphere Feeding Regions, Antarctic Areas I-VI

The southern hemisphere humpback whales have a summer feeding range comprising the entire Antarctic Zone (Rice 1998). Humpback whales are said to have a circumpolar distribution in Antarctica that is not necessarily continuous, as they can be found in high concentration in some areas and scarce in other regions (Mackintosh 1942). The Antarctic feeding grounds for humpback

whales are considered to be south of 60°S latitude, and were originally divided into five areas based on the distribution of the whaling fleet (Mackintosh 1942). Later, using data from the abundance of whales in the feeding season, Antarctica was divided into Areas I-VI (Figure 1.3) (Mackintosh 1942).

Until recently the only data on the humpback whale's migration came from whaling records (Townsend 1935, Mackintosh 1942). The original link of migration destinations were '*Discovery*' tags (stainless steel tags shot into the whale's blubber and later recovered when the whale was killed and flensed). These provided the first information on the humpback whale's previously unknown migration in the Southern Hemisphere (Mackintosh 1942; Dawbin 1966). This established relationships between 3 areas in the Antarctic and the northern breeding grounds closest to them (Dawbin 1966). Humpback whales from the South Pacific breeding grounds are thought to feed in Areas IV, V, VI, and possibly the Antarctic Peninsula, but information of connections is still limited (Figure 1.4) (IWC report SC-58-Rep 5 2006).

1.5 Exploitation and stock depletion

South Pacific humpback whale stocks were subject to hunting throughout the 19th and 20th centuries resulting in severe decline of the species (Dawbin 1966). They were first taken by open-boat whalers in their tropical breeding grounds in the 19th century (Smith *et al.* 2006; Townsend 1935). These takes peaked in Western Australia, the South Pacific and western South America breeding grounds (IWC stocks D-G) (Figure 1.4) between 1850 and 1880 with almost 9,000 whales killed (Smith *et al.* 2006). In the South Pacific these takes were largely from Tonga, with a smaller number of whales (n = 42) taken from New Caledonia (Smith *et al.* 2006). In the 20th century, Southern Hemisphere humpback whales were exploited in their Antarctic feeding grounds (Clapham &

Baker 2008). This large scale commercial exploitation was responsible for the population hovering near the brink of extinction by 1966 when the IWC banned hunting of humpback whales. Despite the protection status, the Soviet Union continued hunting humpback whales illegally until 1973 (Mikhalev 2000). This illegal hunting involved taking as many whales as were seen with complete disregard to location and regulation of open season (Berzin 2008). In addition, the numbers that were reported by the Soviet Union were blatantly wrong (e.g. 7,500 killed and 450 reported, more than 4,000 killed and fewer than 100 reported) (Berzin 2008). The effect of this hunting left over 37,000 humpback whales dead in just under a five year period (Table 1.1). Over 25,000 of these whales were killed in Areas V and VI during the 1959/1960 and 1960/1961 seasons (Clapham *et al.* 2009).

“In the case of whales, the Soviet Union pillaged and destroyed foreign and international natural resources, and the leaders behind these acts thus became malicious domestic and international criminals” (Berzin 2008).

The Soviet Union was not the only country hunting illegally. During the summer of 1954-1955 a Panamanian whaling ship slaughtered humpback whales in the Antarctic without regard for time of open season or minimum length and then falsified their statistics. The records showed 170 humpbacks were killed when actually 1,125 humpback whales were taken from Area IV and V that season (Chittleborough 1965). The effects of this cumulative deceitful hunting left biologist baffled, thinking perhaps a biological agent of some sort was responsible for the huge loss of humpback whales (Berzin 2008).

Despite official protection from the IWC beginning in 1966, the implications of such intense hunting in the Antarctic areas south of the Oceania breeding stocks are still apparent today. These breeding stocks have been slow to recover, with a current abundance estimate of all four Oceania regions (New

Caledonia, Tonga, Cook Islands and French Polynesia) to be 3,827 (C.V. 0.12) (Baker *et al.* 2006). For comparison, the breeding grounds of Oceania are thought to have a carrying capacity of 17,800-20,600 (based on median posterior estimates from Jackson *et al.* 2008). In addition, the recovery estimates for Oceania are substantially lower than Eastern Australia (Breeding Stock E1) which also is thought to use Antarctic Area V. The median recovery estimates for a two-stock model show Oceania was 23-30% compared to 44-46% for Eastern Australia (Jackson *et al.* 2008), and models run of the population trajectory illustrate that Oceania is recovering more slowly than Eastern Australia (Figure 1.5). This indicates that Antarctic catches have had a long term impact on these small breeding stocks of Oceania (Clapham *et al.* 2009). To ensure proper recovery and management regarding catch allocations in the future it is important to monitor the abundance and migratory allocation of these breeding stocks.

1.6 The Comprehensive Assessment and South Pacific Stock Structure

After the moratorium on whaling began the IWC devised a Comprehensive Assessment to provide the scientific committee with information on whale stocks in light of management objectives (Donovan 1989). This assessment addressed what conceptual approaches might be used to provide the Commission with 'more effective scientific advice and recommendations for management; to determine the studies required to implement these approaches; and to establish a time-table for the in-depth assessment of whale stocks' (Donovan 1989). Although this has now been accomplished for several whale species including Bowhead and western Pacific Gray whales it is still in progress for the Southern Hemisphere humpback whales. Key to this assessment is defining the breeding stocks and any knowledge regarding movement patterns of

these stocks. Comparisons of distinct fluke photos of individual humpback whales in South Pacific breeding grounds have suggested that these populations may be somewhat isolated, with limited movement between regions (Figure 1.6) (Garrigue *et al.* 2004; Garrigue *et al.* 2007). In a photo-identification comparison study across Oceania and Eastern Australia for the years 1999-2006 only a limited number of matches were made (Figure 1.6) despite the fact that the number of comparisons was large (East Australia catalogue $n = 1,292$, Oceania $n = 692$; Garrigue *et al.* 2007). French Polynesia matches included American Samoa ($n = 4$) and Tonga ($n = 7$). Genotype matches have also been found between breeding regions for the years 1991-2007. Specific to French Polynesia are matches to New Caledonia ($n = 1$), Cook Islands ($n = 1$), American Samoa ($n = 6$), Tonga ($n = 7$) and Colombia ($n = 1$). In addition, using genetic analyses, the population structure of these stocks was investigated (Olavarría *et al.* 2007) suggesting significant segregation for breeding stocks D (Western Australia), E1 (Eastern Australia), E2 (New Caledonia), E3 (Tonga), Fi (Cook Islands) and F2 (French Polynesia) (Figure 1.4) (IWC report 2006; Olavarría *et al.* 2007).

1.7 Molecular Markers- a technique to study whale populations

Many of the 'classical' methods of estimating abundance and other biological parameters depended on information from dead whales (Donovan 1989). Over the last decade, genetic analysis has been widely used to enhance our understanding of cetacean phylogeography and population dynamics (Lambertson *et al.* 1987). Biopsy sampling is used to collect skin samples of wild-ranging cetaceans in the field. These skin samples are extracted for DNA and amplified in order to sequence a specific region to use as a genetic marker (Sambrook *et al.* 1989; Baker *et al.* 1994). Genetic analyses and fluke photo-

identification allow less invasive ways to study populations of whales using non-lethal study techniques.

The use of genetic markers represents a viable alternative to traditional methods of individual and stock identification (Figure 1.7), because they are permanent and exist in all individuals (Palsboll *et al.* 1997). From nuclear and mitochondrial (mt) DNA analyses information can be obtained on sex, individual identification, migratory connections, population size and stock identity which are used to identify critical conservation needs for whales. MtDNA is a maternally inherited genetic marker powerful for describing population structure in maternal lineages, and sensitive to demographic changes in the population (Baker *et al.* 1993). An F_{ST} index is used to measure population differentiation of mtDNA. This statistic compares the genetic variability within and between populations using a quantitative value ranging from 0 to 1 based on the proportion of haplotypes found in each population (Wright 1969). A value of 0 indicates there is no differentiation and all haplotypes are shared in equal proportions between the populations. A value of 1 indicates the populations are completely differentiated sharing no haplotypes.

Specific to this project, mtDNA is used to clarify stock identity and infer migratory allocations of feeding areas to breeding grounds of humpback whales in the South Pacific. This work builds on the previous study of Olavarria *et al.* (2007) who identified 110 unique haplotypes by 71 variable sites based on a 470 base pair portion of the mitochondrial DNA control region of the southern hemisphere humpback whales from the eastern Indian and South Pacific Oceans. In addition, 392 samples have been added from the breeding grounds in Oceania and 142 samples from Areas IV, V, VI and I from the Antarctic feeding areas (Steel *et al.* unpublished).

1.8 Mixed Stock Analysis

The knowledge of migratory connections of humpback whales in the South Pacific is still limited. Molecular genetic markers have proven useful for inferring migration patterns by matching start and end point observations with population identity (Bowen *et al.* 2007). Since the Oceania breeding stocks are considered genetically differentiated (Overall F_{ST} value = 0.027; p-value < 0.001), genetic markers can be used to assess migratory allocation from whales in the feeding area to the breeding ground. Mixed-stock analysis, commonly used in salmon populations to allocate runs to natal breeding grounds (Grant *et al.* 1980), has the ability to apportion components among individuals in a mixture to one or several breeding populations based on the proportion of haplotype frequencies from each population.

1.9 Photo Identification – a method for individual identification of cetaceans

Natural markings have been successfully used to individually identify many cetacean species (Hammond *et al.* 1990). The ventral side of the humpback whale fluke in most cases provides a unique pattern and pigmentation allowing for individual identification (Katona *et al.* 1979). Despite the fact that scarring can sometimes alter the humpback fluke it is still a reliable method for matching to previous years (Perry *et al.* 1990). For several regions in the South Pacific and Antarctica humpback whale fluke photographs are taken each season and the best photograph of each individual whale is catalogued by the principal investigator of the region after annual within region reconciliation to be used for comparison with other regions.

1.10 Capture-Recapture Analysis

The Scientific Committee of the International Whaling Commission has agreed that the examination of marked whales for the purpose of capture-

recapture analysis can provide valuable information on questions of location of boundaries and rates of mixing across boundaries (Donovan 1989). Capture-recapture data originally collected using ultimately lethal *Discovery* tags (Dawbin 1964), are now obtained using non-lethal genetic markers (a skin biopsy taken of a whale) or photo-identification markers (a photograph taken of the unique ventral side of the humpback whale fluke). In both instances the original biopsy skin sample or fluke photograph acts as the first capture of the whale and subsequent biopsies or photographs act as the recapture. Once the data are collected over a period of capture occasions, or breeding seasons in the case of French Polynesia humpback whales, a capture probability is calculated as described in Otis *et al.* (1978).

Different programs can then be used to estimate the abundance of a population depending on biological parameters. Open population models allow for births and deaths, immigration and emigration (Jolly 1965) while closed population models allow for variations in individual capture probabilities in a population (White *et al.* 1982). Using these genetic and photo-identification techniques it is possible to assess the abundance, survival rates or movement patterns to monitor the recovery of populations (Hammond *et al.* 1990). This type of capture-recapture method using natural markings or skin samples has been successful for measuring abundance in whale sharks (Meekan *et al.* 2006) and several cetacean species including humpback whales and Hector's dolphins (Hammond *et al.* 1990; Calambokidis *et al.* 1990; Perry *et al.* 1990; Mizroch *et al.* 2004; Gormley *et al.* 2007). For this project photo-identification is used to estimate abundance of the French Polynesia humpback whales (Stock F2) to monitor the population as part of the IWC's Comprehensive Assessment of southern hemisphere humpback whales.

1.11 French Polynesia humpback whales breeding stock F

French Polynesia encompasses over 5,000,000 square km and lies almost directly north of the Antarctic Area VI (Figure 1.4). There is little known about migratory feeding ground destinations for French Polynesia. Though it is thought that these whales feed in Antarctic Area VI (IWC report 2006), no connections have yet been established.

Humpback whales have been observed in almost all island groups in French Polynesia, with the island of Rurutu in the Austral Islands and Moorea in the Society Islands appearing to be the most populated with humpback whales (Gannier 2004; Poole 2006). The field work for this study was carried out in Rurutu and Moorea generally within 500 meters of the coral reef. French Polynesia had been considered to be a transitory location, but the high percentage of young calves (~10%) and singers observed during the breeding season over the last decade suggest French Polynesia is now a breeding ground destination (Poole 2006). Analysis of mtDNA shows significant segregation within Breeding Stock F, suggesting French Polynesia is a discrete breeding ground (Olavarría *et al.* 2003, 2007). An abundance estimate using photo identification with a limited number of photos has shown that French Polynesia's humpback whale population remains low despite the moratorium on whaling (Baker *et al.* 2006).

1.12 Scope of thesis

This thesis examines the little known humpback whale breeding ground of French Polynesia. Chapter 2 considers migratory connections between breeding grounds in Oceania, including French Polynesia and feeding areas in the Antarctic Areas IV, V, VI and I. Chapter 3 provides information on the current population abundance of French Polynesia humpback whales. To explore

migratory connections using a different method chapter 4 considers a comparison using fluke identification photographs between French Polynesia and the Antarctic Peninsula to investigate if the Antarctic Peninsula may be a primary feeding area of the French Polynesia breeding ground.

This work provides new information on the French Polynesia breeding stock F2 and possible feeding area connections of South Pacific humpback whales. Since whaling activities in the feeding areas are to be a future consideration this data is imperative to the sustainability of South Pacific humpback whales.

Data collection for genetic analyses of humpback whales has been an ongoing collaborative effort in multiple areas throughout the South Pacific. I benefitted by using published and unpublished data from the South Pacific Whale Research Consortium (SPWRC), Instituto Antártico Chileno (INACH) and Centro de Estudios del Cuaternario (CEQUA). The SPWRC is widely recognized as the lead forum for exchange of scientific information and coordination of research throughout the South Pacific region. It is through this organization that I obtained genetic data from Colombia, French Polynesia, Cook Islands, Tonga, New Caledonia, Eastern Australia and Western Australia for the period of 1991-2007. The SPWRC also assembles fluke photographs of humpbacks taken by scientists in the field. These photographs are verified through a Quality Control process arranged by breeding region, and updated annually. The principal investigator is Dr. Rochelle Constantine. The French Polynesia photo identification catalogue has been compiled by Dr. Michael Poole of SPWRC since 1990. The Antarctic Peninsula catalogue was collected by Carlos Olavarria, Jorge Acevedo and Anelio Aguayo-Lobo. For complete information on co-authors see the section 'Contribution of Authors'.

LITERATURE CITED

- Baker, C.S., C. Garrigue, R. Constantine, B. Madon, M. Poole, N. Hauser, P. Clapham, Donoghue, K. Russell, T. O'Callahan, D. Paton, and D. Mattila. 2006. Abundance of humpback whales in Oceania (South Pacific), 1999 to 2004. Unpublished report SC/A06/HW51 for consideration by the inter-sessional workshop for the comprehensive assessment of Southern Hemisphere humpback whales, Hobart, Tasmania. 2006.
- Berta, Annalisa; Sumich, James L.; Kovacs, Kit M.; (2006) *Marine Mammals Evolutionary Biology*. Academic Press.
- Berzin, A. A. (2008) The truth about Soviet whaling. In Y. V. Ivashchenko, P. J. Clapham, and R. L. Brownell, Jr. (editors), *The truth about Soviet whaling: a memoir*, p. 1-59. [Transl. by Y. V. Ivashchenko]. *Mar. Fish. Rev* 70(2).
- Bromley, D.W. (2006) The dynamic between social systems and ocean ecosystems: Are there lessons from commercial whaling? In *Whales, Whaling and Ocean Ecosystems*. Ed. Estes, J. et al. University of California Press Berkley and Los Angeles, California; Chapter 28.
- Calambokidis J, J. C. Cubbage, G. H. Steiger. (1990) Population estimates of humpback whales in the Gulf of the Farallones, California. *Rep Int Whal Comm* 325-333.
- Chittleborough, R.G. (1965) Dynamics of two populations of humpback whales, *Megaptera novaeangliae* (Borowski). *Aust. J. Mar. Freshw. Res.* 16:33-128.
- Clapham, P.J. and Mead, J.G. (1999) *Megaptera novaeangliae*. *Mamm.Species* 604:1-9.
- Clapham PJ (2002) The humpback whale. Seasonal feeding and breeding in a baleen whale. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds) *Cetacean Societies Field studies of dolphins and whales*. The University of Chicago Press, Chicago and London, p 173-196.
- Clapham, P.J. and Baker, C.S. (2008) Modern Whaling. In: Perrin, W.F., Wursig, B. and Thewissen, J.G.M. (eds.) *Encyclopedia of Marine Mammals*, pp.1328-1332. Academic Press, San Diego.
- Clapham PJ, Mikhaliev YA, Franklin W, Paton DA, Baker CS, Ivanshchenko YV, Brownell Jr. RL (2009) Catches of Humpback Whales by the Soviet Union and Other Nations in the Southern Ocean, 1947-1973.
- Dawbin WH (1966) The seasonal migratory cycle of humpback whales. In: Norris KS (ed) *Whales, Dolphins, and Porpoises*. University of California Press, Berkeley and Los Angeles, p 145-171.

- Donovan GP (1989) Preface. In: Donovan GP (ed) The comprehensive assessment of whale stocks: the early years. Report of the International Whaling Commission (Special Issue 11). International Whaling Commission, Cambridge.
- Gales NJ, Kasuya T, Clapham PJ, Brownell Jr. RL (2005) Japan's whaling plan under scrutiny. Useful science or unregulated commercial whaling? *Nature* 435:883-884.
- Gannier A (2004) The large-scale distribution of humpback whales (*Megaptera novaeangliae*) wintering in French Polynesia during 1997-2002. *Aquatic Mammals* 30:227-236.
- Garrigue, C., Dodemont, R., Steel, D., Baker, C.S., (2004) Organismal and 'genetic' capture-recapture using microsatellite genotyping confirm low abundance and reproductive autonomy of humpback whales on the wintering grounds of New Caledonia. *Marine Ecology Progress Series* 274: 251-262.
- Gormley, AM and Dawson SM (2005) Capture-recapture estimates of Hector's dolphin abundance at Banks Peninsula, New Zealand. *Marine Mammal Science* 21: 204-216.
- Hauser N, Zerbini A, Geyer Y, Heide-Jørgensen MP, Clapham, PJ. In press. Migratory destination of a satellite-tagged humpback whale in the Cook Islands. *Marine Mammal Science*.
- Jackson JA, Patenaude NJ, Carroll EL, Baker CS (2008) How few whales were there after whaling? Inference from contemporary mtDNA diversity. *Molecular Ecology* 17:236-251.
- Jolly, G. M. (1965) Explicit estimates from capture-recapture data with both death and immigration | Stochastic model. *Biometrika* 52 225-247.
- Mackintosh, N.A. (1942) The southern stocks of whalebone whales. *Discov Rep* 22:197-300.
- Mackintosh, N.A. (1965) The stocks of whales. Fishing News Books Ltd. London.
- Olavarria C, Baker CS, Bannister JL, Brasseur M, Caballero S, Capella J, Clapham PJ, Dodemont R, Donaghue M, Jenner C, Jenner MM, Moro D, Florez-Gonzalez L, Hauser N, Oremus M, Paton DA, Poole MM, Rosenbaum H, Russell K (2007) Population structure of South Pacific humpback whales and the origin of the eastern Polynesian breeding grounds. *Marine Ecology Progress Series* 330:257-268.
- Mizroch SA, Herman LM, Straley JM, Glockner-Ferrari DA and 6 others (2004) Estimating the adult survival rate of central North Pacific humpback whales (*Megaptera novaeangliae*). *J Mammal* 85: 963-972.
- Otis D, K. P. Burnham, G. C. White (1978) Statistical inference for capture data on closed animal populations. *Wildlife Monographs* 62: 1-135.

- Paterson RA, Paterson P, Cato DH (2001) Status of humpback whales, *Megaptera novaeangliae*, in east Australia at the end of the 20th century. *Memoirs of the Queensland Museum* 47:579-586.
- Palsbøll PJ, Allen J, Bérubé M, Clapham PJ, Feddersen TP, Hammond PS, Hudson RR, Jørgensen H, Katona S, Larsen AH, Larsen F, Lien J, Mattila DK, Sigurjonsson J, Sears R, Smith T, Sponer R, Stevick P, Øien N (1997a) Genetic tagging of humpback whales. *Nature* 388:767-769.
- Perry, A., C. S. Baker and L. M. Herman. (1990) Population characteristics of individually identified humpback whales in the central and eastern North Pacific: a summary and critique. *Rep Int Whal Comm* pp 307-318.
- Poole MM (2006) An update on the occurrence of humpback whales in French Polynesia. *International Whaling Commission SC/A06/58*:6pp.
- Smith TD, Josephson E, and Reeves RR (2006) 19th Century Southern Hemisphere Humpback Whale Catches. Report SC/A06/HW53 to the Scientific Committee of the International Whaling Commission. Hobart Australia.
- Steel D, Garrigue C, Poole MM, Hauser N, Olavarria C, Florez-Gonzalez L, Constantine R, Caballero S, Thiele D, Paton DA, Clapham PJ, Donoghue M, Baker CS (2008) Migratory connections between humpback whales from South Pacific breeding grounds and Antarctic feeding areas. *International Whaling Commission SC/60/SH13*:6pp.
- Stevick PT, Aguayo-Lobo A, Allen J, Avila I, Capella J, Castro C, Chater K, Dalla Rosa L, MH E, Felix F, Florez-Gonzalez L, Freitas A, Haase B, Llano M, Lodi L, Munoz E, Olavarria C, Secchi ER, Scheidat M, Siciliana A (2004) Migrations of individually identified humpback whales between the Antarctic Peninsula and South America. *Journal of Cetacean Research and Management* 6:109-113.
- Townsend CH (1935) The distribution of certain whales as shown by logbook records of American whaleships. *Zoologica* 19:1-50.
- White, GC, D. R. Anderson, K. P. Burnham, D. L. Otis. (1982) Capture-recapture and removal methods for sampling closed populations. LA-8787-NERP Los Alamos National Laboratory, Los Alamos, New Mexico.
- Wright, S. (1969) *Evolution and the Genetics of Populations Volume 2: the Theory of Gene Frequencies*, pp 294–295. Univ. of Chicago Press, Chicago.

Table 1.1 Known total post-war catches (USSR and other nations) of humpback whales from Areas IV, V and VI, and migratory corridors directly north of these areas (e.g. Australia and New Zealand). There were an additional 7,177 Soviet catches that were not assignable to Area. (Source: Clapham *et al.* 2009).

Year/Source	Area IV	Area V	Area VI	Total
USSR	-	11,778	1,167	12,945
1959/60				
USSR	242	8,630	3,617	12,489
1960/61				
Other USSR, 1949-73	8,779	2,161	2,411	13,351
Australia/NZ 1949-62	18,180	15,577	-	33,757
Total	27,201	38,146	7,195	72,542

Figure 1.1. Morphological characteristics of humpback whales.
 Photo left: the unique markings of the ventral side of the humpback whale fluke.
 Photo top right: the tubercles can be seen on the dorsal side of the rostrum.
 Photo lower right: the long flipper unique to humpback whales.



Figure 1.2 Humpback whale southern hemisphere geographic distribution. Solid sections represent winter breeding stocks or populations including IWC stock designations A-G. Circles represent what are thought to be feeding Area designations. IWC Area designations I-VI are sections with a dashed line. Arrows represent migratory connections, dashed is inferred and solid is known connection (IWC SC-58-Rep 5 2006).

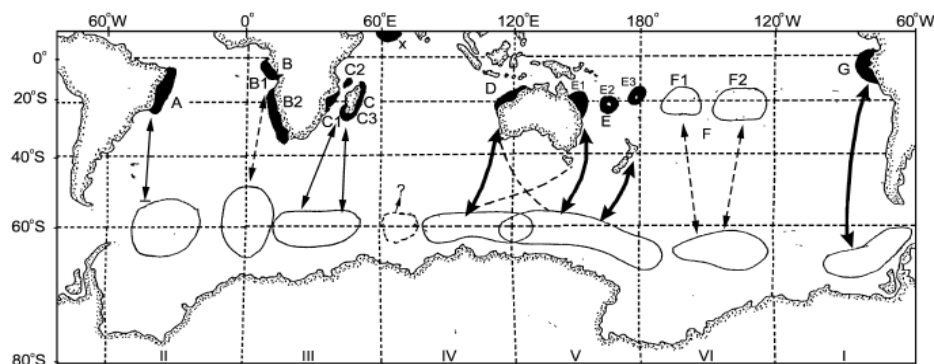


Figure 1.3. Antarctic management areas as currently designated by the IWC.

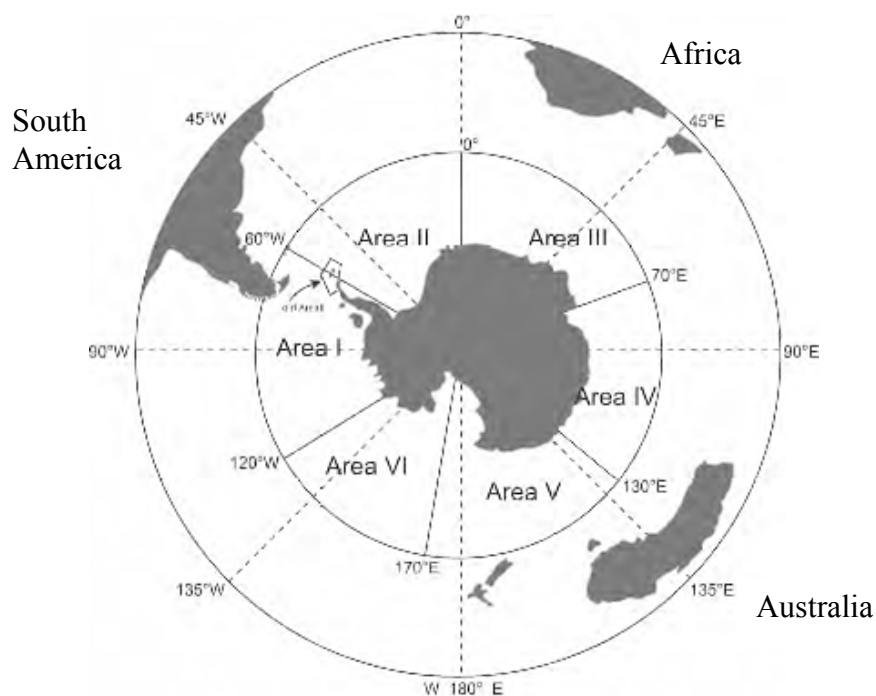


Figure 1.4 South Pacific humpback whale breeding stocks and feeding areas. IWC breeding stock designation are shown as ovals representing stocks D, E, F, and G. Smaller ovals represent the further stock segregation found after mtDNA analysis (Olavarría *et al.* 2007).

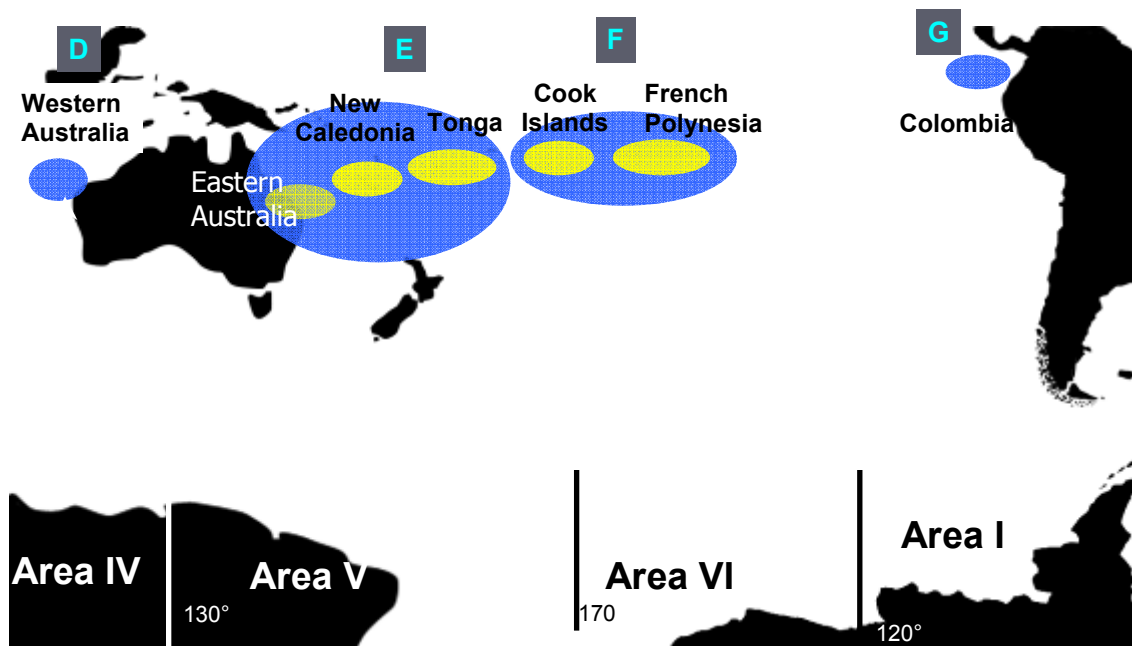


Figure 1.5. Population trajectories for Oceania as compared to east Australia showing changes in population abundance (N) over time. Median trajectory (solid line) and 95% posterior probability intervals (dashed lines) are shown in bold for Oceania and East Australia (Source: Jackson *et al.* 2008).

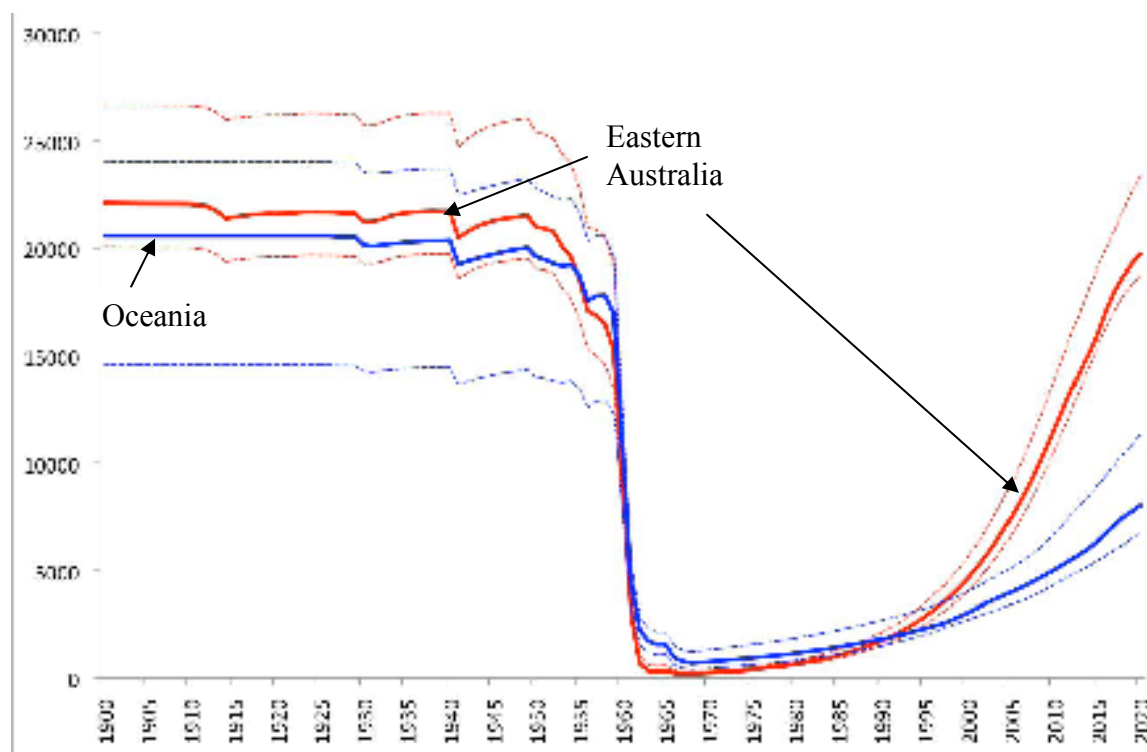


Figure 1.6 - Summary of Photo ID matches 1999-2006 between catalogues from Eastern Australia (n = 1242) and Oceania (n = 692). Specific to French Polynesia there are only matches between Tonga and French Polynesia and American Samoa and French Polynesia.

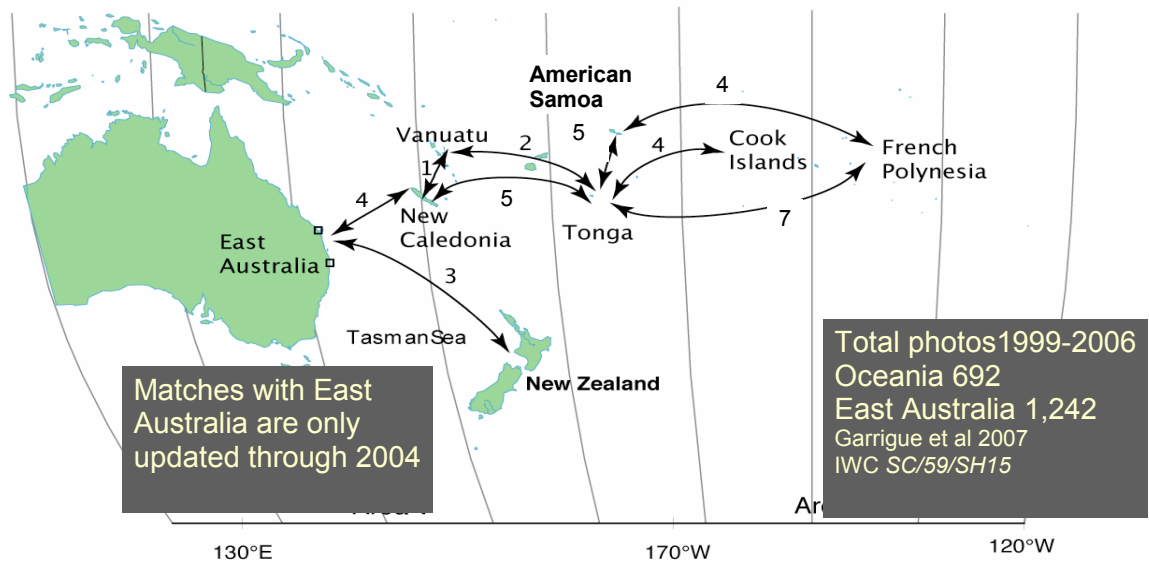
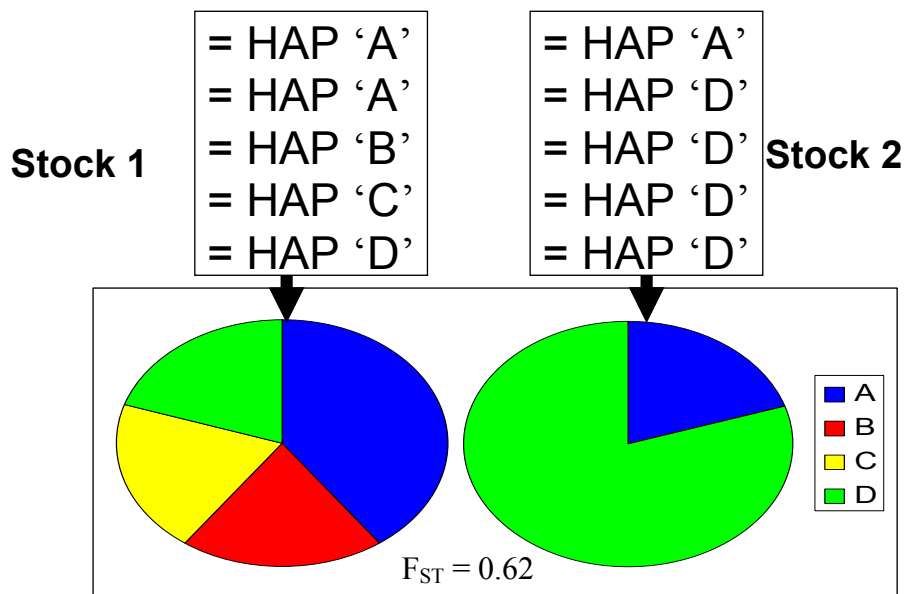
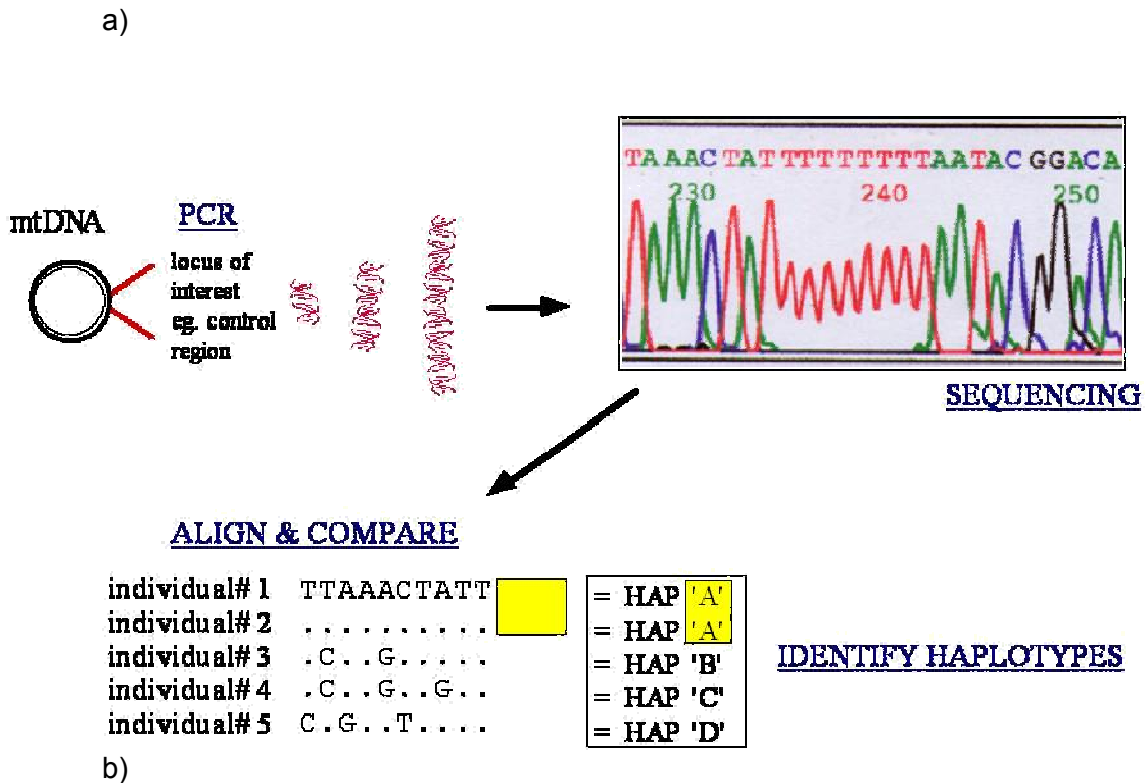


Figure 7a – The use of mitochondrial DNA in cetacean research. MtDNA is extracted from skin samples, and copied many times in a polymerase chain reaction (PCR). The copies are then sequenced and aligned in order to compare to other individuals. Unique sequences are assigned a haplotype. 7b - These haplotypes are then compared between populations to determine how closely related stocks are quantitatively (the F_{ST} diversity index) and qualitatively (pie charts).



Chapter 2 - Using Mixed-Stock Analysis of Humpback Whales (*Megaptera novaeangliae*) to estimate migratory allocation from Antarctic Feeding Areas to South Pacific Breeding Grounds

R. ALBERTSON-GIBB¹, C. OLAVARRÍA², D. STEEL¹, L. FLÓREZ-GONZÁLEZ⁶, C. GARRIGUE³, N. HAUSER⁴, M. POOLE⁵, M. ANDERSON⁸, M. BRASSEUR¹⁰, J. BANNISTER⁹, J. JACKSON¹, C. ANTOLIK¹, and C. S. BAKER^{1,7}

¹ Marine Mammal Institute and the Department of Fisheries and Wildlife, Oregon State University, 2030 SE Marine Science Dr, Newport Oregon 97365 USA

² Proyecto INACH 163 Ecología de Cetáceos Antárticos. Instituto Antártico Chileno, Punta Arenas, Chile

³ Opération Cétacés BP 12827 98802 Nouméa, New Caledonia

⁴ Cook Islands Whale Research Takuvaine Valley PO Box 3069, Avarua Rarotonga, The Cook Islands

⁵ Marine Mammal Research Program, BP 698 98728 Maharepa, Moorea, French Polynesia

⁶ Fundacion Yubarta, Carrera 24F Oeste No. 3-110, Tejares de San Fernando, Cali, Colombia

⁷ School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

⁸ Southern Cross University Whale Research Centre Military Road East, Lismore, Australia

⁹ Western Australian Museum, Francis Street, Perth, Western Australia 6000, Australia

¹⁰ Edith Cowan University School of Natural Sciences 270 Joondalup Drive Joondalup Western Australia

ABSTRACT

Very few migratory connections have been documented between humpback whale (*Megaptera novaeangliae*) breeding grounds and feeding areas in the South Pacific Ocean. Understanding these migratory connections is crucial to management strategies especially for the allocation of historical Antarctic catches in population dynamic models used to assess the current recovery of these small, isolated breeding stocks. Here we use mixed-stock analysis of mtDNA haplotypes as described in Olavarría *et al.* (2007) to apportion samples from four Antarctic feeding areas (IWC Areas IV, V, VI* and I*) (n = 142) to seven breeding grounds, including: Western Australia; Eastern Australia; New Caledonia; Tonga; Cook Islands; French Polynesia; and Colombia (n = 1,504). Assuming that the breeding grounds represent ‘source stocks’ and that each feeding area represents ‘mixed-stocks’, results showed Area IV apportioned primarily to

Western Australia (71.6%, SE 1.1%), Area VI* apportioned primarily to Tonga (78.4%, SE 24.5%), and Area I* whales apportioned primarily to Colombia (76.5%, SE 8.1%). Although limited by small sample size, Area V apportionment was close to evenly split between New Caledonia (44.4%, SE 28.4%) and Eastern Australia (51.0%, SE 26.4%). These results agree with previous *Discovery* marking, photo-identification and genetic studies of individuals suggesting that mixed-stock analysis could prove to be a useful tool for modeling the apportionment of feeding areas to breeding stocks for the purpose of assessing recovery and evaluating the impact of any future Antarctic catches.

KEY WORDS: GENETICS; HUMPBAC WHALE; MIGRATION; SOUTHERN HEMISPHERE; BREEDING GROUNDS; FEEDING AREAS; MOVEMENTS

2.1 INTRODUCTION

Humpback whales in the Southern Hemisphere undertake the annual migration from tropical breeding grounds to Antarctic feeding areas (Mackintosh 1942). These breeding stocks experienced severe population declines due to commercial whaling in their associated Antarctic feeding areas that occurred legally and illegally until the mid-1960's (Clapham 2009). The number of humpback whales killed in the Southern Hemisphere was more than 200,000 in the 20th century (Clapham & Baker 2008). The small breeding regions in Oceania have been slow to recover from this hunting. In the South Pacific Ocean very few connections have been documented for humpback whale migratory connections. Describing connections between their breeding grounds and feeding areas is crucial for management strategies, especially for historical catches and modeling of current population dynamics (e.g., Jackson *et al.* 2008).

The International Whaling Commission (IWC) has divided the tropical breeding grounds into several stocks for management purposes based on

distribution and *Discovery* tag returns, and divided Antarctica into feeding Areas I-VI based on summer catch distributions in the feeding season (Mackintosh 1942; Mackintosh 1965; IWC 2006). In the South Pacific and eastern Indian Ocean, these breeding regions were assigned stock designation D, E, F and G (Figure 2.1). Severe reduction in most Southern Hemisphere whale populations prompted the IWC to offer protection for humpback whales from whaling in 1966, and a moratorium was put into place in 1986. Recovery of stocks has been variable, and some stocks remain small despite decades of protection (Clapham & Baker 2008). The Eastern Australia humpbacks appear to have recovered more quickly (Paterson *et al.* 2006) than humpbacks in most of Oceania (Baker *et al.* 2006).

Genetic markers have been informative for estimating population differentiation and designation of subpopulation status. Recent analyses of mtDNA suggest that the sub-stocks within E and F are genetically differentiated, separating New Caledonia (Stock E2) and Tonga (E3) from Eastern Australia (Stock E1); and Cook Islands (Stock F1) from French Polynesia (Stock F2) (Garrigue *et al.* 2006; Olavarría *et al.* 2007). This sub-stock designation is summarized in an IWC Report (2006). Comparison of photo-identification catalogues between breeding sub-stocks E1, E2, E3, F1 and F2 has also confirmed that these populations are somewhat isolated, with limited movement between regions (Garrigue *et al.* 2004; 2008). Although the breeding stocks have shown significant genetic differentiation of mtDNA there still remains uncertainty in the feeding areas about genetic differentiation (Loo *et al.* 2006).

Despite the known history of humpback whales in the South Pacific, very few direct connections between breeding stocks and their Antarctic feeding areas have been documented. Limited migratory information comes from early

Discovery tag records (Dawbin 1966), photo-identification matches (Stone *et al.* 2000; Franklin *et al.* 2008) and recent genotype matches (Steel *et al.* 2008). In the absence of direct observations of migratory pathways, molecular genetic markers have proven useful for inferring migration patterns by matching start and end point observations with population identity (Bowen *et al.* 2007). Mixed-stock analysis (MSA), originally developed for salmon management programs (Grant *et al.* 1980), provides an estimate of the most likely proportion of ‘source populations’ represented in a ‘mixed population’ sample using the frequencies of genetic markers (Bass *et al.* 2004). In fisheries, MSA is used to estimate what proportion of a population in a mixture came from each of a number of most likely source populations (Manel *et al.* 2005).

We used MSA with mtDNA haplotypes to examine what proportion of a humpback whale population in an Antarctic feeding mixture came from each of the breeding stock source populations. MtDNA haplotypes were derived from skin biopsy samples from seven breeding grounds (IWC breeding stocks D, E1, E2, E3, F1, F2 and G) and four IWC Antarctic feeding Areas (Areas IV, V, VI* and I*). This dataset revises and extends that reported previously in Olavarria *et al.* (2007), removing samples identified as replicates by genotyping (Steel *et al.* 2008) and including 392 previously unanalyzed samples from Oceania as well as 142 individual whales from four Antarctic Areas. An Analysis of Molecular Variance (AMOVA) of this dataset first confirmed differentiation between breeding grounds and between the four feeding areas. This was followed by mixed-stock analysis (MSA) with a Bayesian baseline to estimate the migratory apportionment of each feeding area to the seven breeding grounds. The Bayesian approach allows for the uncertainty of rare haplotypes that may not be detected in source population samples (Pella and Masuda 2001).

2.2 METHODS

2.2.1 Field collection

A total of $n = 1,713$ samples were collected from live whales in the seven breeding grounds (Table 2.1). In addition to the samples described in Olavarria *et al.* (2007) ($n = 1,112$), biopsy and sloughed skin tissue samples ($n = 392$) were collected from humpback whales on breeding grounds of the South Pacific during the Austral winters of 2003 through 2007. Western Australia samples (biopsy only) were collected from North West Cape in 2002 as described in (Brasseur 2007) with additional samples collected in 1990, 1993 and 1994 (Baker *et al.* 1994; 1998). Eastern Australia samples were collected from humpback whales off Byron Bay and Ballena (sloughed skin only) as described in Olavarria *et al.* (2006). Oceania samples were collected primarily by members of the South Pacific Whale Research Consortium during synoptic surveys from 1999-2007 but also include smaller numbers of samples collected during surveys of some regions dating back to 1991. Samples collected from the Colombian breeding grounds were collected by members of Project Yubarta from 1991 to 1998 (Flórez-González 1991; Baker *et al.* 1998; Caballero *et al.* 2001; Steel *et al.* 2008). Sampling on breeding grounds was carried out aboard dedicated small boat surveys. Biopsy samples were collected using a stainless steel biopsy dart deployed from a crossbow (Lambertsen 1987) or a modified veterinary capture rifle (Krutzen *et al.* 2002).

In the feeding areas, biopsy samples ($n = 214$) were collected from living whales during the Austral summers of 1989 to 2005, during surveys by the International Decade of Cetacean Research and Southern Ocean Whale and

Ecosystem Research Cruise (IDCR/SOWER) under supervision of the IWC (Report 2006), and during more localized surveys of the Antarctic Peninsula by the Chilean Antarctic Institute (INACH).

2.2.2 *MtDNA amplification and sequencing*

As described in detail by Olavarria *et al.* (2007) genomic DNA was extracted from tissue samples using a standard phenol/chloroform extraction protocol (Sambrook *et al.* 1989) modified for small skin samples by Baker *et al.* (1994). An approximately 800 base-pair (bp) fragment of the 5'-end of mtDNA control region (i.e. D-loop) was amplified via the Polymerase Chain Reaction (PCR) using the primers, light-strand tPro-whale Dlp1.5 and heavy-strand Dlp8G as reported in Garrigue *et al.* (2004). Amplification and temperature profiles were followed as documented in Olavarria *et al.* (2007). Unincorporated primers and nucleotides were removed from PCR products using exonuclease (Exo I) and shrimp alkaline phosphatase (SAP) and sequenced on an ABI3730xl DNA sequencer (Applied Biosystems) using the primer M13Dlp-1.5.

2.2.3 *Data Analyses*

Sequences were aligned and edited using SEQUENCHER (version 4.1.2, Gene Codes Co.) and checked visually by comparison to other chromatographs. Unique haplotypes were defined by 71 variable sites resolved from the 470 bp consensus region as discussed in Olavarría *et al.* (2007). The potential for replicate samples of individual whales was considered for each regional sample set. Replicates were removed where microsatellite genotyping allowed for individual identification (Steel *et al.* 2008). After sequencing corrections five of

the original 115 haplotypes were removed from Olavarria *et al.* (2007) (Final n = 110).

A pairwise comparison at the haplotype level was performed using the program ARLEQUIN (version 3.1, Schneider *et al.* 2000) to compare the degree of genetic diversity between breeding and feeding regions. An Analysis of Molecular Variance (AMOVA) was performed in using 10,000 permutations to measure the differentiation between breeding stocks at the haplotype level.

MSA was conducted using the Statistical Program for Analyzing Mixtures (SPAM; version 3.7b; Alaska Department of Fish and Game (ADF&G 2003)) for haplotype data with 10,000 iterations and 1,000 bootstrap resamples. For the future purposes of allocating historical catches to breeding stocks, we assumed that the breeding ground samples represented the 'source stocks' in the MSA program and the feeding area samples represented the 'mixed-stocks'. In this framework, each feeding area was analyzed separately, and component estimates were apportioned to the seven breeding grounds.

Given the large number of haplotypes (Olavarria *et al.* 2007) a Bayesian method was implemented in the estimation mode of SPAM. The Bayesian approach allows for the uncertainty of rare haplotypes that are actually present in a breeding ground, but not detected in a small sample (Pella & Masuda 2001). Thus the Bayesian method has the potential to correct for small samples or rare haplotypes better than the standard Maximum Likelihood methods (Luke *et al.* 2004). Previous studies (Templin *et al.* 2003; Pella & Masuda 2002) emphasized that Bayesian modeling of baseline frequencies is an acceptable way to account for any negative bias in analyses caused by sparse data.

The simulation mode in SPAM was used to assess whether differences in haplotype frequencies among breeding regions were large enough to estimate

the origins of feeding areas. The simulation mode assigns one breeding region 100% apportionment as a possible mixture scenario to evaluate performance for a given source stock or breeding region (ADF&G 2003), and then reports what percentage could actually be detected by the program. These simulations work similarly to a jack-knife estimate evaluating how well the program can assign haplotypes correctly back to their respective breeding ground. Typically results of 90% or better have been used in fisheries studies to indicate sufficient power among data to differentiate between each of the source stocks and to determine relative mixture proportions reasonably accurately (Templin *et al.* 2003).

2.3 RESULTS

2.3.1 *Revised Antarctic Areas*

After reviewing sample locations of Antarctic samples, we modified the boundaries of Area VI and Area I to reflect apparent geographic groupings of samples (Figure 2.2). For Area VI*, we included three samples from the eastern edge of Area VI and included seven samples collected in the western edge of Area I (n = 27). For Area I*, we excluded one additional sample in the central region and included all samples from the Antarctic Peninsula (n = 68). The four samples from the western boundary of Area V and the four samples from the eastern boundary of Area V were not considered sufficient for statistical analysis, but are included here for an initial assessment of Area V. Although we did not attempt to adjust for differences in sample size due to very limited numbers from the Antarctic region, the number of haplotypes was similar in each of the four areas with the exception of findings for Area V (Table 2.1).

2.3.2 *Population Diversity and Differentiation*

After removal of replicates within regions, a total of $n = 1,713$ samples representing 1,504 individual humpback whales from 7 discrete breeding regions and $n = 214$ samples representing 142 individuals from four feeding areas were available to determine genetic diversity and differentiation. Once this was established a MSA program was implemented to apportion Antarctic feeding areas to component estimates for South Pacific breeding stocks (Table 2.2). Of the 110 haplotypes observed in this study, only four occurred in all seven of the breeding grounds, and 41 occurred in only one breeding ground. The number of haplotypes was greatest for New Caledonia (55), as reported previously in Baker *et al.* (1998) and Olavarría *et al.* (2003). However, based on increased samples size, this study found Colombia to have the lowest number of haplotypes (25) (Table 2.1) contrary to previous studies sighting French Polynesia having the lowest. Within the feeding areas, the number of haplotypes was similar, ranging from 18 in Area VI to 27 in Area IV; the exception being Area V (seven haplotypes represented) where only eight samples were analyzed.

Differentiation between breeding grounds and feeding areas was quantified by an AMOVA. The proposed subdivisions of IWC breeding stock E into E1, E2, and E3, as described previously, and all pair-wise comparisons were supported by significant overall differences ($F_{ST} = 0.027$; $P < 0.001$). For breeding grounds, pairwise F_{ST} values (Table 2.2) illustrated a greater difference between Colombia and the Oceania breeding grounds than between Western Australia and Oceania as shown in Olavarría *et al.* (2007). For feeding areas all pair-wise comparisons were supported by significant overall differences ($F_{ST} = 0.023$; $P < 0.001$). For feeding areas all pair-wise F_{ST} values (Table 2.2) illustrated the greatest difference between Area I* and Area VI*. Pairwise comparisons of feeding areas to breeding grounds showed significant F_{ST} values

for all but three cases: Area IV to Western Australia, Area VI* to Tonga, and Area I* to Colombia. The exception was Area V which was only significant with French Polynesia and Colombia (Table 2.2).

2.3.3 Migratory Apportionments

Apportionments to breeding grounds from feeding areas were inferred from the MSA program. Area IV was apportioned primarily to Western Australia (71.6% SE 10.8%) with a small percentage to Tonga (28.8% SE 13.4%). Although sample size was small, there was an almost equal split of Area V between New Caledonia (44.1% SE 28.3%) and Eastern Australia (51.1% SE 26.5%) and a small contribution to Western Australia (4.6% SE 9.0%). Area VI* was apportioned primarily to Tonga (81.4% SE 22.5%), with a smaller percentage apportioned to the Cook Islands (5.0% SE 15.9%). A large percentage of Area I* was apportioned to Colombia (88.3% SE 7.5%) with a smaller percentage (8.8% SE 7.4%) to the Cook Islands. French Polynesia had very low apportionments from any of these areas (< 3%). The mixed-stock simulation in the MSA program indicated that the population of each breeding ground could be correctly re-assigned with at least 83% accuracy, with the exception of the Cook Islands (73%) (Table 2.3).

2.4 DISCUSSION

The management of whale stocks becomes more effective if it can be determined how stocks assemble on the breeding grounds especially if less abundant stocks can be protected in both breeding and feeding areas. Mixed-stock analysis provides insight into this organization provided that different breeding grounds are genetically differentiated. The mixed-stock analysis strengthened results from previous photo-identification and genotype studies

(Table 2.3, Figure 2.1) by providing general population apportionments instead of individual connections. This analysis has shown that the prevailing trends identified here are that each feeding area is apportioned to one primary breeding region. In addition, the population trends revealed here are consistent with previous analyses investigating individual matches (Steel *et al.* 2008).

2.4.1 Area IV

Historically Western Australia (breeding stock D) was associated with Antarctic Area IV stock for management purposes (Mackintosh, 1942). Here using mtDNA data and MSA, the larger apportionment of Area IV to Western Australia supports these previous findings linking individuals using historical whaling data (*Discovery* tags) and more recent photo-identification (Chittleborough 1965; Dawbin 1964; Gill & Burton *et al.* 1995, Franklin 2008). However, the smaller apportionment of Area IV to Tonga is puzzling. Although Eastern Australia has closer proximity to Area IV than Tonga, no significant Eastern Australia apportionment was made. This could possibly be explained by the AMOVA results and recent photo-identification matchings. Olavarria *et al.* (2007) found low level haplotype frequency matches between Western Australia and breeding stock E (Tonga and New Caledonia) which they used to predict possible movements between Western Australia and Stock E despite the large geographic distance between them. Photo-identification studies comparing breeding stocks D and E have shown Tonga to be a possible stopover for other breeding grounds to the west (Eastern Australia, Stock E1 and New Caledonia, Stock E2) and to the east (Cook Islands, Stock F1) (SPWRC report 2009). Therefore, the small apportionment of Area IV to Tonga suggests Tonga may be a stopover for some whales headed to other areas in Stock E and these animals may be using Area IV feeding area. In addition, there was a *Discovery* tag found

in a whale from Tonga on the border of Area IV/V (Dawbin 1966), suggesting some of these whales may feed in the eastern portion of Area IV. Another possibility is that the smaller apportionments indicated by SPAM may have higher degrees of uncertainty as shown by the higher standard errors associated with these estimates.

2.4.2 Area V

The illegal Soviet Whaling from 1959/60-1961/62 (Clapham *et al.* 2009; Berzin 2008) that targeted Area V so intensely demonstrates why Area V is arguably the most important area for apportionment of historical catches. However, sample size for this region was too small to provide significant statistical power. Despite this statistical limitation these samples provide intriguing insight into possible migratory destinations. Our results show almost equal apportionment to Eastern Australia and New Caledonia. This strengthens previous individual connection studies including *Discovery* tags, photo identification and genotype matches (Dawbin 1964; Franklin *et al.* 2006; Olavarría *et al.* 2006) linking Eastern Australia to Antarctic Area V (Franklin *et al.* 2008), and New Caledonia to Area V (Steel *et al.* 2008). The possible evidence of migration from New Caledonia to Area V, the location of Japan's proposed hunting grounds, suggests that whales from small breeding stocks in the South Pacific could be at risk from hunting events in Area V. This reiterates the vital need for additional Antarctic samples from these areas to help clarify migration destinations.

2.4.3 Area VI*

A close connection between Area VI* and Tonga is indicated by the lack of significance in the AMOVA, and the large apportionment of Area VI* to Tonga in the MSA analysis. These results agree with recent genotype matching and

limited *Discovery* tags, which have provided evidence of connections between the two regions (Dawbin *et al.* 1964; Steel *et al.* 2008). There was a 5.0% apportionment from Area VI* to the Cook Islands which has also been proposed as a component of the Area VI stock (Hauser *et al.* 2000). Recently a humpback whale tagged in the Cook Islands in September of 2006 was located on the border of Area VI and Area I in December of 2006. This implies that at least some humpbacks wintering in the Cook Islands feed in Area VI with perhaps some interchange between Area VI and Area I (Hauser *et al.* in press), or what is referred to here as Area VI*. In addition, the whale was recorded heading southeast from the Cook Islands suggesting areas to the east of the Cook Islands, possibly French Polynesia, may host some whales that feed primarily in the western part of Area I (Hauser *et al.* in press).

Surprisingly, Area VI* showed no apportionment to French Polynesia (<3.0%) despite the geographic proximity of these seasonal habitats and the large sample size of French Polynesia. This suggests the whales in French Polynesia may be traveling to an as of yet unsampled component of Area VI or Area I, or that breeding stocks like Tonga and Colombia, the main apportionment from Area VI* and I* respectively, have sufficiently larger proportions of haplotype frequencies to these feeding areas masking what would be otherwise a small apportion to French Polynesia. Despite the fact that French Polynesia had very low apportionments from Area VI*, these recent findings reveal an interesting combination of results that should be explored further.

2.4.4 Area I*

The large apportionment from Area I* to Colombia confirms a strong association between Colombia and the Antarctic Peninsula. These differences support earlier conclusions that Antarctic Peninsula and Colombia are somewhat

isolated from Oceania. Genetic markers and naturally marked individuals have confirmed that there is a connection between Colombia and Area I around the Antarctic Peninsula (Olavarria *et al.* 2007, Stevick *et al.* 2006, Caballero *et al.* 2001, Stone *et al.* 1990). Our results are in agreement with previous investigators (Olavarria *et al.* 2007; Stone *et al.* 1990), who have suggested that many humpbacks from the Antarctic Peninsula migrate along the western coast of South America to Colombia. The AMOVA here and in Olavarria *et al.* (2007) suggest these regions are somewhat isolated from Oceania and Antarctic Areas V and VI as shown in the higher degree of differentiation in the pair-wise F_{ST} values (Table 2.2).

2.4.5 Implications of the Study

Mixed-Stock Analysis has shown considerable promise as a method for assisting the proportional component estimates of feeding grounds to breeding stocks (Figure 2.1). Sample sizes from most breeding grounds were considerably larger ($n > 100$) and more representative of the known distribution of humpbacks in the South Pacific. Unfortunately, sample sizes for the feeding areas were relatively small resulting in large standard errors for some apportionments (Table 2.3) implying results for the smaller apportionments should be approached with caution. A more concerted and systematic sampling of feeding areas, especially in Area V, is needed to complement the coordinated sampling of breeding grounds in Oceania. This analysis also provided some unexpected results, including the Area IV apportionment to Tonga (28.0%), Area I* apportionment to Cook Islands (8.8%) and the absence of any apportionment of Area VI* to French Polynesia.

South Pacific humpback whale data has three primary shortfalls: 1. a large number of different haplotypes, 2. variation in population size 3. generally

sparse data. Although Maximum Likelihood methods have previously been used for data with these limitations in MSA, contributions from abundant stocks are underestimated and those from less common or even absent stocks are overestimated (Pella & Masuda 2001; Bolker *et al.* 2003). Previous studies (Templin *et al.* 2003; Pella & Masuda 2002) emphasized that Bayesian modeling of baseline frequencies is an acceptable way to account for any negative bias in analyses caused by sparse data.

Other limitations of this study include the exclusion of lesser South Pacific breeding grounds where sample sizes were too small ($n < 5$) for consideration in this analysis, (American Samoa, Vanuata and Fiji) and the impact their absence might have on apportionments from feeding areas. Despite these limitations, MSA provided the first population analysis of South Pacific humpback whales providing additional inference to associate feeding areas and breeding grounds.

2.4.6 The future of MSA for migratory connections

Although the simulation mode in the MSA program is intended to assess power among specific data more concise methods are beginning to be developed. These show that 100% simulation algorithms of current MSA programs tend to have a positive bias in the simulation results overstating the power of assignment (Anderson *et al.* 2008). This bias is thought to be exacerbated when F_{ST} values indicate that relationships are relatively close among breeding populations as shown here. This is something that should be considered in future MSA studies.

These results help determine the utilization of the feeding areas by different breeding stocks, and present a means to assess the direction of future research. The use of microsatellites in MSA has been very successful in salmon and turtle populations. However, with the use of assignment tests a different

question is addressed. The population is not examined. Instead, individual genotypes are investigated. Expected genotypic probabilities are calculated in the MSA program from samples from each potential source population, and genotypes are assigned to the population in which that genotype is most likely to occur (Manel *et al.* 2005). Mixed-stock analysis using microsatellites possibly could provide fine-scale figures for management (see Appendix A) and may become a preferred method of stock identification as it has in fisheries management (Habricht *et al.* 2007) especially if additional Antarctic samples from Areas V and VI became available.

ACKNOWLEDGEMENTS

Sample collection in Oceania was supported by the International Fund for Animal Welfare (IFAW). The collection of samples around the Antarctic Peninsula was supported primarily by the Instituto Antártico Chileno (INACH). Funding for laboratory analysis was provided by the Regional Natural Heritage Program, Department of Environment and Heritage, Government of Australia, and the endowment of the Marine Mammal Institute, Oregon State University. We thank the South Pacific Whale Research Consortium for access to the data, and Thomas Follet for GIS assistance with the Antarctic Map.

LITERATURE CITED

- Alaska Department of Fish and Game. (2003). SPAM Version 3.7: Statistics Program for Analyzing Mixtures. Alaska Department of Fish and Game, Commercial Fisheries Division, Gene Conservation Lab.
- Anderson, E.C., Waples, R.S., and Kalinowski, S.T. (2008). An improved method for predicting the accuracy of genetic stock identification. *Can. J. Fish. Aquat. Sci.* 65: 1475-1486.
- Baker, C.S., Perry, A., Bannister, J.L., Weinrich, M.T. Abernethy, R.B., Calambokidis, J., Lien, J., Lambertsen, R.H., Urbán-Ramírez, J., Vásquez, O., Clapham, P.J., Alling, A., O'Brien, S.J., Palumbi, S.R. (1993) Abundant mitochondrial DNA variation and worldwide population structure in humpback whales. *Proc Natl Acad Sci USA* 90:8239–8243.
- Baker, C.S., Slade, R.W., Bannister, J.L., Abernethy, R.B., and 7 others. (1994) Hierarchical structure of mitochondrial DNA gene flow among humpback whales *Megaptera novaeangliae*, world-wide. *Mol Ecol* 3:313–327.

- Baker, C.S., Flórez-González, L., Abernethy, B., Rosenbaum, H.C., Slade, R.W., Capella, J., Bannister, J.L. (1998) Mitochondrial DNA variation and maternal gene flow among humpback whales of the southern hemisphere. *Mar Mamm Sci* 14:721–737.
- Baker, C.S., Garrigue, C., Constantine, R., Madon, B., Poole, M., Hauser, N., Clapham, P., Donoghue, M., Russell, K., O'Callahan, T., Paton, D., and Mattila, D. (2006) Abundance of humpback whales in Oceania (South Pacific), 1999-2004. Paper SC/A06/HW51 presented to the IWC Scientific Committee. May 2006. 10pp.
- Banks, M.A. and W. Eichert. (2000) WHICHRUNBayes (Version 4.2) A computer program for population assignment of individuals based on multilocus genotype data. *Journal of Heredity*. 91:87-89
- Bass, A.L., Epperly, S.P., & Braun-McNeill, J. (2004) Multi-year analysis of stock composition of a loggerhead turtle (*Caretta caretta*) foraging habitat using maximum likelihood and Bayesian methods. *Conservation Genetics* 5: 783-796.
- Bolker, B., Okuyama, T., Bjørndal, K., Bolten, A. (2003) Sea Turtle Stock Estimation Using Genetic Markers: Accounting for sampling error of rare genotypes. *Ecological Applications* 13(3):763-775.
- Bowen, B.W., Grant, W.S., Hills-Starr, Z., Shaver, D.J., Bjørndal, A., Bolten, A.B., Bass, A.L. (2007) Mixed-stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricate*) in the Caribbean Sea. *Molecular Ecology*. 16: 49-60.
- Brasseur MM (2007) Population structure and management of the humpback whale (*Megaptera novaeangliae*) in Western Australia: investigation of the genetic status and structure of Stock D/Antarctic Area group IV. Edith Cowan University
- Chittleborough, R.G. (1965) Dynamics of two populations of humpback whales, *Megaptera novaeangliae* (Borowski). *Aust. J. Mar. Freshw. Res.* 16:33-128.
- Clapham, P.J. and Baker, C.S. (2008) Modern Whaling. In: Perrin, W.F., Wursig, B. and Thewissen, J.G.M. (eds.) *Encyclopedia of Marine Mammals*, pp.1328-1332. Academic Press, San Diego.
- Clapham, P.J. and Mead, J.G. (1999) *Megaptera novaeangliae*. *Mamm. Species* 604:1-9.
- Clapham P.J. and Zerbini A. (2006) Is social aggregation driving high rates of increase in some Southern Hemisphere humpback whale populations? Paper SC/58/SH3 presented to the IWC Scientific Committee, May 2006 (unpublished). 12pp.

- Dawbin, W.H. (1964) Movements of humpback whales marked in the southwest Pacific Ocean 1952 to 1962. *Norsk Hvalf. Tid.* 53:68-78.
- Flórez-González L (1991) Humpback whales *Megaptera novaeangliae* in the Gorgona island, Colombian Pacific breeding waters: population and pod characteristics. *Memoirs of the Queensland Museum* 30:291-295.
- Franklin, W., Franklin, T., Brooks, L., Gibbs, N., Childerhouse, S., Smith, F., Burns, D., Paton, D., Garrigue, C., Constantine, R., Poole, M.M., Hauser, N., Donoghue, M., Russell, K., Mattila, D., Robbins, J., Oosterman, A., Leaper, R., Baker, S., and P. Clapham. (2008) Migratory movements of humpback whales (*Megaptera novaeangliae*) between Eastern Australia and the Balleny Islands, Antarctica, confirmed by photo-identification. Paper SC/60/SH2 presented to the IWC Scientific Committee, June 2008 (unpublished). 12pp.
- Garrigue, C., Aguayo, A., Baker, C.S., Caballero, S., Clapham, P., Constantine, R., Denkinger, J., Donoghue, M., Flórez-González, L., Greaves, J., Hauser, N., Olavarria, C., Pairoa, C., Peckham, H. and Poole, M. (2000) Migratory movements of humpback whales in Oceania, South Pacific. Paper SC/52/IA6 presented to the IWC Scientific Committee, June 2000, (unpublished).
- Garrigue, C., Dodemont, R., Steel, D., Baker, C.S., (2004) Organismal and 'gametic' capture-recapture using microsatellite genotyping confirm low abundance and reproductive autonomy of humpback whales on the wintering grounds of New Caledonia. *Marine Ecology Progress Series* 274: 251-262.
- Garrigue, C., Baker, C.S., Constantine, R., Poole, M., Hauser, N., Clapham, P., Donoghue, M., Russell, K., Paton, D., Mattila, D. (2006) Interchange of humpback whales in Oceania (South Pacific). Report SC/A06/HW55, Presented to the IWC Scientific Committee. (unpublished).
- Garrigue, C., T. Franklin, K. Russell, D. Burns, M. Poole, D. Paton, N. Hauser, M. Oremus, R. Constantine, S. Childerhouse, D. Mattila, N. Gibbs, W. Franklin, J. Robbins, P. Clapham, C.S. Baker. First assessment of interchange of humpback whales between Oceania and the east coast of Australia. (2008) *J. Cetacean Res. Manage.* (Submitted March 2008).
- Gill PC, Burton CLK (1995) Photographic resight of a humpback whale between Western Australia and Antarctic Area IV. *Marine Mammal Science* 11:96-100
- Grant, W.S., Milner, G.B., Krasnowski, P., Utter, F.M. (1980) Use of biochemical genetic variants for identification of sockeye salmon (*Oncorhynchus nerka*) stocks in Cook Inlet, Alaska. *Can.J. Fish. Aquat. Sci.*, 37:1236-1247.
- Habicht, C., Seeb, L., Seeb, J. (2007) Genetic and ecological divergence defines population structure of Sockeye Salmon populations returning to Bristol Bay, Alaska, and provides a tool for admixture analysis. *American Fisheries Society* 136: 82-94.
- Hauser, N., Peckham, H. and Clapham, P. (2000) Humpback whales in the Southern Cook Islands, South Pacific. *J. Cetacean Res. Manage.* 2(3):159-64.

- Hauser, N., Zerbini, A., Geyer, Y., Heide-Jorgensen, M-P. and Clapham, P. (2009) Movements of satellite-monitored humpback whales, *Megaptera novaeangliae*, from the Cook Islands *Mar Mamm Sci* In press.
- Jackson, J.A., Zerbini, A., Clapham, P., Constantine, R., Garrigue, C., Hauser, N., Poole, M.M., Baker, C.S. (2008) Progress on a two-stock catch allocation model for reconstructing population histories of east Australia and Oceania. Paper SC/60/SH14 presented to the IWC Scientific Committee, June 2008 (unpublished). 12 pp.
- Loo, J., Pomilla, C., Olavarria, C., Aguayo, A., Thiele, D., Baker, S., Ensor, P. and Rosenbaum, H. (2006) Genetic structure of feeding aggregations of humpback whales in the Southern Ocean. Paper SC/59/SH24. Presented to the IWC Scientific Committee, June 2006 (unpublished). 6pp.
- Luke, K., Horrocks, J.A., LeRoux, R.A., Dutton, P.H. (2004) Origins of green turtle (*Chelonia mydas*) feeding aggregations around Barbados, West Indies. *Marine Biology* 144: 799-805.
- Koljonen, M.L., Pella, J.J., Masuda, M. (2005) Classical individual assignments versus mixture modelling to estimate stock proportions in Atlantic salmon (*Salmo salar*) catches from DNA microsatellite data. *Can. J. of Fisheries and Aquatic Science*. 62: 2143-2158.
- Krutzen M, Barre LM, Moller LM, Heithaus MR, Simmer C, Sherwin WB (2002) A biopsy system for small cetaceans: darting success and wound healing in *Tursiops spp.* . *Marine Mammal Science* 18:863-878.
- Loo, J., Pomilla C., Best, P.B., Findlay, K.P., Rosenbaum, H.C. (2006) Structure and diversity between feeding aggregations of humpback whales (*Megaptera novaeangliae*) using mitochondrial and nuclear DNA. Paper SC/A06/HW26. Presented to the IWC Scientific Committee, June 2006 (unpublished). 6pp.
- Mackintosh, N.A. (1942) The southern stocks of whalebone whales. *Discov Rep* 22:197–300.
- Mackintosh, N.A. (1965) The stocks of whales. Fishing News Books Ltd. London.
- Manel, S., Gaggiotti, O., and Waples, R.S. (2005) Assignment methods: matching biological questions with appropriate techniques. *Trends in Ecology and Evolution*. 20: 136-142.
- Olavarria, C., Anderson, M., Paton, D., Burns, D., Brasseur, M., Garrigue, C., Hauser, N., Poole, M., Caballero, S., Flórez-González, L., Baker, C.S. (2006) Eastern Australia humpback whale genetic diversity and their relationship with Breeding Stocks D, E, F and G. Paper SC/58/SH25 Presented to the IWC Scientific Committee, June 2006 (unpublished). 10pp.
- Olavarria, C., Baker, C.S., Bannister, J., Brasseur, M., Caballero, S., Capella, J., Clapham, P., Dodemont, R., Donaghue, M., Jenner, C., Jenner, M.M., Moro, D.J., Florez-González, L., Hauser, N., Oremus, M., Paton, D., Poole, M.,

- Rosenbaum, H., Russell, K. (2007) Population structure of South Pacific humpback whales and the origin of the eastern Polynesian breeding grounds. *Marine Ecology Progress Series*. 330: 257-268.
- Paterson, R. and Paterson, P. and Cato, D.H. (1994) The status of humpback whales (*Megaptera novaeangliae*) in East Australia thirty years after whaling. *Biol. Conserv.* 70: 135-142.
- Pella, J.J., Masuda, M. (2001) Bayesian methods for analysis of stock mixtures from genetic characters. *Fish.Bull.* 99:151-167.
- Poole, M. (2006) An update on the occurrence of humpback whales in French Polynesia. SC/A06/58 Presented to the IWC Scientific Committee, June 2006 (unpublished). 6 pp.
- Roberts, M.A., Anderson, C.J., Stender, B., Seagars, A., Whittaker, J.D., Grandy, J.M., & Quattro, J.M. (2005) Estimated contribution of Atlantic Coastal loggerhead turtle nesting populations to offshore feeding aggregations. *Conservation Genetics* 6:133-139.
- Sambrook, J., Fritsch, E.F., Maniatis, T. (1989) Molecular cloning: a laboratory manual, 2nd edn. Cold Spring Harbor Laboratory Press, New York.
- Schneider, S., Roeslly, D., Excoffier, L. (2000) Arlequin. A software program for population genetics data analysis.
- Stevick, P.T., Aguayo-Lobo, A., Allen, J.M., Chater, K., Dalla-Rosa, L., Olavarria, C., Secchi, E., (2006) Mark-recapture abundance estimates for humpback whales in the Antarctic Peninsula. SC/A06/HW54. 2006. Presented to the IWC Scientific Committee, June 2006 (unpublished). 6pp.
- Steel, D., Garrigue, C., Poole, M., Hauser, N., Olavarria, C., Flórez-González, L., Constantine, R., Caballero, S., Thiele, D., Paton, D., Clapham, P., Donoghue, M., and Baker, C.S. (2008) Migratory connections between humpback whales from South Pacific breeding grounds and Antarctic feeding areas demonstrated by genotype matching. Paper SC/60/SH13. Presented to the IWC Scientific Committee, June 2008 (unpublished). 6pp.
- Stone, G.S., Florez-González, L and Katona, S. (1990) Whale migration record. *Nature* 346: 705.
- Townsend, C.H. (1935) The distribution of certain whales as shown by logbook records of American whaleships. *Zoologica* 19:1-50.

Table 2.1. A summary the South Pacific humpback whale samples collected including the number of individuals, the number of haplotypes in each region out of the total 110, and the number of unique haplotypes relative to seasonal habitats. Individual samples were collected from 1991-2005 and replicates within regions were deleted. Area I* is solely the Antarctic Peninsula, and Area VI* includes 7 individuals from Area I/VI border (Figure 2.2).

Region	Years Samples Collected	Individuals	Haplotypes	Unique Haplotypes by seasonal habitat
Breeding Regions				
Western Australia	1990, 1993, 1994, 2002	174	53	21
Eastern Australia	2002, 2003	156	38	0
New Caledonia	1995-2005	367	55	10
Tonga	1991, 1994-1996, 1998-2003, 2005	355	51	2
Cook Islands	1998-2003, 2005	101	29	1
French Polynesia	1997-2007	247	30	2
Colombia	1991-1998	104	25	9
Total Breeding regions		1504		
Feeding Areas				
Antarctic Area IV	1999	39	27	16
Antarctic Area V	1991, 1999, 2001	8	7	4
Antarctic Area VI*	1990, 2001	27	18	5
Antarctic Area I*	1990, 1994, 1996, 1997, 1998, 1999	68	20	14
Total Feeding Areas		142		

Table 2-2. Updated South Pacific humpback whale F_{ST} values corrected for replicate samples. Pair-wise test of differentiation between all areas for mtDNA control region sequences. Values in bold represent a significant difference based on 10,000 random permutations of the data matrix ($P < 0.05$). Symbols above matrix represent significant difference (+) between regions or no significant difference (-) between regions.

Region	WA	EA	NC	Tg	CI	FP	Col	Area IV	Area V	Area VI*	Area I*
Western Australia D		+	+	+	+	+	+	-	-	+	+
Eastern Australia E1	0.019		+	+	+	+	+	-	-	+	+
New Caledonia E2	0.013	0.010		+	+	+	+	+	-	-	+
Tonga E3	0.013	0.018	0.007		+	+	+	+	-	-	+
Cook Islands F1	0.028	0.043	0.033	0.015		+	+	+	-	-	+
French Polynesia F2	0.029	0.046	0.032	0.021	0.005		+	+	+	+	+
Colombia G	0.060	0.047	0.056	0.057	0.080	0.078		+	+	+	-
Area IV	0.001	0.005	0.006	0.007	0.027	0.029	0.060		-	-	+
Area V	0.024	0.001	0.005	0.014	0.047	0.047	0.070	0.014		-	+
Area VI*	0.007	0.012	0.001	0.001	0.014	0.022	0.060	0.001	0.009		+
Area I*	0.040	0.045	0.038	0.038	0.054	0.052	0.001	0.041	0.052	0.039	

Table 2.3 Percent apportionments using SPAM 3.7 of South Pacific humpback whale breeding populations including (standard errors) from the feeding areas IV, V, VI* and I*. Listed in the Simulation Apportionment column is the actual apportionment the program could assign given the baseline data using the simulation mode of SPAM 3.7. The simulation mode assigns one breeding region 100% apportionment as a possible mixture scenario using 10,000 iterations.

Region	AREA IV	AREA V	AREA VI*	AREA I*	Simulation Apportionment
Western Australia Sub-stock D	71.1 (10.8)	4.64 (9.0)	0.00 (.000)	0.00 (.000)	95.0%
Eastern Australia Sub-stock E1	0.00 (.000)	51.1 (26.5)	0.00 (.000)	0.00 (.000)	89%
New Caledonia Sub-stock E2	0.00 (.00)	44.1 (28.3)	12.9 (13.7)	0.00 (.000)	91%
Tonga Sub-stock E3	28.8 (13.4)	0.02 (8.0)	81.4 (22.5)	0.00 (.000)	83%
Cook Islands Sub-stock F1	0.00 (8.0)	0.01 (2.4)	5.0 (15.9)	8.8 (7.4)	73%
French Polynesia Sub-stock F2	0.00 (.000)	0.03 (3.2)	0.71 (12.3)	2.7 (8.2)	85%
Colombia Sub-stock G	0.00 (.000)	0.04 (2.2)	0.01 (0.6)	88.3 (7.5)	95%
Unknown	0.03	0.01	1.16	0.66	

Figure 2.1 South Pacific humpback whale breeding grounds (Stocks D, E, F, G) and feeding areas (Area IV, V, VI* and I*). Arrows show the results from the South Pacific humpback whale mixed-stock apportionments greater than 10% for breeding grounds from the feeding areas. Included in the boxes is the number (n) of individuals from each region.

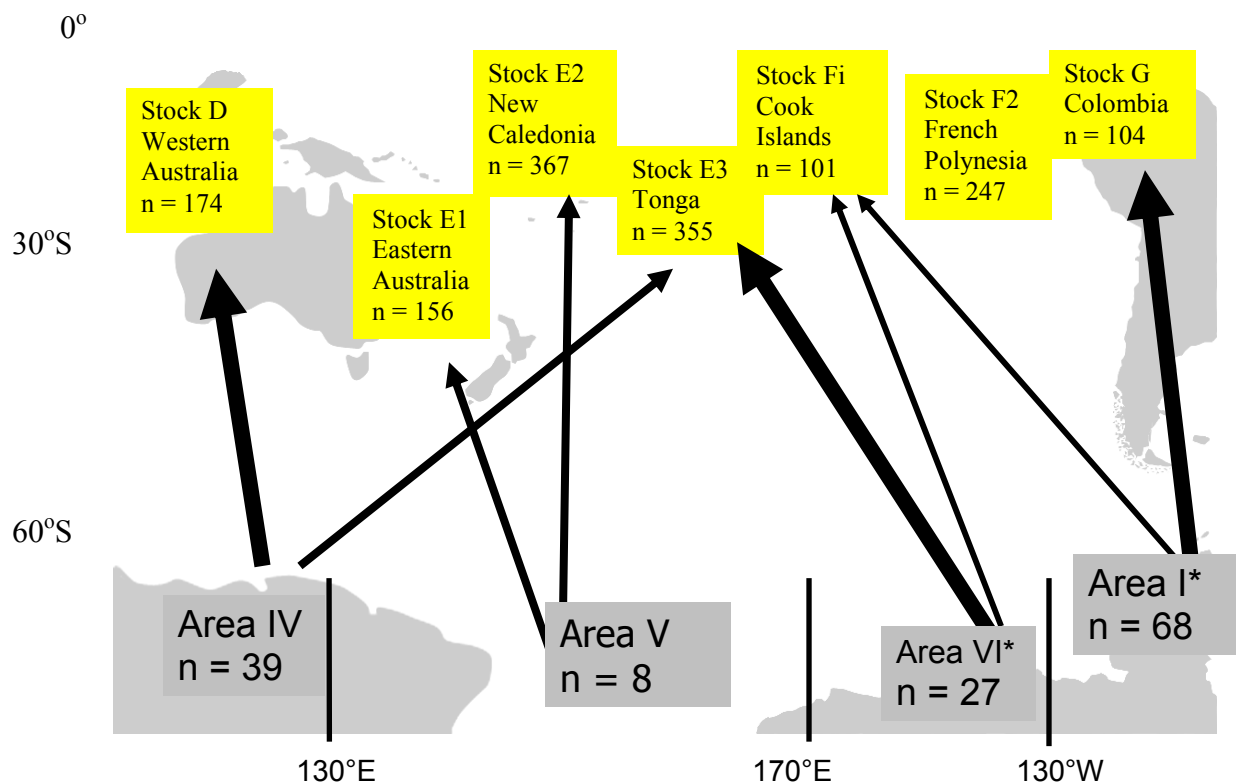
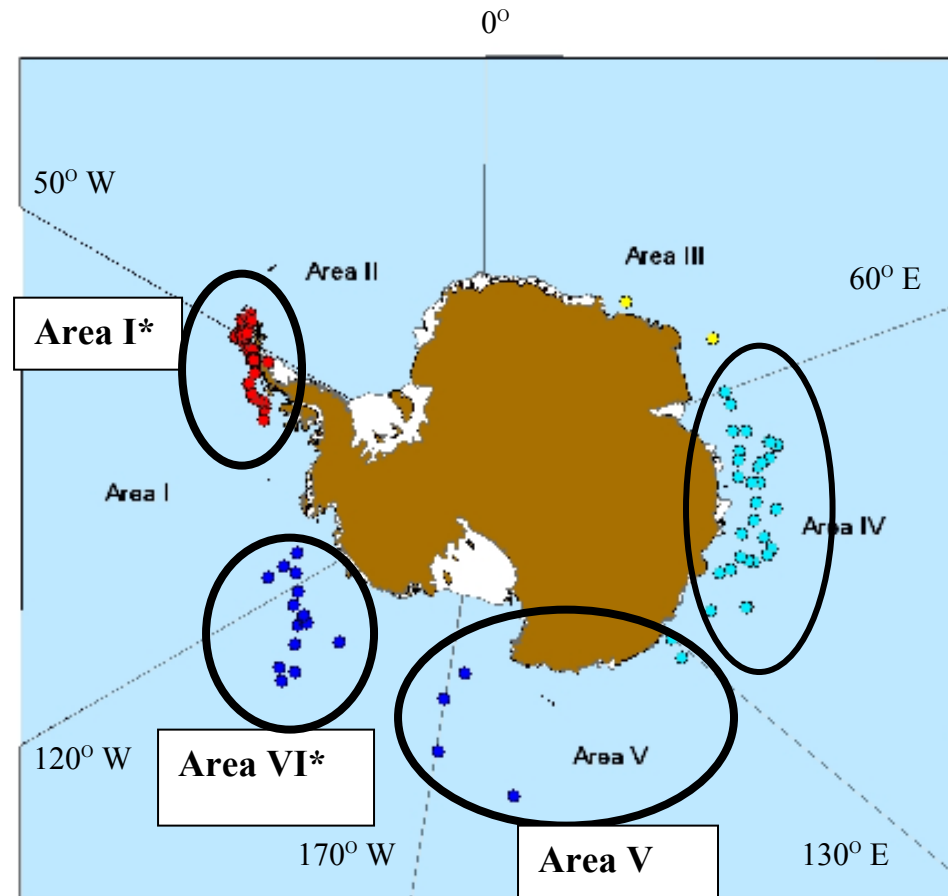


Figure 2.2. Distribution in the Antarctic feeding grounds of humpback whale samples taken during the IWC-SOWER cruises (1989, 1994, 1996-1999, 2001, 2002, 2003-2005), and INACH Antarctic Peninsula cruises. Individuals outside a circle were not used in analyses after regrouping of available samples. Actual Area boundaries as implemented by the IWC are shown with lines and labeled with degrees. Circled portions designate samples used in analysis.



CHAPTER 3 - Capture-recapture estimation of abundance for humpback whales of French Polynesia (Breeding Stock F) using photo-identification

Renee Albertson-Gibb¹, Michael Poole^{2,4} Rochelle Constrantine^{3,4} and C. Scott Baker^{1,4}

1. Marine Mammal Institute, Oregon State University, Newport, Oregon USA
2. Marine Mammal Research Program, BP 698 98728 Maharepa, Moorea, French Polynesia
3. School of Biological Sciences, University of Auckland, Private Bag 92010, Auckland, New Zealand
4. South Pacific Whale Research Consortium, P.O. Box 3069, Avarua, Rarotonga, Cook Islands

ABSTRACT

The abundance of humpback whales in French Polynesia was estimated using capture-recapture analysis of individual fluke photographs collected from 1999 to 2007. Photographs were reconciled annually and cross-matched for resights between years. The Usable Photos catalogue for these years contains 411 individual whales represented by photographs considered to be of usable quality. All Usable Photos were also reviewed according to five Quality Control criteria evaluating the clarity of the photos in five categories resulting in a catalogue of 264 individual whales defined as the Quality Control catalogue. Estimates of abundance were calculated for both the Usable Photos and Quality Control catalogues using CAPTURE, a closed population model, (adjusted for time and heterogeneity, but unadjusted for mortality) and JOLLY, an open population model (adjusted for time and survival). The CAPTURE and JOLLY estimates for the Usable Photos were 2,046 (CV 0.16) and 1,225 (CV 0.40) respectively. The CAPTURE and JOLLY Quality Control estimates were much smaller; 949 (CV 0.16) and 564 (CV 0.90) respectively. To alleviate the assumption of a closed population for nine years, an additional CAPTURE closed population estimate was calculated using only the years 2003-2007. For this 5-year period the

estimate for the Usable Photos was 1,849 (CV 0.16), and the Quality Control estimate was 853 (CV 0.24).

3.1 INTRODUCTION

Although many humpback whale stocks appear to be recovering from whaling in the southern hemisphere, several small breeding stocks in Oceania in the South Pacific remain low despite an almost 50 year moratorium on whaling (Clapham *et al.* 2009). Monitoring abundance of these recovering populations is crucial, providing important information for the International Whaling Commission's Comprehensive Assessment on southern hemisphere humpback whales.

Mackintosh (1965) assumed the number of humpback whales in Oceania directly above Area VI was relatively small compared to Areas IV and V. French Polynesia is considered part of the International Whaling Commission breeding stock F in Oceania north of Antarctic Area VI. Historically, French Polynesia was considered a transitory location, but more recently has been recognized as a breeding ground (Poole 2006). Although it has been established that French Polynesia is genetically differentiated from other Oceania breeding stocks, (Olavarria *et al.* 2007) there has been a small degree of interchange documented by photo-identification between French Polynesia and Tonga (n=4 Garrigue *et al.* 2007) and between French Polynesia and American Samoa (n=4 Garrigue *et al.* 2007).

Fluke photo-identification has been collected consistently in French Polynesia since 1999. A preliminary estimate of Oceania, including French Polynesia, was first presented to the IWC by Baker *et al.* (2006) using a multi-year closed population model of fluke photograph catalogues compiled by the

principal investigator from each Oceania region. In this study we seek to improve this abundance estimate for French Polynesia humpback whales by using both open and closed population models. We compared results from two photo catalogues where one is a subset of the original principal investigator's photo catalogue that has passed additional quality criteria for the purpose of minimizing bias in matching (Garrigue *et al.* 2007).

3.2 METHODS

3.2.1 *Field Surveys*

Fluke identification photographs were taken of humpback whales (Katona *et al.* 1979) on dedicated and opportunistic surveys throughout the breeding ground in various islands of French Polynesia. The collection of fluke photographs most often occurred around the island of Moorea in the Society Islands, less often around the island of Rurutu in the Austral Islands and rarely around smaller islands within the Society Islands (Poole 2006; Figure 3-1) although all resightings were in Moorea. Photographs were taken aboard one of two vessels between the months of July and November from 1999-2007. Some, but not all, years had similar sampling effort. Differences in sampling effort included opportunities lost due to weather and availability of volunteers.

3.2.2 *Photograph matching procedure*

The photographs were reconciled annually, within and between years, by the principal investigator in order to exclude all poor quality photographs and to record any possible recaptures identified from previous years. After photographs were reconciled the best fluke photograph per individual was chosen by the principal investigator to become a part of the Usable Photos catalogue. This catalogue currently consists of 411 individual humpback whales seen in French

Polynesia waters for the years 1999-2007. Annually this catalogue is submitted to the South Pacific Whale Research Consortium's synoptic study of humpback whales in Oceania (Garrigue *et al.* 2007) for Quality Control analysis and assessment of possible matches between breeding regions.

All images of the Usable Photos catalogue were reviewed according to a standard set of Quality Control criteria that were originally developed for the SPLASH program in the North Pacific. This is a scoring system based on quality measures of the photos that are irrespective of distinctiveness of the fluke (Calambokidis *et al.* 2001, Garrigue *et al.* 2007). It consists of five quality criteria using a score between 1 and 5 in each category to accept or reject photographs (Figure 3-2). These five criteria categories were: (i) proportion of the fluke visible, (ii) fluke angle, (iii) the lateral angle of the photographer, (iv) exposure quality, and (v) contrast quality as described in Calambokidis *et al.*, (2001). All the images were graded from the highest quality (1) to the lowest quality (5). A score of 4 or 5 in any of the five categories was considered to be of insufficient quality for a representative comparison of resights and was therefore excluded from the Quality Control catalogue (Garrigue *et al.* 2007). For a complete description of the implementation of the SPLASH criteria see Garrigue *et al.* (2007).

3.2.3 Data sets

As a result of the review, two data sets, or photo catalogues, were used for this analysis (Table 3-1).

- 1) Usable Photos (n = 411) included photographs of unique individuals of the primary investigator excluding those of extremely poor quality.
- 2) Quality Control catalogue (n = 264) included photographs which scored between 1 and 3 for each of the SPLASH criteria.

Photographs taken before 2006 were taken with film. These photos were scanned in December 2005 at the highest quality resolution and were used for exchange here and in all subsequent comparisons of Oceania that have taken place at the annual South Pacific Whale Research Consortium (Garrigue *et al.* 2007). All photos after 2005 have been taken digitally.

All matches within and between regions were checked for accuracy by two scientists to reduce the likelihood of bias discussed in Perry *et al.* (1990). This bias considers the effect of two types of errors. Type one error occurs when two photographs are considered a match when they were not. This would lead to a negative bias in the abundance estimate of individuals in the population. Type two errors occur if a match was missed between two photographs. This would result in a positive bias in a population estimate because the individual would be counted as two individuals rather than a resight.

3.2.4 Exploration of model selection and assumption violation

The following assumptions are considered for almost all capture-recapture models (Begon 1979):

- 1) 'The markings used for sightings and resightings are permanent.' Specific to humpback whales this includes the unique markings on the underside of the fluke. These markings are considered to be permanent on adult whales with the exception of scars that may be accumulated over the life of the whale (Friday *et al.* 2000). Flukes have been used successfully world-wide for humpback whale abundance studies, and some individuals have been resighted successfully using this technique over a period of 16 years in the northern hemisphere (e.g. Baker *et al.* 1988). This study excluded any photographs of sub-adult, juvenile or calves as the coloration of the fluke on some humpback whales has been known to change in the first three years of life (Perry *et al.* 1990).

- 2) 'The actual marking of the animal has no effect on subsequent recaptures.'

Capture recapture studies on cetaceans have shown a majority of the animals are unaffected by the boat being in close enough proximity to take a fluke photograph, and photographing a whale does not necessarily make it easier or more difficult to photograph again (Katona & Beard 1990; Clapham and Mattila, 1993).

- 3) 'The marking of animals has no effect on death or emigration.' Photographing a whale does not directly affect its mortality (Katona & Beard 1990). Many studies have followed individuals for decades, and have found no negative effects on mortality of a whale from approaching a whale with a boat (Calambokidis 1990).

- 4) 'There is no inherent difference between the catchability of individuals.' This assumption is often violated in humpback whale studies which have been shown to demonstrate variations in heterogeneity and time effects (Pledger *et al.* 1998; Chao 1992). Violating this assumption can create a negative bias in population estimates (Pleger *et al.* 1998; Chao 1992; Otis *et al.* 1978). This violation and how it was addressed in this study will be discussed in model selection with Program CAPTURE.

- 5) 'There are no births or immigrations or no deaths or emigrations.' Due to the length of our study period this assumption is violated. It has been shown that a violation of this assumption can result in a positive bias in abundance estimates (Otis *et al.* 1978) and will be addressed in the Results and Discussion sections with Program JOLLY.

- 6) Sampling periods are short in relation to total time of the life history of the whale. This is a nine year study. Humpback whales are assumed to have a life span of at least fifty years (Clapham 2002).

3.2.5 Abundance estimation procedure

3.2.5.1 Chapman modified Lincoln-Petersen estimator

Pair-wise estimates were calculated using the Chapman modified Lincoln-Petersen estimate. It is considered a closed model allowing for no changes in the population and no variability in capture (Begon 1979). We used the Chapman modification of the Lincoln-Petersen estimate to calculate 2-year abundance estimates to look for variation in time periods. The Chapman modification to the Lincoln-Petersen estimate is shown below:

The unbiased estimate of $\hat{N}$ is:
$$\frac{(n_1 + 1)(n_2 + 1)}{(m_2 + 1)}$$

where $\hat{N}$ is our estimate of population size, n_1 is the number of individuals captured, on the first occasion, n_2 is the number of individuals captured on the second occasion and m_2 is the number of individuals previously marked (or resighted) that are captured on the second occasion (Amstrup *et al.* 2005). The difference between the Lincoln-Petersen and Chapman's estimator is small when the number of recaptures is large relative to n_1 and n_2 (Amstrup *et al.* 2005).

3.2.5.2 Schnabel weighted mean model

The Schnabel method is a multi-year extension of the Petersen estimate (Begon 1979). It is a closed model assuming no changes in the population and, like the Petersen estimate, does not account for time or heterogeneity (Begon 1979).

3.2.5.3 Program CAPTURE

We applied a series of models implemented in Program CAPTURE (Rexstad & Burnham, 1991) within Program MARK to generate the abundance covering the entire study period 1999-2007. To alleviate the violation of the closed population assumption in CAPTURE we ran an additional analysis including only the last five years 2003-2007. Different models were used for both study periods in Program CAPTURE to account for sources of variation in capture probabilities unique to humpback whales. These included but weren't limited to, Darroch's model for time (M_t) and Chao's model for time in combination with individual heterogeneity (M_{th}) (Otis *et al.* 1979; Chao *et al.* 1992; Norris & Pollock 1996).

Several different models were designed in Program CAPTURE to account for three sources of variation in capture probabilities. The model for time, M_t , assumes capture probability varies from one occasion to another but that animals are equally catchable on all occasions. This implies there is a difference only in the ability of the animal to be located by the observer due to uncontrolled variables such as weather. The second source of variation is heterogeneity. Heterogeneity, Model M_h , does not assume all animals to be equally catchable due to individual differences (Chao *et al.* 1992; Norris & Pollack 1996). This could be because part of an animal's range exists outside the study area (White *et al.* 1981). Heterogeneity may also be caused by transient animals or permanent emigration of subpopulations (Schwarz & Seber 1999) where animals show up once in the population and are not captured subsequently. The third source of variation is Behavior, Model M_b . This is primarily a problem in populations of animals that are being traditionally captured in a trap, inviting the problem in recapture of animals either being "trap happy" or "trap shy". In general this has not usually been a problem in cetacean capture-recapture

estimations (Clapham & Mattila 1993; Wursig & Jefferson 1990). Therefore, only two of these sources, time and heterogeneity, were considered here.

3.2.5.4 Open-population model: the Jolly-Seber model

The open-population models allow for demographic changes in the population over time. It is imperative that demographic changes are considered for both survival and capture probabilities to differ for each sampling period in studies of long lived species (Pollock *et al.* 1990; Schwarz & Arneson 1996). This is done with stochastic models and is referred to as the standard Jolly-Seber model, or Model A (Time dependent and capture dependent) (Jolly 1965; Jolly 1982). Other models within Program JOLLY are available for variations of these parameters including Model B (constant survival), Model C (constant capture) and Model D (constant survival and capture). These additional models perform well when capture probabilities are high (>0.5) (Pollock *et al.* 1990). Program JOLLY also performs a Likelihood Ratio Test (LRT) to test for an affect of first capture on survival probabilities.

3.2.6 Transient individuals

Due to the low number of resights, or recaptures in these data, it is of interest to test if there are transients in the population. Program U-Care version 2.2 (Choquet *et al.*, 2005) conducts goodness-of-fit tests as well as specific tests for transience (test 3.SR). This allows for the following hypothesis to be tested: H_0 : there is no difference between the “new” and the “old” individuals captured at occasion t in the probability of being later encountered.

Alternatively

H_1 : there is a difference in the probability of being later encountered between the “new” and the “old” individuals captured at occasion t .

Difference is tested by a chi-squared test.

3.3 RESULTS

Using the distinct coloration patterns of the ventral side of the fluke photographed between the years 1999-2007, 411 humpback whales were identified in French Polynesia waters. A series of capture-recapture models were used to determine abundance estimates for both the Usable Photos and Quality Control catalogues, and with the exception of the estimates generated by Program JOLLY all estimates assumed a closed population. Within-year sample sizes varied for both catalogues, ranging from 27-62 for the Usable Photos catalogue and 15-44 for the Quality Control catalogue (Table 3-1). Resighting rates were relatively low, with only 39 individuals sighted twice (34 individuals sighted twice for Quality Control) and 5 individuals sighted three times (for both Usable Photos and Quality Control catalogues) (Figure 3-3). Abundance estimates ranged from 1,225-2,046 for the Usable Photos catalogue and 564-949 for the Quality Control catalogue. All results are summarized in Table 3-2.

3.3.1 Catalogue Results

The Lincoln-Petersen estimate (Figure 3-4) gave a mean estimate of 1,000 individuals but displayed wide variation between some years with 2-year population estimates ranging from 600 to 3,000 depending on the years calculated. A similar pattern was seen for the Quality Control catalogue with a mean of 400 individuals and 2-year estimates ranging from 200-850. The Schnabel weighted mean of the Petersen estimate for the entire study period was 1,679 (CV 0.15) for Usable Photos and 825 (CV 0.16) for Quality Control.

For the period 1999-2007, among the multiple-occasion closed population CAPTURE models the M_{th} Chao gave the largest estimate for both Usable Photos (2,046, CV 0.16) and Quality Control (949, CV 0.16). Similarly, the model

chosen by Program CAPTURE was M_t Darroch for both Usable Photos (1,824, CV 0.13) and Quality Control (861, CV 0.13). For the period 2003-2007 the largest estimate was M_{th} Chao for both Usable Photos (1,849, CV 0.16) and Quality Control (853, 0.24 CV). Once again the model chosen by Program CAPTURE was M_t Darroch (Usable Photos 1,724, CV 0.13; Quality Control 803, CV 0.20).

In the open population model, Program JOLLY mean results were much lower than the closed population model Usable Photos (1,225, CV 0.40) Quality Control (564, CV 0.90). These individual year results (not shown) contained large CVs (>0.40) and wide confidence intervals, sometimes including zero. A Likelihood Ratio Test in Program JOLLY was significant implying Model A (time dependent survival and capture) was the appropriate model to use compared to Model D (constant survival and capture). The survival rate calculated by Jolly for Usable Photos (0.82) and Quality Control (0.78) demonstrated about an 80% survival rate from one capture occasion to the next.

3.3.2 Transience

The test 3.SR provided by U-CARE did not reveal a transience problem (p-value = 0.15 Usable photos; p-value = 0.30 Quality Control) contending many of the whales only seen once do not necessarily have low probability of being captured again on subsequent occasions. However, the scope of this test is limited if heterogeneity is a component of the population.

3.4 DISCUSSION

3.4.1 Lincoln-Petersen and Schnabel estimates

The Chapman modified Lincoln-Petersen estimates revealed either an inconsistency in sampling from year to year, or changes in the number of whales

entering the sampling area (Figure 3.6). This most likely occurred from non-uniform sampling effort, which is continuously a challenge in cetacean field surveys due to practicalities of weather and the long time interval of each capture occasion; although some variation could be natural. The Lincoln-Petersen estimate and the Schnabel weighted mean model do not allow for variation in capture probability, so the estimates are negatively biased for populations showing degrees of heterogeneity or time effects (Amstrup 2005; Begon 1979).

3.4.2 Closed population model five year study

There were several challenges in the analysis of these data including violations of a closed population assumption and limitations from sparse data. To assume a closed population of humpback whales for an extended study period is not biologically realistic (Calambokidis *et al.* 1990) and will have a positive bias on the abundance estimate (White *et al.* 1982). An additional analysis with a shorter time period was used in Program CAPTURE (2003-2007). These results revealed similar abundance estimates to the nine year study, but larger standard errors most likely due to the reduction in captures and recaptures (Schwarz & Seber 1999). Despite this statistical quandary, the results from the five-year study period appear to be the most sensible to this study given that they address the heterogeneity issue and still have reasonable confidence intervals unlike the open model Program JOLLY.

3.4.3 Preferred model in Program CAPTURE

The model chosen by Program CAPTURE for both the Usable Photos and Quality Control catalogue was Darroch's M_t which assumes capture probability varies from one occasion to another (time) but do not vary in individual capture probabilities (heterogeneity). However, heterogeneity becomes apparent with large variability in capture probabilities (White *et al.* 1982) which was shown

in our data to vary from 0.02 to 0.06. Our analysis revealed both time and heterogeneity to be factors as shown with a low number of recaptures (~10% of sightings per year) and sampling variability. Chao's model for both time and heterogeneity (Model M_{th}) has been shown to work well for sparse data and large variation in capture probability (Chao *et al.* 1989; Chao *et al.* 1992). Although models containing only time give reasonable estimates, if heterogeneity is present both of these models will have a negative bias (Otis *et al.* 1978; Hammond & Anthony 2006). Both time and heterogeneity effects have been shown to be important in migratory animals including some cetacean species (Calambokidis *et al.* 1990; Gormley *et al.* 2007). Based on the information in Program CAPTURE and the known biology of the species, the appropriate model appears to be M_{th} Chao.

3.4.4 Limitation of open population model

The open population model requires more data per capture period (>100 captures) than the closed population models in order to provide equally as precise of estimates (White *et al.* 1982). Our number of individuals per capture occasion was < 60 which resulted in large standard errors and high CVs. Although it is imperative that demographic changes are considered in studies of long lived species (Pollock *et al.* 1990; Schwarz & Arneson 1996), in cetacean studies this can be challenging due to sparse data (Cerchio *et al.* 2006). In this study a precise open population estimate could not be achieved with any precision.

3.4.5 Quality Control

Compared with the results obtained with the Usable Photo catalogue estimates produced from the Quality Control catalogue results were substantially smaller. The Quality Control criteria reduced the number of photographs by 156

from the Usable Photos catalogue, but also resulted in 5 individuals lost in recaptures (Figure 3-3). This created slightly larger capture probabilities despite the lower number of photographs demonstrating these data are possibly more robust than the Usable Photos catalogue. The loss of the large number of photographs could bias the abundance estimate if these are indeed animals that represent the population. The removal of marginal quality photographs should have reduced the probability of a 'missed match' (calling two sightings different when they were in fact the same) potentially improving the precision of the estimate (Perry *et al.* 1990; Stevick *et al.* 2001). However, this removal also reduces the sample size of both sightings and resightings, perhaps because of other underlying factors such as fluking behavior. In which case, the Quality Control could result in an unintended negative bias. A third possibility is that individuals represented by poorer quality photographs include a higher proportion of transients. The continued use of the Quality Control catalogue could assist in answering the question of transience. If after several years there are still a large number of individuals only seen once in the population, it is most likely due to transience and not to low quality photographs. 'Double tagging' using genotypes would also provide information needed to evaluate these effects (Garrigue *et al.* 2004).

3.4.6 Heterogeneity

The reduction of heterogeneity would generate a more robust estimate and allow flexibility in the types of models that could be used. Although some estimators can account for heterogeneity as shown with Program Capture, it is also important to try and deemphasize heterogeneity in the field, if possible. When capture probability is low and heterogeneity is apparent investigators should use methods to increase capture and recapture events (i.e. longer days in

the field covering larger areas) to provide larger numbers of individuals in a capture occasion and improve parameter estimation (Rosenberg et al. 1995). If this could be a priority in annual field studies (i.e. the funding was available to meet these criteria) allowing the population to be modeled in open and closed parameters, and use only Quality Control photos to reduce error in matching and possibly assess the issue of transience, monitoring this critical population could produce a truly robust estimate.

3.4.6 *Summary and future direction*

In summary, we have performed an extensive evaluation of humpback whale population abundance for breeding stock F2 in the South Pacific and discussed the advantage of using Quality Control photographs to carry out this evaluation. Sample size limitations and low capture probabilities resulted in low precision for open population models. Considering the overlap of confidence intervals for Usable Photos and Quality Control we propose a range for the population between 853-1,849 individual humpback whales from the closed population Model M_{th} including the years 2003-2007. This suggests potential vulnerability of a recovering population that is thought to have low interchange with other regions of Oceania (Garrigue *et al.* 2007).

Future surveys should include remote outlying areas within French Polynesia that are virtually unexplored for humpback whales, especially in the eastern Tuamotu Islands and northern Gambier Islands (Gannier 2004). If whales in outer islands are new individuals utilizing other habitat within the vast territory of French Polynesia they may need to be estimated independently. In contrast, if whales in outlying areas are also seen in well surveyed regions like Moorea or Rurutu within the same season this could provide critical data on residence times for some French Polynesia humpback whales.

ACKNOWLEDGEMENTS

The authors greatly appreciate Kirsten Thompson, Claire Garrigue and members of the South Pacific Whale Research Consortium who reviewed photographs tirelessly from the entire region of Oceania for Quality Control and interchange. We also wish to thank Dr. Robert Anthony for his time and efforts on various sections of this manuscript. His sound advice through meetings and emails was greatly appreciated. The International Fund for Animal Welfare graciously provided funding for the fieldwork in French Polynesia.

LITERATURE CITED

- Amstrup, S.C., McDonald, T.L., and Manly, B.F.J. (2005) Handbook of Capture-Recapture Analysis. Princeton University Press. Princeton New Jersey.
- Baker, C.S., C. Garrigue, R. Constantine, B. Madon, M. Poole, N. Hauser, P. Clapham, Donoghue, K. Russell, T. O'Callahan, D. Paton, and D. Mattila. 2006. Abundance of humpback whales in Oceania (South Pacific), 1999 to 2004. (2006) Unpublished report SC/A06/HW51 for consideration the inter-sessional workshop for the comprehensive assessment of Southern Hemisphere humpback whales, Hobart, Tasmania. 2006.
- Baker CS, Perry A, Vequist G (1988) Humpback whales of Glacier Bay, Alaska. *Whalewatcher* 22:13-17.
- Begon, M (1979) Investigating animal abundance: capture-recapture for biologists. University Park Press, Baltimore.
- Burnham KP, Anderson DR (2002) Model selection and multimodal inference: a practical information-theoretic approach. *Springer-Verlag*, New York.
- Calambokidis J, Cubbage JC, Steiger GH (1990) Population estimates of humpback whales in the Gulf of the Farallones, California. *Rep Int Whal Commn*: pp. 325-333.
- Calambokidis J, G. H. Steiger, J. M. Straley, L. M. Herman, S. Cerchio, D. R. Salden, R. J. Urban, J. K. Jacobson, O. Von Ziegesar, C. K. Balcolmb, C. M. Gabriele, M. E. Dahlheim, S. Uchida, G. Ellis, Y. Miyamura, P. P. Ladron de Guevara, M. Yamaguchi, F. Sato, S. A. Mizroch, L. Schlender, K. Rasmussen, J. Barlow, J. T. Quinn II. (2001) Movements and population

- structure of humpback whales in the North Pacific. *Marine Mammal Science* 17:769-794.
- Cerchio S (1998) Estimates of humpback whale abundance off Kauai, 1989-1993. Evaluating biases associated with sampling the Hawaiian Islands breeding assemblage. *Mar Ecol Prog Ser* 175: 23-23.
- Chao A (1989) Estimating population size for sparse data in capture-recapture experiments. *Biometrics* 35:327-338.
- Chao A, Lee S-L, Jeng S-L (1992) Estimating population size for capture-recapture data when capture probabilities vary by time and individual animal. *Biometrics* 38:201-216.
- Childerhouse, S., J. Jackson, C.S. Baker, N. Gales, P.J. Clapham, and R.L. Brownell, Jr. (2008) *Megaptera novaeangliae*, Oceania subpopulation. IUCN Red List of Threatened Species (<http://www.iucnredlist.org/details/132832>)
- Clapham, PJ, Y. Mikhalev, W. Franklin, D. Paton, C. S. Baker, Y. V. Ivashchenko and R. L. Brownell, Jr. Catches of Humpback Whales by the Soviet Union and Other Nations in the Southern Ocean, 1937-1973.
- Gannier A. (2004) The large-scale distribution of humpback whales (*Megaptera novaeangliae*) wintering in French Polynesia during 1997-2002. *Aquatic Mammals* 30:227-236.
- Garrigue, C. South Pacific Whale Research Consortium (2007) First assessment of interchange of humpback whales between Oceania and the east coast of Australia SC/59/SH15. Presented to the IWC Scientific Committee, June 2007 (unpublished). 9 pp.
- Garrigue C, R. Dodemont, D. Steel, C. S. Baker. (2004) Organismal and 'gametic' capture-recapture using microsatellite genotyping confirm low abundance and reproductive autonomy of humpback whales on the wintering grounds of New Caledonia. *Marine Ecology Progress Series* 274:251-262.
- Hammond, E.L., and Anthony, R.G. (2006) Mark-recapture estimates of population parameters for selected species of small mammals. *Journal of Mammalogy*, 87(3):618-627.
- Jolly, G. M. (1965). Explicit estimates from capture-recapture data with both death and immigration | Stochastic model. *Biometrika* 52 225-237.
- Katona S, Baxter B, Brazier O, Kraus S, Perkins J, Whitehead H (eds) (1979) Identification of humpback whales by fluke photographs, Vol 3. Plenum Press, New York.
- Mackintosh, N.A. (1965) The stocks of whales. Fishing News Books Ltd. London.
- Norris, J. L. and Pollock, K. H. (1996). Nonparametric MLE under two closed capture-recapture models with heterogeneity. *Biometrics* 52 639-639.

- Otis D, Burnham KP, White GC (1978) Statistical inference for capture data on closed animal populations. *Wildl Monogr* 62: 1-135.
- Olavarría, C., Baker, C.S., Bannister, J., Brasseur, M., Caballero, S., Capella, J., Clapham, P., Dodemont, R., Donaghue, M., Jenner, C., Jenner, M.M., Moro, D.J., Florez-González, L., Hauser, N., Oremus, M., Paton, D., Poole, M., Rosenbaum, H., Russell, K. (2007) Population structure of South Pacific humpback whales and the origin of the eastern Polynesian breeding grounds. *Marine Ecology Progress Series*. 330: 257-268.
- Perry, A., C. S. Baker and L. M. Herman. (1990) Population characteristics of individually identified humpback whales in the central and eastern North Pacific: a summary and critique. *Rep Int Whal Comm* pp 307-318.
- Pledger, S. and E_ord, M. (1998). Correction of bias to heterogeneous capture probability in capture-recapture studies of open populations. *Biometrics* 53 319-329.
- Poole, M.M. (2006) An update on the occurrence of humpback whales in French Polynesia. SC/A06/58 Presented to the IWC Scientific Committee, June 2006 (unpublished). 12 pp.
- Rexstad, E., and K.P. Burnham. (1991) User's Guide for Interactive Program CAPTURE. Colorado Cooperative Fish & Wildlife Research Unit, Colorado State University, Fort Collins, Colorado.
- Rosenburg, D. K., Overton, W. S. and Anthony, R. G. (1995). Estimation of animal abundance when capture probabilities are low and heterogeneous. *Journal of Wildlife Management* **59** 252-261.
- Schwarz CJ, Arnason AN (1996) A general methodology for the analysis of open-model capture recapture experiments. *Biometrics* 52: 860-873.
- Stevick PT, Palsboll PJ, Smith TD, Bravington MV, Hammond PS (2001) Errors in identification using natural markings: rates, sources, and effects on capture–recapture estimates of abundance. *Can J Fish Aquat Sci* 58.
- White, GC, Anderson, DR, Burnham, KP, Otis, DL (1982) Capture-recapture and removal methods for sampling closed populations. LA-8787-NERP Los Alamos National Laboratory, Los Alamos, New Mexico.

Table 3-2: Abundance estimates of Usable Photos and Quality Control tail fluke photo-identification catalogues for humpback whales of French Polynesia using the Schnabel estimate, closed models calculated by CAPTURE within Program MARK and an open model calculated by JOLLY.

Usable Photos						Quality Control				
	N	SE	CV	95% CI	Model Selection	N	SE	CV	95% CI	Model Selection
Schnabel 1999-2007	1,679	254	0.15	1,181-2,177	--	825	132	0.16	566-1,084	--
Darroch's M(t) 1999-2007	1,824	235	0.13	1,437-2,389	1.0	861	112	0.13	678-1,124	1.0
Darroch's M(t) 2003-2007	1,724	112	0.13	678-1,124	1.0	803	160	0.20	561-1,203	1.0
M _{th} Chao 1999-2007	2,046	318	0.16	1,532-2,798	0.80	949	154	0.16	708-1,321	0.66
M _{th} Chao 2003-2007	1,849	439	0.16	1,197-2,970	0.73	853	206	0.24	556-1,392	0.72
Program Jolly 1999-2007	1,225	500	0.40	246-2,203	--	564	509	0.90	0-1,587	--
Survival Rate Φ	0.82	0.17	--	--	--	0.78	0.15	--	--	--

Figure 3-1: French Polynesia including the two locations (circled) humpback whale data has mostly been collected, Moorea in the Society Islands and Rurutu in the Austral Islands (Poole 2006).

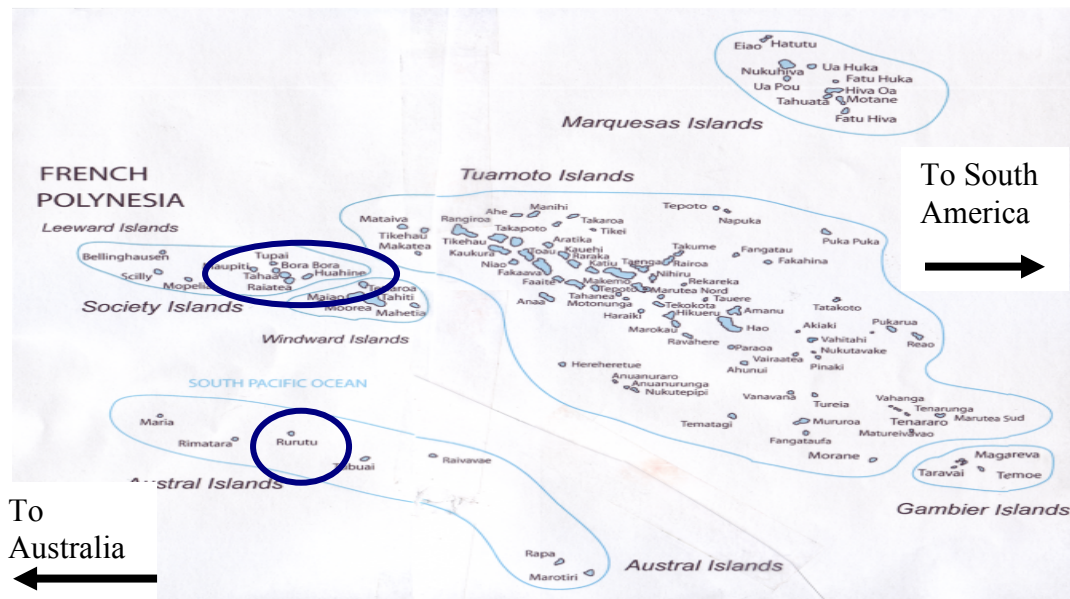


Figure 3-2: Examples of humpback whale fluke photos. The left photo was considered part of the Usable Photos catalogue due to the unique markings visible in the middle and to the right of center on the fluke, but was removed after Quality Control due to a score of 4 in the categories of % visible, fluke angle, and focus. The one on the right has passed all five Quality Control categories scoring a 3 or less for each.



Figure 3-3: The number of times individual humpback whales were sighted in French Polynesia 1999-2007.

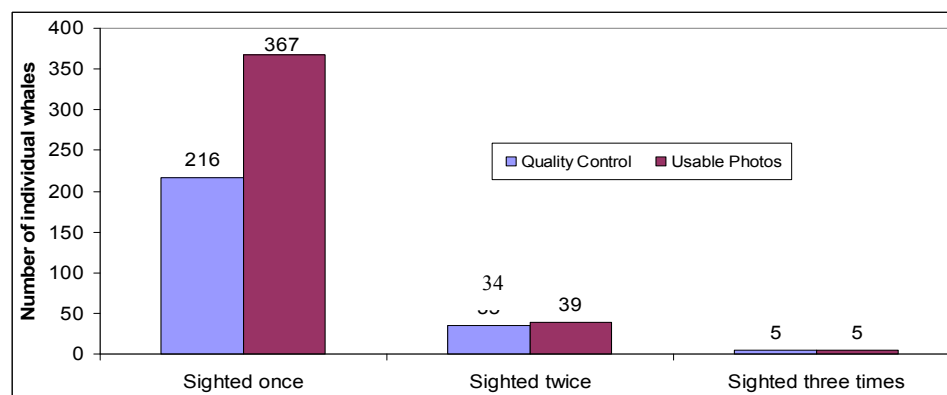
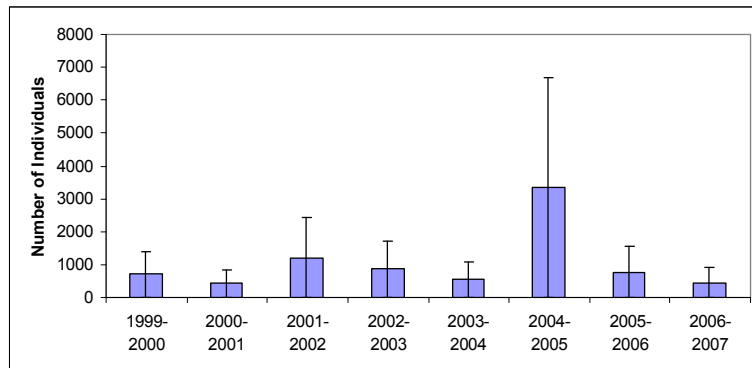
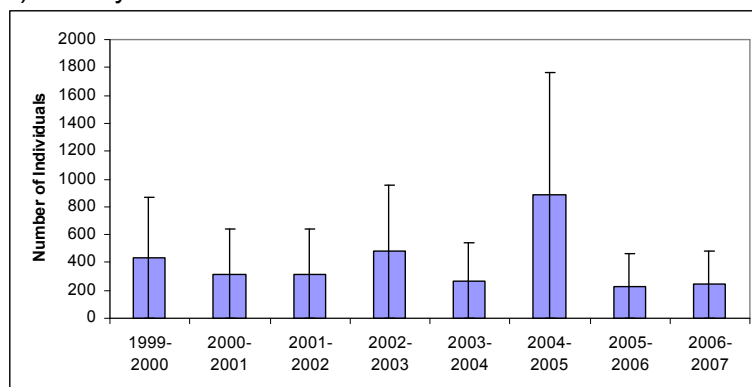


Figure 3-4 Year to year estimates of French Polynesia humpback whale population size using the Chapman modified Lincoln-Petersen Estimate for a) Usable Photos and b) Quality Control including 95% confidence intervals. The figure shows that elimination of photos for the Quality Control catalogue has a negative effect on the abundance estimate (note the scale is less than half the value of the Usable Photos scale).

a) Usable Photos



b) Quality Control



FOR CONSIDERATION BY THE SCIENTIFIC COMMITTEE OF
THE INTERNATIONAL WHALING COMMISSION
MADEIRA, PORTUGAL JUNE 2009

CHAPTER 4 - Photo-identification comparison of humpback whales from the Antarctic Peninsula/Strait of Magellan and French Polynesia, (Breeding Stock F)

Renee Albertson-Gibb¹, Jorge Acevedo^{2,3}, Carlos Olavarría^{2,3}, Anelio Aguayo^{2,4}, M. Michael Poole⁵ and C. Scott Baker¹

1. Marine Mammal Institute, Oregon State University, Newport, Oregon USA

2. Proyecto INACH 163 Ecología de Cetáceos Antárticos. Instituto Antártico Chileno, Punta Arenas, Chile

3. Fundación Centro de Estudios del Cuaternario. Avda. Bulnes 01890, Punta Arenas, Chile

4. Instituto Antártico Chileno. Plaza Muñoz Gamero 1055, Punta Arenas, Chile.

5. Marine Mammal Research Program, BP 698 98728 Maharepa, Moorea, French Polynesia

ABSTRACT

Humpback whales (*Megaptera novaeangliae*) are a highly migratory species found in all the world's oceans. However, in the South Pacific Ocean very few connections have been documented between their low latitude breeding grounds and their high latitude feeding areas. An understanding of these connections is an important component of the IWC Comprehensive Assessment in determining historic catch allocations, and the modeling of current population dynamics. In light of the discovery of recent connections between breeding stock F2 and breeding stock G and between American Samoa and the Antarctic Peninsula, a fluke photo-identification comparison was undertaken between French Polynesia and the Antarctic Peninsula and Strait of Magellan. The French Polynesia catalogue (n=450) spans 1990-2007 seasons, and the Antarctic Peninsula/Strait of Magellan (n=369) catalogue includes the 1994/1995 season through the 2007/2008 season. These three photographic catalogues were compared by two researchers independently to search for possible matches between the two regions. No conclusive matches were found. This is not conclusive evidence

against some whales migrating to the Antarctic Peninsula from the French Polynesia breeding ground. However, it does suggest that the Antarctic Peninsula is not the primary migratory destination of the French Polynesia breeding stock (Stock F2).

4.1 INTRODUCTION

4.1.1 Previous documentation of connections between Oceania and the Antarctic Peninsula

Little is known about the humpback whale migratory connections of breeding stocks E and F in the South Pacific to the Antarctic. For management purposes the IWC (Report SC-58-Rep-5 2006) considers South Pacific humpback whale migration as generally the Antarctic feeding areas IV, V, VI and I and the South Pacific breeding grounds directly above them. However, documented connections of specific breeding grounds to specific feeding areas are relatively few, and those that are known are not always directly north-south (Figure 4.1). For example, two genotype matches were recently found between Tonga and Area I (Steel *et al.* 2008), and several *Discovery* tags were recovered from Areas in the Antarctic that were not directly south of the breeding ground at which they were implanted (Dawbin 1966; Figure 4.1). In September 2006 a satellite tag was implanted in a humpback whale in the Cook Islands (breeding stock F) and in December 2006 the whale was subsequently located on the border of Area VI and Area I demonstrating at least some whales may travel in a southeasterly direction to adjacent feeding areas (Hauser *et al.* in press). In addition, in 2008 a photo-identification match was found between American Samoa (border of breeding stock E/F) and the Antarctic Peninsula (Robbins *et al.* 2008).

4.1.2 Regions used in the comparison

French Polynesia comprises 118 islands almost directly north of Antarctic Area VI (Figure 3.1). Although humpback whales have been observed in all of French Polynesia's archipelagoes, the island of Rurutu in the Austral Islands and Moorea in the Society Islands appear to have the highest concentrations of whales (Poole 2006). Despite extensive search effort by whalers in the 19th century in the South Pacific breeding grounds, few regions, including French Polynesia and Cook Islands, were thought to contain many humpback whales (Townsend 1935). Until recently it was assumed that the regions east of Tonga did not contain autonomous breeding populations (Mackintosh 1942). However, since 1990 boat surveys in French Polynesia have collected fluke photos, skin samples, song recordings and general field data including observations of mother/calf pairs that indicate that humpback whales are using French Polynesia's waters as a breeding ground (Poole 2006). Fluke photo-identification comparisons across South Pacific breeding grounds (Stocks E and F) have revealed that these populations are relatively isolated, with limited movement between regions either within or across years (Garrigue *et al.* 2004). Genetic analyses have shown French Polynesia to be genetically differentiated from other South Pacific breeding grounds (Olavarria *et al.* 2007), and the IWC now recognizes French Polynesia as breeding stock F2, separate from the Cook Islands and other areas to the west in breeding stock E (IWC report 2008). Although some limited exchange has been documented between French Polynesia and other breeding grounds in the South Pacific, there are no documented accounts of migratory connections between this region and any Antarctic feeding areas.

Humpback whales from the Antarctic Peninsula migrate mainly along the west coast of South America to Ecuador and Colombia (Acevedo *et al.* 2008; Albertson-Gibb *et al.* 2008; Castro *et al.* 2008; Olavarría *et al.* 2007; Stevick *et al.* 2004; Caballero *et al.* 2001; Flórez-González *et al.* 1998; Stone *et al.* 1990), while a high proportion of the Strait of Magellan humpback whales are thought to migrate to Central America (Panama and Costa Rica) (Acevedo *et al.* 2007; Acevedo *et al.* 2008). In addition, whales along the west coast of South America (breeding stock G) are genetically differentiated from other breeding stocks in the South Pacific, including breeding Stock F (mtDNA control region $F_{ST} = 0.076$), and are genetically very similar to whales from the Antarctic Peninsula (mtDNA control region $F_{ST} = 0.001$) (Olavarría *et al.* 2007; Albertson-Gibb *et al.* 2008). However, recently there has been more documentation on connections between whales in Breeding Stock F and whales along the coast of South America and the Antarctic Peninsula. A photo-identification match was identified between American Samoa, on the border of breeding stocks E and F, and the Antarctic Peninsula (Robbins *et al.* 2008). In addition, a genotype match was identified between French Polynesia (Stock F) and Colombia (Stock G) (Donoghue *et al.* 2008), the first documented movement between breeding stocks F and G. Since the Antarctic Peninsula is considered the primary feeding area of breeding stock G this discovery presents the possibility that some whales from French Polynesia may migrate to the Antarctic Peninsula. The individual was seen in Colombia in 1995 (Mno95Co052) and French Polynesia in 2003 (Mno03FP017) which most likely implies the transition between the two regions happened in the feeding areas and not the breeding grounds. The individual could have migrated to the Antarctic Peninsula from Colombia, and at some point migrated to French Polynesia from the Antarctic Peninsula feeding area.

The comparison of photographs of the ventral side of the humpback whale flukes has successfully shown migratory links from breeding grounds to feeding areas. In the Southern Hemisphere these connections include Western Australia to Antarctic Area IV (Gill & Burton *et al.* 1995); Eastern Australia to Antarctic Area V (Franklin *et al.* 2008), and Colombia to the Antarctic Peninsula (Stevick *et al.* 2004). In this report, we present a collaborative comparison of individual humpback whale fluke photographs to explore possible migratory connections between French Polynesia and the Antarctic Peninsula/Strait of Magellan (AP/SM).

4.2 MATERIALS AND METHODS

4.2.1 Sample Collection

Identification photographs were collected from three study sites. The photo-identification surveys were carried out opportunistically in French Polynesia beginning in 1990 with dedicated surveys beginning in 1999 (Table 4.1). These surveys were generally conducted within 500 meters of shore during the Austral winter between the months of July through November. However, surveys are conducted year round for other species, and if whales were seen outside of these months every effort was made to attain photos of the flukes. In the AP/SM dedicated boat surveys have been conducted annually. In the Antarctic Peninsula these surveys are conducted between December and February, and in the Strait of Magellan they are conducted between December and May (Table 4.1).

4.2.2 Photo-identification catalogues

Photos were reconciled within regions annually by the primary catalogue holders and new individual whales were assigned a unique number for

identification purposes. Beginning in 1999 as part of the South Pacific Whale Research Consortium's interchange comparison, French Polynesia photos have been compared annually with all other Oceania breeding grounds (stocks E and F). In order to decrease the human error rate in matching of our comparison, two researchers compared all photos independently of each other. A total of 450 French Polynesia photos were compared against 276 photos from the Antarctic Peninsula and 93 photos from the Strait of Magellan.

4.3 RESULTS

4.3.1 *Photo matching*

Capture-recapture methodology using fluke photo-identification of whales' flukes has proven to be a powerful tool to link individual whales from breeding grounds to feeding areas. Comparisons of the French Polynesia catalogue to each of the AP, and SM catalogues were made using 450 individual humpback whale photographs from the French Polynesia breeding ground and 276 and 93 photographs from AP and SM feeding areas respectively (Table 4.1). A possible match was first identified by Jorge Acevedo in November of 2008 between Antarctic Peninsula INACH photo 076 taken January 12, 1997 and French Polynesia photo 0014 taken in September 2000 (Figure 4.2). These photos were later examined by members of the South Pacific Whale Research Consortium at the annual meeting in February 2009. It was agreed that there were similarities between the two photographs however, it could not be concluded that this was a match due to poor clarity of the French Polynesia photo. No other putative matches were found between the two catalogues, by either of the two independent researchers.

4.3.2 Probability of capture

In an attempt to accept or reject the hypothesis that French Polynesia whales use the AP/SM as the primary breeding ground I considered approximately how many humpback whales would likely be “captured” or sighted between the two regions if French Polynesia humpbacks were completely intermingling with humpbacks from Breeding Stock G in the Antarctic Peninsula. To illustrate this I used population sizes from current abundance estimates for French Polynesia, (Breeding Stock F2 $N_{2008} = 1,724$ CI 1,187-2,583; Albertson-Gibb *et al.* unpublished) and AP/SM (Breeding Stock G $N_{2006} = 6,847$ CI 5,243-8,632; IWC Report 2008). A modification of the Lincoln-Petersen estimate yields:

Equation 1 $\frac{(C_{FP})(C_{AP/SM})}{N_{AP}} = N_{match}$, number of matches that should be found

$$N_{AP}$$

Where

C_{FP} is the number of French Polynesia individuals in the photo catalogue

$C_{AP/SM}$ is the number of AP/SM individuals in the photo catalogue

N_{AP} is the number of individuals assumed to be sharing the feeding area (sum of N_{2006} Breeding Stock G and N_{2008} Breeding Stock F2).

Equation 1 then yields $\frac{(450)(369)}{(8,571)} = 19$

This equation indicates in order for the Antarctic Peninsula to be the primary feeding area of French Polynesia we should have seen approximately 19 matches between the French Polynesia and AP/SM catalogues.

4.4 DISCUSSION

Although the possibility exists of migratory movements between breeding stock F and the Antarctic Peninsula, similar to those detected between American Samoa (border of breeding stock E/F) and the Antarctic Peninsula (Robbins *et al.* 2008) we documented no such connection here. Despite making 166,050 comparisons, no conclusive matches were found between French Polynesia and the AP/SM. Only one possible French Polynesia-AP/SM match was found, and due to the poor clarity of one of the photos we cannot confidently conclude that it is indeed, a match. Since we found zero conclusive matches we can reject the null hypothesis that the Antarctic Peninsula/Strait of Magellan is the primary feeding area of French Polynesia. However, given the known limitations of photo-identification matching, in particular the limited number of whales sampled compared to the current population estimates, these findings do not rule out the possibility of whales from French Polynesia traveling to the Eastern South Pacific waters especially in light of the genetic match between French Polynesia and Colombia (Donoghue *et al.* 2008). Given that there seems to be great complexity in humpback whale population structure (Calambokidis *et al.* 2001), possible migratory connections that are not directly north-south should continue to be investigated. Long term photo-identification studies and genetic analyses can provide accurate definition of stocks and migration between them which is essential to the recovery of the South Pacific humpback whale population.

ACKNOWLEDGEMENTS

The authors wish to thank the International Fund for Animal Welfare for providing funding for the fieldwork in French Polynesia. Rochelle Constantine,

Claire Garrigue and the South Pacific Whale Research Consortium kindly provided information on photo matches between the South Pacific breeding regions.

LITERATURE CITED

- Acevedo J., Rasmussen K., Félix F., Castro C., Llano M., Secchi E., Saborío M., Aguayo-Lobo A., Haase B., Scheidat M., Dalla-Rosa L., Olavarria C., Forestell P., Acuña P., Kaufman G. and Pastene LA. (2007) Migratory destinations of humpback whales from the Magellan Strait feeding ground, Southeast Pacific. *Mar. Mammal Sci.* 23(2): 453-463.
- Acevedo J. , Allen J. , Castro C., Félix F., Rasmussen K., Flórez-González L., Aguayo-Lobo A., Secchi E., Llano M. , Garita F. , Forestell P. , Haase B. , Capella J., Dalla Rosa L., Ferrina D., Plana J., Tobón IC., Kaufman G., Flak P., Scheidat M. & Pastene LA (2008). Migratory destination of humpback whales from the Eastern South Pacific population as revealed by photo-identification analysis. Paper SC/60/SH20 Presented to the IWC Scientific Committee, June 2008 (unpublished). 8pp.
- Albertson-Gibb, R., C. Olavarria, D. Steel, L. Florez-González, C. Garrigue, N. Hauser, M. Poole, M. Anderson, J. Bannister, J. Jackson, C. Antolik, and C. S. Baker (2008). Mixed-Stock Analysis of Humpback Whales (*Megaptera novaeangliae*) from Antarctic Feeding Areas and South Pacific Breeding Grounds. Paper SC/60/SH15 Presented to the IWC Scientific Committee, June 2008 (unpublished). 6pp.
- Calambokidis J, Steiger GH, Straley JM, Herman LM, Cerchio S, Salden DR, Urbán R. J, Jacobson JK, vonZiegesar O, Balcomb KC, Gabrielle CM, Dahlheim ME, Uchida S, Ellis G, Miyamura Y, Ladrón de Guevara P. P, Yamaguchi M, Sato F, Mizroch SA, Schlender L, Rasmussen K, Barlow J, Quinn II TJ (2001) Movements and population structure of humpback whales in the North Pacific. *Marine Mammal Science* 17:769-794.
- Castro, C., Acevedo J., Allen J., Dalla Rosa L., Flórez-González L., Aguayo-Lobo A., Rasmussen K., Llano M., Garita F., Forestell P., Secchi E., García-Godos I., Ferrina D., Kaufman G., Scheidat M. & Pastene LA. (2008) Migratory movements of humpback whales (*Megaptera novaeangliae*) between Machalilla National Park, Ecuador and Southeast Pacific. Paper SC/60/SH23. Presented to the IWC Scientific Committee, June 2008 (unpublished). 6pp.
- Clapham, P.J. and Baker, C.S. (2008) Modern Whaling. In: Perrin, W.F., Wursig, B. and Thewissen, J.G.M. (eds.) *Encyclopedia of Marine Mammals*, pp.1328-1332. Academic Press, San Diego.

- Dalla Rosa, L, Secchi, E.R., Maia, Y.G., Zerbini, A., Heide-Jorgensen, M.P. (2008). Movements of satellite-monitored humpback whales on their feeding ground along the Antarctic Peninsula. *Polar Biol* 31: 771-781.
- Dawbin, W.H. (1966) The seasonal migratory cycle of humpback whales. Pages 145-171 in K.S. Norris, ed. Whales, dolphins and porpoises. University of California Press, Berkeley.
- Donoghue, M. (2008) Report of the Annual Meeting of the South Pacific Whale Research Consortium. Paper SC/60/SH21 presented to the IWC Scientific Committee, June 2008 (unpublished). 14pp.
- Florez -Gonzalez L., Capella J., Haase B., Bravo G.A., Felix F. and Gerrodette T. (1998). Changes in winter destinations and the northernmost record of southeastern pacific humpback whales. *Mar. Mammal Sci.* 14(1)189-196.
- Franklin, W., Franklin, T., Brooks, L., Gibbs, N., Childerhouse, S., Smith, F., Burns, D., Paton, D., Garrigue, C., Constantine, R., Poole, M.M., Hauser, N., Donoghue, M., Russell, K., Mattila, D., Robbins, J., Oosterman, A., Leaper, R., Baker, S., and P. Clapham. (2008). Migratory movements of humpback whales (*Megaptera novaeangliae*) between Eastern Australia and the Balleny Islands, Antarctica, confirmed by photo-identification. Paper SC/60/SH2. Presented to the IWC Scientific Committee, June 2008 (unpublished). 6pp.
- Gill PC, Burton CLK (1995) Photographic resight of a humpback whale between Western Australia and Antartic Area IV. *Marine Mammal Science* 11:96-100.
- Hauser, N., Zerbini, A., Geyer, Y., Heide-Jorgensen, M-P. and Clapham, P. (2009) Movements of satellite-monitored humpback whales, megaptera novaeangliae, from the Cook Islands *Mar Mamm Sci* in press.
- Katona S, Baxter B, Brazier O, Kraus S, Perkins J, Whitehead H (1979) Identification of humpback whales by fluke photographs. In: Winn HE, Olla BL (eds) *Behavior of Marine Animals*, Vol. 3. Plenum Press, New York, p 33-44.
- International Whaling Commission Report on southern hemisphere humpback whales (2006). SC-58-Rep 5.
- International Whaling Commission Report of the Sub-Committee on Other Southern Hemisphere Whale Stocks (SH) (2008) Annex H. 30 pp.
- Olavarría, C., Baker, C.S., Bannister, J., Brasseur, M., Caballero, S., Capella, J., Clapham, P., Dodemont, R., Donaghue, M., Jenner, C., Jenner, M.M., Moro, D.J., Florez-González, L., Hauser, N., Oremus, M., Paton, D., Poole, M., Rosenbaum, H., Russell, K. (2007) Population structure of South Pacific humpback whales and the origin of the eastern Polynesian breeding grounds. *Marine Ecology Progress Series*. 330: 257-268.
- Poole, M.M. (2006) An update on the occurrence of humpback whales in French Polynesia. SC/A06/58 Presented to the IWC Scientific Committee, June 2006 (unpublished). 12 pp.

- Robbins J., Dalla Rosa L., Allen JM., Mattila DK & Secchi ER (2008) Humpback whale photo-identification reveals exchange between American Samoa and the Antarctic Peninsula, and a new mammalian distance record. Paper SC/60/SH5. Presented to the IWC Scientific Committee, June 2008 (unpublished). 4 pp.
- Steel, D., Garrigue, C., Poole, M., Hauser, N., Olavarria, C., Flórez-González, L., Constantine, R., Caballero, S., Thiele, D., Paton, D., Clapham, P., Donoghue, M., and Baker, C.S. (2008) Migratory connections between humpback whales from South Pacific breeding grounds and Antarctic feeding areas demonstrated by genotype matching. Paper SC/60/SH13. Presented to the IWC Scientific Committee, June 2008 (unpublished). 9pp.
- Stevick, P.T., Palsbøll, P.J., Smith, T.D., Bravington, M.V. and Hammond, P.S. (2001) Errors in identification using natural markings: rates, sources and effects on capture-recapture estimates of abundance. *Can. J. Fish. Aquat. Sci.* 58:1861-70.
- Stevick P.T., Aguayo-Lobo A, Allen J, Avila IC, Capella J, Castro C, Chater K, Dalla Rosa L, Engel MH, Félix F, Flórez-González L, Freitas A, Haase B, Llano M, Lodi L, Muñoz E, Olavarria C, Secchi E, Scheidat M and Siciliano S (2004) Migrations of individually identified humpback whales between the Antarctic Peninsula and South America. *Journal of Cetacean Research and Management* 6: 109-113.
- Stone G., Flórez-González L. and Katona S. (1990) Whale migration record. *Nature* 346: 705.
- Townsend CH (1935) The distribution of certain whales as shown by logbook records of American whaleships. *Zoologica* 19:1-50.

Table 4-1. Antarctic Peninsula (INACH), and Strait of Magellan (CEQUA) and French Polynesia humpback whale photo-identification catalogues used in the comparison of the Feeding Regions and Breeding Stock.

Year	Antarctic Peninsula Feeding Region Area I		Strait of Magellan Feeding Region Area I		French Polynesia Breeding Stock F2	
	Number of Individuals	Time Period	Number of Individuals	Time Period	Number of Individuals	Time Period
1990- 1993	--	--	--	--	11	July-Nov.
(1994) 1995	23	Dec.-Jan.	--	--	2	July -Nov.
1996	40	Jan.-Feb.	--	--	5	July -Nov.
1997	46	Jan.-Feb.	--	--	17	July -Nov.
1998	20	Jan.- Feb.	--	--	9	July -Nov.
1999	39	Jan.-Feb.	--	--	46	July -Nov.
2000	--	--	--	--	29	July -Nov.
2001	--	--	--	--	27	July -Nov.
2002	--	--	--	--	42	July -Nov.
2003	--	--	11	March	59	July -Nov.
(2003) 2004	--	--	27	Dec.-Mar.	62	July -Nov.
(2004) 2005	--	--	28	Dec.-April	52	July -Dec.
(2005) 2006	55	January	16	Dec.- May	28	July -Nov.
(2006) 2007	9	January	11	Dec.-June	61	July -Dec.
2008	44	Jan.-Feb.	--	--	--	--
Total	276		93		450	

Figure 4.1 Map of South Pacific humpback whale migratory connections of genotype data (solid line) and *Discovery Mark* data and one satellite tag from Cook Islands (dashed line) and photo-identification (dotted line) (Steel *et al.* 2008; Stevick *et al.* 2004; Franklin *et al.* 2008; Gill & Burton 1995; Hauser *et al.* in press; Robbins *et al.* 2008; Donoghue *et al.* 2008)

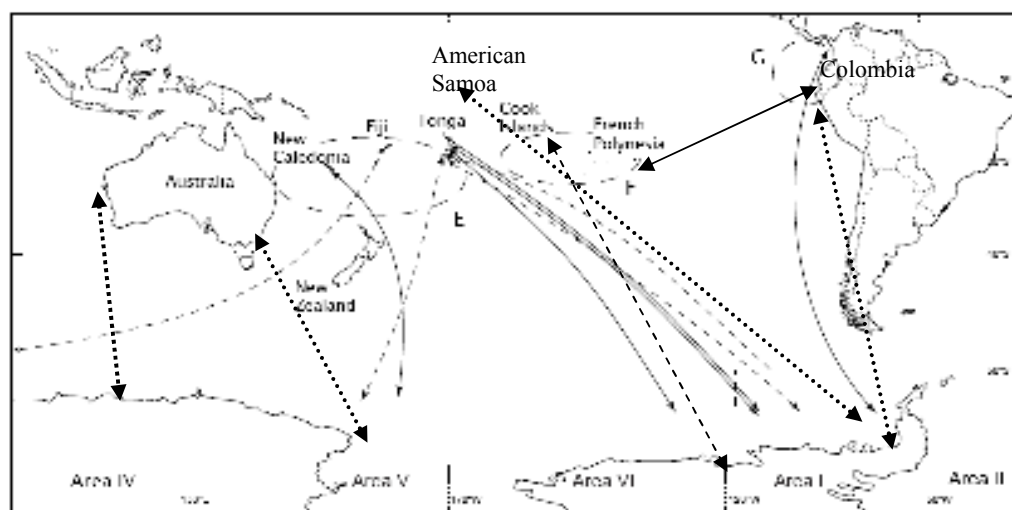
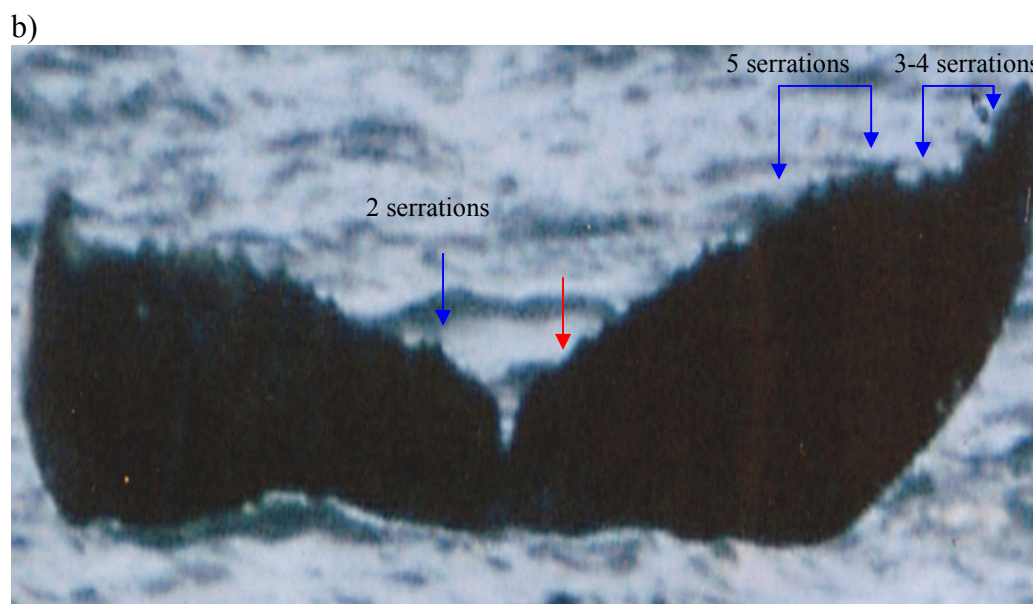
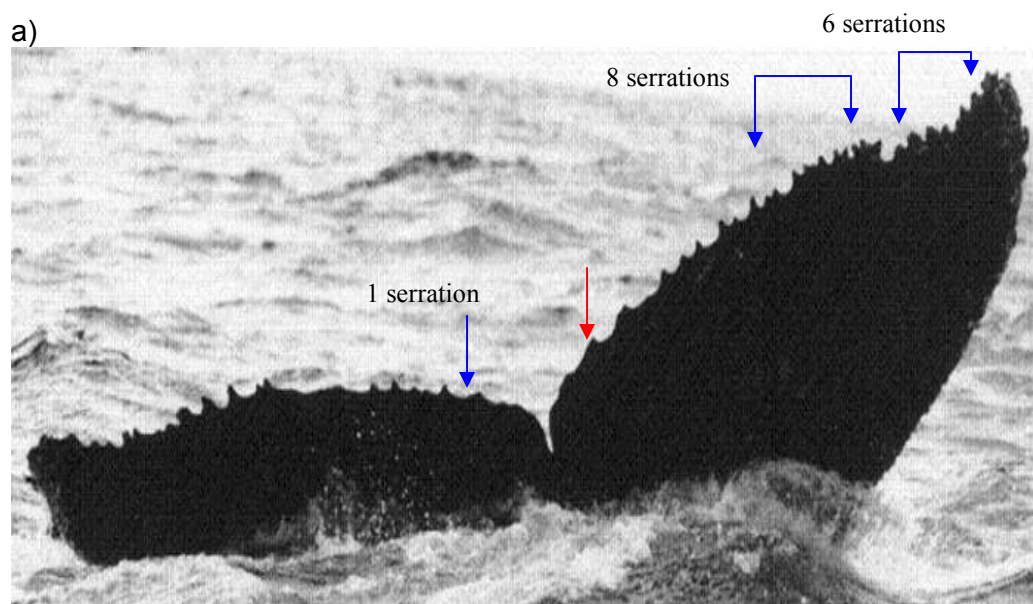


Figure 4.2. Two humpback whale fluke photos identified as showing many similarities a) INACH 076 Antarctic Peninsula photo and b) French Polynesia photo FP 0014.



Chapter 5 – General Conclusion

Effective conservation strategies need to consider the temporal distribution of species throughout their range. This study represented the continuation of the efforts of Olavarria *et al.* (2007) on the population structure of South Pacific humpback whales, and specifically French Polynesia, to better understand migratory connections and current abundance. Genetic markers were implemented to infer migratory apportionments of feeding areas to breeding grounds at the population level (mtDNA haplotypes). In addition photo-identification was used to estimate abundance for French Polynesia, one of the least studied breeding stocks in the South Pacific, and investigate the possibility of migratory connections between French Polynesia and the Antarctic Peninsula/Strait of Magellan.

This work was driven by the limited information available regarding migratory connections and abundance of the South Pacific humpback whales, breeding stocks considered 'Endangered' by the IUCN. The illegal whaling by the Soviets until 1974 including the intensive hunting of humpbacks for the seasons 1959/60-1960/61 in Areas V and VI, has had a lasting impact on these populations, and surely contribute to their slow recovery (Clapham *et al.* 2009). A comprehensive understanding of population structure in the South Pacific requires allocation of historical catches be carried out to determine connections of feeding areas to breeding grounds. French Polynesia remains one of the only breeding stocks in the South Pacific where no previous connections to Antarctic feeding areas have been made. In addition, other quantitative population dynamic components including abundance can be used as a baseline for future

measurements of population growth to test for recovery from commercial whaling.

5.1 Mixed stock analysis of Oceania and West and East Australia

In chapter 2 I examined the first population analysis to allocate South Pacific breeding grounds from Antarctic feeding areas. Based on data from individual studies I hypothesized that humpback whales may be migrating to adjacent feeding areas as opposed to traditional management of the breeding stocks which assume a north south direction. My results indicated Area VI and at least the western edge of Area I should be considered a possible feeding area destination for the further assessment of Tonga and Cook Islands. Despite a somewhat large sample size for French Polynesia it was not apparent where these whales were migrating although it is suggested by preliminary microsatellite analysis (Appendix A) they may migrate near the border of Area VI/I.

Area V is also important given the proposal by the Japanese government to allocate an annual catch of humpback whales in this region for scientific purposes. If whales from New Caledonia are using this area, as shown by the preliminary mixed-stock analysis of Area V, it is imperative to understand the degree of mixing by smaller, slower recovering stocks from Oceania with more abundant stocks like East Australia (Gales *et al.* 2007).

5.2 French Polynesia abundance estimate

French Polynesia is one of the least studied areas in Oceania, so an abundance estimate was employed as part of the International Whaling Commission's (IWC) Comprehensive Assessment to gain fundamental information on South Pacific breeding stocks. It has been demonstrated here that the use of Quality Control photographs is an important component of a

photo-identification abundance estimate. Quality Control is used to minimize the likelihood of missing a match by removing marginal quality photographs which can introduce a positive bias in estimates. However, by removing marginal quality photographs in the Quality Control process a reduction in the sample size is created of both sightings and resightings and could pose an unintended negative bias. Despite the possible biases in Quality Control my results showed the confidence intervals overlapped for the Usable Photos and Quality Control catalogues presenting a range estimate incorporating both Usable Photos and Quality Control of the 5-year closed population model of 853-1,849 individuals. In addition, I recommended the continued use of Quality Control and the use of microsatellite genotypes in the future to help assess heterogeneity in the population including fluking behavior and possible sex bias dispersal shown to be factors in other South Pacific humpback stocks.

5.3 Photo Comparison of French Polynesia and Antarctic Peninsula/Magellan Strait

To date there are no migratory connections between French Polynesia and the Antarctic. However, there was a microsatellite genotype match between French Polynesia and Colombia. In Chapter 4 I hypothesized that the Antarctic Peninsula was the primary feeding area of French Polynesia. Since the Antarctic Peninsula appears to be the primary feeding area of Colombia as presented in Chapter 2 it is possible that this individual who was first seen in Colombia, migrated to the feeding area in the Antarctic Peninsula before migrating at some later time to French Polynesia and therefore, the Antarctic Peninsula may also be the primary feeding area of French Polynesia. I examined fluke photo-identification catalogues comparing French Polynesia to the Antarctic Peninsula and Strait of Magellan for a possible match. I did not find any conclusive matches. Since I should have found approximately 19 matches considering the

size of the photo catalogues and the size of the Antarctic Peninsula population if the French Polynesia humpback whales are truly intermingling with the Antarctic Peninsula whales, I rejected the null hypothesis that the Antarctic Peninsula/Strait of Magellan are the primary feeding areas of French Polynesia. Although it was not determined where the primary feeding area of French Polynesia is, this study provides baseline information on French Polynesia humpback whales and does corroborate with the population analysis in Chapter 2 that French Polynesia humpback whales may have a primary feeding area in the Antarctic that is yet to be comprehensively sampled.

5.4 Management implications

The greatest threat to South Pacific humpback whales is scientific whaling. The degree of mixing on the feeding grounds is still relatively unknown, but has been shown to be very complex (Calambokidis *et al.* 2001, Dalla Rosa *et al.* 2008). The low abundance and low interchange in the breeding grounds of Oceania present too many uncertainties to allow catch allocations while still striving to reach sustainable levels in the humpback whale population.

A more concerted and systematic sampling of the Antarctic areas, especially Areas V and VI is needed to complement the coordinated sampling of breeding grounds in Oceania. This study, and several individual migratory connection studies previously, (Steel *et al.* 2008, Robbins *et al.* 2008, Franklin *et al.* 2008, Gill & Burton 1995, Acevedo *et al.* 2008) have found humpback whales may not be traveling directly north south in their migration. Management considerations need to include the possibility of humpback whale breeding stocks traveling to adjacent feeding areas.

In French Polynesia little has been documented on the use of islands other than Moorea and Rurutu by humpback whales. From previous work it

appears the humpbacks around Moorea and Rurutu are different whales than the whales found in the Tuamotus and Gambier islands (Gannier 2004, Poole 2006). A study collecting biopsy and fluke photographs from whales in the outer Tuamotus and northern Gambier island groups coupled with the continuation of sample collection in Moorea and Rurutu could allow for a comprehensive study on residence times and the use of French Polynesia waters by humpback whales.

Diverse populations are more productive and resilient than uniform populations. The extirpation of small stocks of humpbacks, especially stocks that are spread throughout vast regions like Oceania and Antarctic Areas V and VI known to have little interchange (Garrigue *et al.* 2007), run the risk of becoming more isolated from each other and further restricting gene flow. Not only does this equate to lower genetic fitness, but in extreme cases can result in hybridization with other closely related species as shown with blue whales (Donoghue *et al.* 2008). Humpback whales in the South Pacific are beginning to show signs of recovery from 20th century commercial whaling. The information presented here regarding migration and abundance is important for the Comprehensive Assessment of Southern Hemisphere humpback whales which the IWC will use to craft informed management decisions for the future of these endangered populations.

LITERATURE CITED

Calambokidis J, Steiger GH, Straley JM, Herman LM, Cerchio S, Salden DR, Urbán R. J, Jacobson JK, vonZiegesar O, Balcomb KC, Gabrielle CM, Dahlheim ME, Uchida S, Ellis G, Miyamura Y, Ladrón de Guevara P. P, Yamaguchi M, Sato F, Mizroch SA, Schlender L, Rasmussen K, Barlow J, Quinn II TJ (2001) Movements and population structure of humpback whales in the North Pacific. *Marine Mammal Science* 17:769-794.

- Franklin, W., Franklin, T., Brooks, L., Gibbs, N., Childerhouse, S., Smith, F., Burns, D., Paton, D., Garrigue, C., Constantine, R., Poole, M.M., Hauser, N., Donoghue, M., Russell, K., Mattila, D., Robbins, J., Oosterman, A., Leaper, R., Baker, S., and P. Clapham. (2008). Migratory movements of humpback whales (*Megaptera novaeangliae*) between Eastern Australia and the Balleny Islands, Antarctica, confirmed by photo-identification. Paper SC/60/SH2. Presented to the IWC Scientific Committee, June 2008 (unpublished). 6pp.
- Gill PC, Burton CLK (1995) Photographic resight of a humpback whale between Western Australia and Antarctic Area IV. *Marine Mammal Science* 11:96-100.
- Gannier A (2004) The large-scale distribution of humpback whales (*Megaptera novaeangliae*) wintering in French Polynesia during 1997-2002. *Aquatic Mammals* 30:227-236.
- International Whaling Commission Report on southern hemisphere humpback whales (2006). SC-58-Rep 5. Unpublished 12 pp.
- Jackson, J.A., Zerbini, A., Clapham, P., Constantine, R., Garrigue, C., Hauser, N., Poole, M.M., Baker, C.S. (2008). Progress on a two-stock catch allocation model for reconstructing population histories of east Australia and Oceania. Paper SC/60/SH14 presented to the IWC Scientific Committee, June 2008 (unpublished). 12 pp.
- Poole M (2006) An update on the occurrence of humpback whales (*Megaptera novaeangliae*) in French Polynesia. Report SC/A06/58 to the Scientific Committee of the International Whaling Commission. Hobart, Australia.
- Robbins J., Dalla Rosa L., Allen JM., Mattila DK & Secchi ER (2008) Humpback whale photo-identification reveals exchange between American Samoa and the Antarctic Peninsula, and a new mammalian distance record. Paper SC/60/SH5. Presented to the IWC Scientific Committee, June 2008 (unpublished). 4 pp.
- Steel, D., Garrigue, C., Poole, M., Hauser, N., Olavarria, C., Flórez-González, L., Constantine, R., Caballero, S., Thiele, D., Paton, D., Clapham, P., Donoghue, M., and Baker, C.S. (2008) Migratory connections between humpback whales from South Pacific breeding grounds and Antarctic feeding areas demonstrated by genotype matching. Paper SC/60/SH13. Presented to the IWC Scientific Committee, June 2008 (unpublished). 9pp.

Bibliography

- Abernethy RB, Baker CS, Cawthorn MW (1992) Abundance and genetic identity of humpback whales (*Megaptera novaeangliae*) in the Southwest Pacific, Report SC/44/O20 to the Scientific Committee of the International Whaling Commission. Glasgow, UK.
- Acevedo J. , Allen J. , Castro C., Félix F., Rasmussen K., Flórez-González L., Aguayo-Lobo A., Secchi E., Llano M. , Garita F. , Forestell P. , Haase B. , Capella J., Dalla Rosa L., Ferrina D., Plana J., Tobón IC., Kaufman G., Flak P., Scheidat M. & Pastene LA (2008). Migratory destination of humpback whales from the Eastern South Pacific Population as revealed by photo identification analysis. Working paper in the 60th meeting of International Whaling Commission Santiago Chile.
- Acevedo J, Rasmussen K, Félix F, Castro C, Llano M, Secchi E, Saborio MT, Aguayo-Lobo A, Haase B, Scheidat M, Dalla-Rosa L, Olavarria C, Forestell P, Acuña P, Kaufman G, Pastene L (2007) Migratory destination of humpback whales from the Magellan Strait feeding ground, Southeast Pacific. *Marine Mammal Science* 23:453-463.
- Acevedo J, Acuña P, Olavarria C, Aguayo-Lobo A, Pastene LA (2004) Report of cetacean surveys in the Magellan Strait in the austral summer 2003/2004, Report SC/56/O7 to the Scientific Committee of the International Whaling Commission. Sorrento, Italy.
- Acevedo-Gutiérrez A, Smultea MA (1995) First records of humpback whales including calves at Golfo Dulce and Isla del Coco, Costa Rica, suggesting 140 geographical overlap of northern and southern hemisphere populations. *Marine Mammal Science* 11:554-560
- Agresti, A (1994) Simple Capture-Recapture Models Permitting Unequal Catchability and Variable Sampling Effort. *Biometrics* 50: 494-500.
- Alaska Department of Fish and Game. 2003. SPAM Version 3.7: Statistics Program for Analyzing Mixtures. Alaska Department of Fish and Game, Commercial Fisheries Division, Gene Conservation Lab.
- Albertson-Gibb, R., C. Olavarria, D. Steel, L. Florez-González, C. Garrigue, N. Hauser, M. Poole, M. Anderson, J. Bannister, J. Jackson, C. Antolik, and C. S. Baker (2008). Mixed-Stock Analysis of Humpback Whales (*Megaptera novaeangliae*) from Antarctic Feeding Areas and South Pacific Breeding Grounds. Working paper SC/60/SH15 in the 60th meeting of International Whaling Commission Santiago Chile.
- Amos W, Hoelzel AR (1991) Long-term preservation of whale skin for DNA analysis. In: Hoelzel AR (ed) Genetic ecology of whales and dolphins, Vol (Special Issue 13). Report of the International Whaling Commission International Whaling Commission, Cambridge, p 99-104.

- Amos W, Whitehead H, Ferrari MJ, Glockner-Ferrari DA, Payne R, Gordon J (1992) Restrictable DNA from sloughed cetacean skin: its potential for use in population analysis. *Marine Mammal Science* 8:275-283
- Anderson, E.C., Waples, R.S., and Kalinowski, S.T. (2008) An improved method for predicting the accuracy of genetic stock identification. *Can. J. Fish. Aquat. Sci.* 65: 1475-1486.
- Árnason Ú, Gullberg A, Widegren B (1991) The complete nucleotide sequence of the mitochondrial DNA of the fin whale, *Balaenoptera physalus*. *Journal of Molecular Evolution* 33:556-568
- Árnason Ú, Gullberg A, Widegren B (1993) Cetacean mitochondrial DNA control region: sequences of all extant baleen whales and two sperm whale species. *Molecular Biology and Evolution* 10:960-970.
- Avise JC (1994) Natural history of genetic markers, Vol. Chapman and Hall, New York.
- Baker, CS, Dalebout, ML (2008) Forensic Genetics. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Academic Press, San Diego, p 453-457.
- Baker CS, Flórez-González L, Abernethy B, Rosenbaum HC, Slade RW, Capella J, Bannister JL (1998a) Mitochondrial DNA variation and maternal gene flow among humpback whales of the Southern Hemisphere. *Marine Mammal Science* 14:721-737.
- Baker CS, Gilbert DA, Weinrich MT, Lambertsen RH, Calambokidis J, McArdle B, Chambers GK, O'Brien SJ (1993a) Population characteristics of DNA fingerprints in humpback whales (*Megaptera novaeangliae*). *The Journal of Heredity* 84:281-290.
- Baker CS, Herman LM, Perry A, Lawton WS, Straley JM, Straley JH (1985) Population characteristics and migration of summer late-season humpback whales (*Megaptera novaeangliae*) in southeastern Alaska. *Marine Mammal Science* 1:304-323.
- Baker CS, Herman LM, Perry A, Lawton WS, Straley JM, Wolman AA, Kaufman GD, Winn HE, Hall JD, Reinke JM, Ostman J (1986) Migratory movement and population structure of humpback whales (*Megaptera novaeangliae*) in the central and eastern North Pacific. *Marine Ecology Progress Series* 31:105-119.
- Baker CS, Lukoschek V, Lavery S, Dalebout ML, Yong-un M, Endo T, Funahashi N (2006) Incomplete reporting of whale, dolphin and porpoise 'bycatch' revealed by molecular monitoring of Korean markets. *Animal Conservation* 9:474-482.
- Baker, C.S., C. Garrigue, R. Constantine, B. Madon, M. Poole, N. Hauser, P. Clapham, Donoghue, K. Russell, T. O'Callahan, D. Paton, and D. Mattila.

- (2006) Abundance of humpback whales in Oceania (South Pacific), 1999 to 2004. Unpublished report SC/A06/HW51 for consideration the inter-sessional workshop for the comprehensive assessment of Southern Hemisphere humpback whales, Hobart, Tasmania. 2006.
- Baker CS, Medrano-González L (2002) World-wide distribution and diversity of humpback whale mitochondrial DNA lineages. In: Pfeiffer CJ (ed) *Molecular and cell biology of marine mammals*. Krieger Publishing Co., Inc, Melbourne, FL, p 84-99.
- Baker CS, Medrano-Gonzalez L, Calambokidis J, Perry A, Pichler FB, Rosembaum H, Straley JM, Urban-Ramirez J, Yamaguchi M, Von Ziegesar O (1998b) Population structure of nuclear and mitochondrial DNA variation among humpback whales in the North Pacific. *Molecular Ecology* 7:695-707.
- Baker CS, Palumbi SR (1997) The genetic structure of whale populations: implications for management. In: Dizon AE, Chivers SJ, Perrin WF (eds) *Molecular genetics of marine mammals*. Special Publication Number 3, *The Society for Marine Mammalogy*, Lawrence, KS, p 117-146.
- Baker CS, Palumbi SR, Lambertsen RH, Weinrich MT, Calambokidis J, O'Brien SJ (1990) Influence of seasonal migration on the distribution of mitochondrial DNA haplotypes in humpback whales. *Nature* 344:238-240.
- Baker CS, Perry A, Bannister JL, Weinrich MT, Abernethy RB, Calambokidis J, Lien J, Lambertsen RH, Urbán-Ramírez J, Vásquez O, Clapham PJ, Alling A, O'Brien SJ, Palumbi SR (1993b) Abundant mitochondrial DNA variation and world-wide population structure in humpback whales. *Proceedings of the National Academy of Sciences, USA* 90:8239-8243.
- Baker CS, Perry A, Herman LM (1987) Reproductive histories of female humpback whales *Megaptera novaeangliae* in the North Pacific. *Marine Ecology Progress Series* 41:103-114.
- Baker CS, Slade RW, Bannister JL, Abernethy RB, Weinrich MT, Lien J, Urbán-Ramírez J, Corkeron P, Calambokidis J, Vásquez O, Palumbi SR (1994) Hierarchical structure of mitochondrial DNA gene flow among humpback whales *Megaptera novaeangliae*, world-wide. *Molecular Ecology* 3:313-327.
- Bannister J (2005) Intersessional working group on Southern Hemisphere humpback whales: revised tables by breeding stock (as at 1 May 2005), Report SC/57/SH11 to the Scientific Committee of the International Whaling Commission. Ulsan, Korea. 30 May – 10 June.
- Bannister JL (1994) Continued increase in Group IV humpbacks off Western Australia. Report of the International Whaling Commission 44:309-310.
- Bannister JL, Hedley SL (2001) Southern Hemisphere group IV humpback whales: their status from recent aerial survey. *Memoirs of the Queensland Museum* 47:587-598.

- Bass, A.L., Epperly, S.P., & Braun-McNeill, J. 2004. Multi-year analysis of stock composition of a loggerhead turtle (*Caretta caretta*) foraging habitat using maximum likelihood and Bayesian methods. *Conservation Genetics* 5: 783-796.
- Berta, Annalisa; Sumich, James L.; Kovacs, Kit M. (2006) Marine Mammals Evolutionary Biology. Academic Press.
- Berube, MH, Jorgensen, H, McEwing R, Palsboll, PJ (2000) Polymorphic dinucleotide microsatellite loci isolated from the humpback whale, *Megaptera novaeangliae*. *Molec. Ec* 9: 2181-2183.
- Berzin, A. A. (2008) The truth about Soviet whaling. In Y. V. Ivashchenko, P. J. Clapham, and R. L. Brownell, Jr. (editors), The truth about Soviet whaling: a memoir, p. 1-59. [Transl. by Y. V. Ivashchenko]. *Mar. Fish. Rev* 70(2).
- Best PB, Bannister JL, Brownell Jr. RL, Donovan GP (eds) (2001) Right whales: worldwide status. *Journal of Cetacean Research and Management* (Special Issue 2), Vol. International Whaling Commission, Cambridge.
- Bolker, B., Okuyama, T., Bjørndal, K., Bolten, A. (2003) Sea Turtle Stock Estimation Using Genetic Markers: Accounting for sampling error of rare genotypes. *Ecological Applications* 13(3):763-775.
- Borge T, Bachmann L, Bjørnstad G, Wiig Ø (2007) Genetic variation in Holocene bowhead whales from Svalbard. *Molecular Ecology* 16:2223-2235.
- Bowen, B.W., Grant, W.S., Hills-Starr, Z., Shaver, D.J., Bjørnadal, A., Bolten, A.B., Bass, A.L. (2007) Mixed stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricate*) in the Caribbean Sea. *Molecular Ecology*. 16: 49-60.
- Branch TA (2006) Humpback abundance south of 60°S from three completed sets of IDCR/SOWER circumpolar surveys, Report SC/AO6/HW6 to the Intersessional workshop for the Comprehensive Assessment of Southern Hemisphere humpback whales Scientific Committee of the International Whaling Commission. Hobart, Australia. 3 – 7 April.
- Breiwick JM & York AE (2008) Stock Assessment In: Perrin WF, Würsig B, Thewissen JGM (eds) *Encyclopedia of Marine Mammals*. Academic Press, San Diego, p 1110-1115.
- Bromley, D.W. (2006) The dynamic between social systems and ocean ecosystems: Are there lessons from commercial whaling? In *Whales, Whaling and Ocean Ecosystems*. Estes, J. et al. Ed. University of California Press Berkeley and Los Angeles, California; Chapter 28.
- Brown GG, Gadeleta G, Pepe G, Saccone C, Sbisà E (1986) Structural conservation and variation in the D-loop containing region of vertebrate mitochondrial DNA. *Journal of Molecular Biology* 192:503-511.

- Brown M, Burt L (1998) Distribution of humpback whales sightings from IWC/IDR surveys. Annex G, Appendix 2. Report of the International Whaling Commission 48:179.
- Caballero S, Hamilton H, Jaramillo C, Capella J, Flórez-González L, Olavarria C, Rosenbaum HC, Guhl F, Baker CS (2001) Genetic characterisation of the Colombian pacific coast humpback whale population using RAPD and mitochondrial DNA sequences. *Memoirs of the Queensland Museum* 47:459-464.
- Calambokidis J, Steiger GH, Evenson JR, Flynn KR, Balcomb KC, Claridge DE, Bloedel P, Straley JM, Baker CS, von Ziegesar O, Dahlheim ME, Waite JM, Darling JD, Ellis G, Green GA (1996) Interchange and isolation of humpback whales off California and other North Pacific feeding grounds. *Marine Mammal Science* 12:215-226.
- Calambokidis J, Steiger GH, Straley JM, Herman LM, Cerchio S, Salden DR, Urbán R. J, Jacobson JK, vonZiegesar O, Balcomb KC, Gabrielle CM, Dahlheim ME, Uchida S, Ellis G, Miyamura Y, Ladrón de Guevara P. P, Yamaguchi M, Sato F, Mizroch SA, Schlender L, Rasmussen K, Barlow J, Quinn II TJ (2001) Movements and population structure of humpback whales in the North Pacific. *Marine Mammal Science* 17:769-794.
- Castro, C., Acevedo J., Allen J., Dalla Rosa L., Flórez-González L., Aguayo-Lobo A., Rasmussen K., Llano M., Garita F., Forestell P., Secchi E., García-Godos I., Ferrina D., Kaufman G., Scheidat M. & Pastene LA. (2008) Migratory movements of humpback whales (*Megaptera novaeangliae*) between Machalilla National Park, Ecuador and Southeast Pacific. Working paper SC/60/SH in the 60th meeting of International Whaling Commission Santiago Chile.
- Chittleborough RG (1959) Australian marking of humpback whales. *Norsk Hvalfangst-Tidende* 48:47-55.
- Chittleborough RG (1960) Intermingling of two populations of humpback whales. *Norsk Hvalfangst-Tidende* 10:510-521.
- Chittleborough RG (1965) Dynamics of two populations of humpback whales, *Megaptera novaeangliae* (Borowski). *Australian Journal of Marine and Freshwater Research* 16:33-128.
- Clapham, P (1997) Whales of the World. Vogageur Press, Inc. USA.
- Clapham P, Mikhalev Y, Franklin W, Paton D, Baker CS, Brownell Jr. RL (2005) Catches of Humpback Whales in the Southern Ocean, 1947-1973, Report SC/57/SH6 to the Scientific Committee of the International Whaling Commission. Ulsan, Korea.
- Clapham PJ (2002) The humpback whale. Seasonal feeding and breeding in a baleen whale. In: Mann J, Connor RC, Tyack PL, Whitehead H (eds).

- Clapham PJ & Baker CS (2008) Whaling, modern. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Academic Press, San Diego, p 1239-1243.
- Clapham PJ, Mattila DK, Palsbøll PJ (1993b) High-latitude-area composition of humpback whale competitive groups in Samana Bay: further evidence for panmixis in the North Atlantic population. *Canadian Journal of Zoology* 71:1065-1066.
- Clapham PJ, Mayo CA (1990) Reproduction of humpback whales (*Megaptera novaeangliae*) observed in the Gulf of Maine. Report of the International Whaling Commission (Special Issue 12):171-175.
- Clapham PJ, Mead JG (1999) *Megaptera novaeangliae*. *Mammalian Species* 604:1-9.
- Clapham PJ, Palsbøll PJ, Mattila DK (1993c) High-energy behaviors in humpback whales as a source of sloughed skin for molecular analysis. *Marine Mammal Science* 9:213-220.
- Clapham P.J. and Zerbini A. (2006). Is social aggregation driving high rates of increase in some Southern Hemisphere humpback whale populations? Paper SC/58/SH3 presented to the IWC Scientific Committee, May 2006 (unpublished). 12pp.
- Constantine R, Russell K, Gibbs N, Childerhouse S, Baker CS (2007) Photo identification of humpback whales (*Megaptera novaeangliae*) in New Zealand waters and their migratory connections to breeding grounds of Oceania. *Marine Mammal Science* 23:715-720.
- Craig AS, Herman LM (1997) Sex differences in site fidelity and migration of humpback whales (*Megaptera novaeangliae*) to the Hawaiian Islands. *Canadian Journal of Zoology* 75:1923-1933.
- Dawbin WH (1956) The migration of humpback whales as they pass the New Zealand Coast. *Transactions of the Royal Society of New Zealand* 84:147-196.
- Dawbin WH (1960) An analysis of the New Zealand catches of humpback whales from 1947 to 1958. *Norsk Hvalfangst-Tidende* 2:61-75.
- Dawbin WH (1964) Movements of humpback whales marked in the southwest Pacific Ocean 1952 to 1962. *Norsk Hvalfangst-Tidende* 53:68-78.
- Dawbin WH (1966) The seasonal migratory cycle of humpback whales. In: Norris KS (ed) Whales, Dolphins, and Porpoises. University of California Press, Berkeley and Los Angeles, p 145-171.
- Dawbin WH (1984) Whaling and its impact on the people of the South Pacific. In: Stanbury P, Bushell L (eds) South Pacific Islands. The Macleay Museum, The University of Sydney, Sydney, Australia, p 77-90.

- Dawbin WH (1997) Temporal segregation of humpback whales during migration in Southern Hemisphere waters. *Memoirs of the Queensland Museum* 42:105-138
- Dawbin WH, Falla RA (1949) A contribution to the study of the humpback whale based on observations at New Zealand shore stations 7th Pacific Science Congress, p 373-382.
- Dizon AE, Chivers SJ, Perrin WF (eds) (1997) Molecular genetics of marine mammals, Vol. Allen Press, Lawrence, Kansas, USA.
- Donovan GP (1989) Preface. In: Donovan GP (ed) The comprehensive assessment of whale stocks: the early years. Report of the International Whaling Commission (Special Issue 11). International Whaling Commission, Cambridge.
- Donovan GP (1991) A review of IWC stock boundaries. In: Hoelzel AR (ed) Genetic ecology of whales and dolphins. Report of the International Whaling Commission (Special Issue 13). International Whaling Commission, Cambridge, p 39-68.
- Ensor P, Matsuoka K, Komiya H, Ljungblad D, Miura T, Morse L, Olson P, Olavarria C, Mori M, Sekiguchi K (2004) 2003-2004 International Whaling Commission-Southern Ocean Whale and Ecosystem Research (IWC-SOWER) Circumpolar Cruise, Area V, Report SC/56/IA13 to the Scientific Committee of the International Whaling Commission. Sorrento, Italy. 29 June – 10 July.
- Ensor P, Matsuoka K, Marques F, Miura T, Murase H, Pitman R, Sakai K, Van Waerebeek K (2001) 2000-2001 International Whaling Commission - Southern Ocean Whale and Ecosystem Research (IWC-SOWER) Circumpolar Cruise, Areas V, VI and I, Report SC/53/IA5 to the Scientific Committee of the International Whaling Commission. London, UK.
- Excoffier L (1995) AMOVA: Analysis of Molecular Variance. University of Geneva, Geneva.
- Excoffier L, Laval G, Schneider S (2005) Arlequin ver. 3.1: An integrated software package for population genetics data analysis. *Evolutionary Bioinformatics Online* 1:47-50.
- Excoffier L, Smouse PE, Quattro JM (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics* 131:479-491.
- Eggert, LS, Eggert, JA, and Woodruff, DS (2003) Estimating population sizes for elusive animals: the forest elephants of Kakum National Park, Ghana. *Molecular Ecology* 12: 1389-1402.

- Félix F, Caballero S, Olavarria C (2007) A preliminary assessment of the genetic diversity in humpback whales (*Megaptera novaeangliae*) from Ecuador and population differentiation with other Southern Hemisphere breeding grounds and feeding areas, Report SC/59/SH11 to the Scientific Committee of the International Whaling Commission. Anchorage, USA.
- Felix F, Palacios DM, Caballero S, Haase B, Falconi J (2006) The Galápagos humpback whale expedition; a first attempt to assess and characterize the population in the archipelago, Report SC/A06/HW15 to the Inter-sessional workshop for the Comprehensive Assessment of Southern Hemisphere humpback whales Scientific Committee of the International Whaling Commission. Hobart, Australia.
- Findlay KP (2001) A review of humpback whale catches by modern whaling operations in the Southern hemisphere. *Memoirs of the Queensland Museum* 47:411-420.
- Flórez-González L (1991) Humpback whales *Megaptera novaeangliae* in the Gorgona island, Colombian Pacific breeding waters: population and pod characteristics. *Memoirs of the Queensland Museum* 30:291-295.
- Flórez-González L, Capella A. J, Haase B, Bravo GA, Félix F, Gerrodette T (1998) Changes in winter destinations and the northernmost record of southeastern Pacific humpback whales. *Marine Mammal Science* 14:189-196.
- Fitzgerald, Erich M. G.; A bizarre new toothed mysticete from Australia and the early evolution of baleen whales. *The Royal Society* 2006. August 16, 2006. pp 2955-2963.
- Frankham R, Ballou, JD, Briscoe, DA (2002) *Conservation Genetics*, Vol. Cambridge University Press, Cambridge, UK.
- Franklin, W., Franklin, T., Brooks, L., Gibbs, N., Childerhouse, S., Smith, F., Burns, D., Paton, D., Garrigue, C., Constantine, R., Poole, M.M., Hauser, N., Donoghue, M., Russell, K., Mattila, D., Robbins, J., Oosterman, A., Leaper, R., Baker, S., and P. Clapham. (2008). Migratory movements of humpback whales (*Megaptera novaeangliae*) between Eastern Australia and the Balleny Islands, Antarctica, confirmed by photo-identification. Paper SC/60/SH2 Working paper SC/60/SH15 in the 60th meeting of International Whaling Commission / Santiago/ Chile.
- Gales NJ, Kasuya T, Clapham PJ, Brownell Jr. RL (2005) Japan's whaling plan under scrutiny. Useful science or unregulated commercial whaling? *Nature* 435:883-884.
- Gambell R (1999) The International Whaling Commission and the contemporary whaling debate. In: Twiss Jr. JR, Reeves RR (eds) *Conservation and management of marine mammals*. Melbourne University Press, Melbourne, p 179-198.

- Gannier A (2004) The large-scale distribution of humpback whales (*Megaptera novaeangliae*) wintering in French Polynesia during 1997-2002. *Aquatic Mammals* 30:227-236.
- Garrigue C, Aguayo A, Amante-Helweg VLU, Baker CS, Caballero S, Clapham P, Constantine R, Denkinger J, Donoghue M, Flórez-González L, Greaves J, Hauser N, Olavarria C, Pairoa C, Peckham H, Poole M (2002) Movements of humpback whales in Oceania, South Pacific. *Journal of Cetacean Research and Management* 4:255-260.
- Garrigue C, Dodemont R, Steel D, Baker CS (2004) Organismal and 'gametic' capture-recapture using microsatellite genotyping confirm low abundance and reproductive autonomy of humpback whales on the wintering grounds of New Caledonia. *Marine Ecology Progress Series* 274:251-262.
- Garrigue C, Forestell P, Greaves J, Gill P, Naessig P, Patenaude NM, Baker CS (2000) Migratory movement of humpback whales (*Megaptera novaeangliae*) between New Caledonia, East Australia and New Zealand. *Journal of Cetacean Research and Management* 2:111-115.
- Garrigue C, Olavarria C, Baker CS, Steel D, Dodemont R, Constantine R, Russell K (2006) Demographic and genetic isolation of New Caledonia (E2) and Tonga (E3) breeding stocks, Report SC/A06/HW19 for consideration of the Inter-session Workshop for the Comprehensive Assessment of Southern Hemisphere humpback whales. Scientific Committee of The International Whaling Commission. Hobart, Australia.
- Gibbs N, Childerhouse S (2000) Humpback whales around New Zealand. *Conservation Advisory Science Notes* 287:1-32.
- Gibbs N, Paton DA, Childerhouse S, Clapham P (2006) Assessment of the current abundance of humpback whales in the Lomaiviti Island Group of Fiji and a comparison with historical data, Report SC/A06/HW34 to the Intersessional workshop for the Comprehensive Assessment of Southern Hemisphere humpback whales Scientific Committee of the International Whaling Commission. Hobart, Australia.
- Gill PC, Burton CLK (1995) Photographic resight of a humpback whale between Western Australia and Antarctic Area IV. *Marine Mammal Science* 11:96-100.
- Gormley, AM and Dawson SM (2005) Capture-recapture estimates of Hector's dolphin abundance at Banks Peninsula, New Zealand. *Marine Mammal Science* 21: 204-216.
- Government of Japan (2005) Plan for the second phase of the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA II) - Monitoring of the Antarctic ecosystem and development of new management objectives for whale resources, Report SC/57/O1 to the Scientific Committee of the International Whaling Commission. Ulsan, Korea. 30 May – 10 June.

- Grant, W.S., Milner, G.B., Krasnowski, P., Utter, F.M. 1980. Use of biochemical genetic variant for identification of sockeye salmon (*Oncorhynchus nerka*) stocks in Cook Inlet, Alaska. *Can.J. Fish. Aquat. Sci.*, 37:1236-1247.
- Griffiths AJF, Miller JH, Suzuki DT, Lewontin RC, Gelbart WM (1996) An introduction to Genetic Analysis, Vol. W. H. Freeman and Company, New York.
- Habicht, C., Seeb, L., Seeb, J. (2007) Genetic and ecological divergence defines population structure of Sockeye Salmon populations returning to Bristol Bay, Alaska, and provides a tool for admixture analysis. *American Fisheries Society* 136: 82-94.
- Hammond PS (2008) Mark-Recapture In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Academic Press, San Diego, p 705-709.
- Hauser N, Peckham H, Clapham P (2000) Humpback whales in the southern Cook Islands, South Pacific. *Journal of Cetacean Research and Management* 2:159-164.
- Hauser, N., Zerbini, A., Geyer, Y., Heide-Jorgensen, M-P. and Clapham, P. (2009) Movements of satellite-monitored humpback whales, megaptera novaeangliae, from the Cook Islands *Mar Mamm Sci* in press.
- Hjort J, Lie J, Ruud JT (1938) Pelagic whaling in the Antarctic VII. The season 1936-1937. *Hvalrådets Skrifter* 18:5-47.
- Hoelzel AR (2008) Molecular Ecology In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Academic Press, San Diego, p 736-741.
- Hoelzel AR (ed) (1991) Genetic ecology of whales and dolphins. Report of the International Whaling Commission (Special Issue 13), Vol. International Whaling Commission, Cambridge.
- Hoelzel AR, Dover GA (1989) Molecular techniques for examining genetic variation and stock identity in cetacean species. In: Donovan GP (ed) The comprehensive assessment of whale stocks: the early years. Report of the International Whaling Commission (Special Issue 11). International Whaling Commission, Cambridge, p 81-120.
- Hoelzel AR, Natoli A, Dahlheim ME, Olavarria C, Baird RW, Black NA (2002) Low worldwide genetic diversity in the killer whale (*Orcinus orca*): implications for demographic history. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269:1467-1473.
- IWC (2005) Report of the Scientific Committee, Annex H, Report of the Subcommittee on other Southern Hemisphere whale stocks. *Journal of Cetacean Research and Management* 7 (Suppl.):235-246.

International Whaling Commission Report on southern hemisphere humpback whales (2006). SC-58-Rep 5. Unpublished 12 pp.

Jackson, J.A., Zerbini, A., Clapham, P., Constantine, R., Garrigue, C., Hauser, N., Poole, M.M., Baker, C.S. (2008) Progress on a two-stock catch allocation model for reconstructing population histories of east Australia and Oceania. Paper SC/60/SH14 presented to the IWC Scientific Committee, June 2008 (unpublished). 12 pp.

Jenner, K.C.S., Jenne, M.N.M., and McCabe, K.A. (2001). Geographical and Temporal Movements of Humpback whales in Western Australian Waters. *APPEA Journal* 749-764.

Johnston SJ, Butterworth DS (2006) Updated assessments of various breeding populations of Southern Hemisphere humpback whales, Report SC/A06/HW22 to the Inter-sessional workshop for the Comprehensive Assessment of Southern Hemisphere humpback whales Scientific Committee of the International Whaling Commission. Hobart, Australia.

Katona S, Baxter B, Brazier O, Kraus S, Perkins J, Whitehead H (1979) Identification of humpback whales by fluke photographs. In: Winn HE, Olla BL (eds) Behavior of Marine Animals, Vol Vol. 3. Plenum Press, New York, p 33-44.

Katona SK, Beard JA (1990) Population size, migration and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. In: Hammond PS, Mizroch SA, Donovan GP (eds) Individual recognition of cetaceans Use of photo-identification and other techniques to estimate population parameters, Vol Report of the International Whaling Commission (Special Issue 12). International Whaling Commission, Cambridge, p 295-306.

Katona SK, Whitehead H (1981) Identifying humpback whales using their natural markings. *Polar Records* 20:439-444.

Kaufman GD, Osmond MG, Ward AJ, Forestell PH (1990) Photographic documentation of the migratory movement of a humpback whales (*Megaptera novaeangliae*) between East Australia and Antarctic Area V. In: Hammond PS, Mizroch SA, Donovan GP (eds) Individual recognition of cetaceans Use of photo-identification and other techniques to estimate population parameters, Vol (Special Issue 12). Report of the International Whaling Commission (Special Issue 12). International Whaling Commission, Cambridge, p 265-268.

Kellogg R (1929) What is known of the migration of some of the whalebone whales. *Smithsonian Institution Annual Report* 1928:467-494.

Kemp S, Bennett AG (1932) On the distribution and movements of whales on the South Georgia and South Shetland whaling grounds. *Discovery Reports* 6:165-190.

- Koljonen, M.L., Pella, J.J., Masuda, M. (2005) Classical individual assignments versus mixture modelling to estimate stock proportions in Atlantic salmon (*Salmo salar*) catches from DNA microsatellite data. *Can. J. of Fisheries and Aquatic Science*. 62: 2143-2158.
- Krützen M, Barre LM, Moller LM, Heithaus MR, Simms C, Sherwin WB (2002) A biopsy system for small cetaceans: darting success and wound healing in *Tursiops* sp. *Marine Mammal Science* 18:863-878.
- Lambertsen RH (1987) A biopsy system for large whales and its use for cytogenetics. *Journal of Mammalogy* 68:443-445.
- Larsen AH, Sigurjonsson J, Øien N, Vikingsson G, Palsbøll PJ (1996) Populations genetic analysis of nuclear and mitochondrial loci in skin biopsies collected from central and northeastern North Atlantic humpback whales (*Megaptera novaeangliae*): population identity and migratory destinations. *Proceedings of the Royal Society of London Series B-Biological Sciences* 263:1611-1618.
- LeDuc RG, Dizon AE, Goto M, Pastene LA, Kato H, Nishiwaki S, LeDuc CA, Brownell JR. RL (2007) Patterns of genetic variation in Southern Hemisphere blue whales and the use of assignment test to detect mixing on the feeding grounds. *Journal of Cetacean Management and Research* 9:73-80.
- Loo J, Pomilla C, Best PB, Findlay KP, Rosenbaum HC (2006) Structure and diversity between feeding aggregations of humpback whales (*Megaptera novaeangliae*) using mitochondrial and nuclear DNA, Report SC/A06/HW26 to the Inter-sessional workshop for the Comprehensive Assessment of Southern Hemisphere humpback whales Scientific Committee of the International Whaling Commission. Hobart, Australia.
- Loo J, Pomilla C, Olavarria C, Aguayo A, Thiele D, Baker CS, Ensor P, Rosenbaum H (2007) Genetic structure of feeding aggregations of humpback whales in the Southern Ocean., Report SC/59/SH24 to the Scientific Committee of the International Whaling Commission. Anchorage, USA.
- Lukacs, PM & Burnham, PM (2005) Review of capture-recapture methods applicable to noninvasive genetic sampling. *Molecular Ecology* 14: 3909-3919.
- Luke, K., Horrocks, J.A., LeRoux, R.A., Dutton, P.H. (2004) Origins of green turtle (*Cheloni mydas*) feeding aggregations around Barbados, West Indies. *Marine Biology* 144: 799-805.
- Mackintosh NA (1942) The southern stocks of whalebone whales. *Discovery Reports* 22:197-300.
- Mackintosh NA (1965) The stocks of whales, Vol. Fishing News (Books) Ltd., London.

- Manel, S., Gaggiotti, O., and Waples, R.S. (2005) Assignment methods: matching biological questions with appropriate techniques. *Trends in Ecology and Evolution*. 20: 136-142.
- Mathews EA, Keller S, Weiner DB (1988) A method to collect and process skin biopsies for cell culture from the free-ranging gray whales (*Eschrichtius robustus*). *Marine Mammal Science* 4:1-12.
- Matthews LH (1937) The humpback whale, *Megaptera novaeangliae*. *Discovery Reports* 17:7-92.
- Mattila DK, Clapham PJ, Katona SK, Stone GS (1989) Population composition of humpback whales, *Megaptera novaeangliae*, on Silver Bank, 1984. *Canadian Journal of Zoology* 67:281-285.
- Maudet C, Miller, C, Bassano, B, Breitenmoser-Wursten, C, Gauthier, D, Obexer-Ruff, G, Michallet, J, Taberlet, P, Luikart G (2002) Microsatellite DNA and recent statistical methods in wildlife conservation management: applications in Alpine ibex. *Molec. Ecology* 11: 421-436.
- Medrano-González L, Baker CS, Robles-Saavedra MR, Murrell J, Vazquez-Cuevas MJ, Congdon BC, Stranley JM, Calambokidis J, Urban-Ramirez J, Flórez-González L, Olavarría C, Aguayo-Lobo A, Nolasco-Soto J, Juarez-Salas RA, Villavicencio-Llamas K (2001) Trans-oceanic population genetics structure of humpback whales in the North and South Pacific. *Memoirs of the Queensland Museum* 47:465-479.
- Mikhalev YA (2000) Biological characteristics of humpbacks taken in Antarctic Area V by the whaling fleets *Slava* and *Sovietskaya Ukraina*, Report SC/52/IA to the Scientific Committee of the International Whaling Commission. Adelaide, Australia.
- Mikhalev YA (2004) Trade and the biological characteristic of humpback whales, caught by Soviet Antarctic flotillas into the season 1960-61, Report SC/56/SH9 to the Scientific Committee of the International Whaling Commission. Sorrento, Italy.
- Mikhalev YA, Tormosov DD (1997) Corrected data about non-Soviet whale marks recovered by Soviet whaling fleets. Report of the International Whaling Commission 47:1019-1027.
- Morin, PA & Dizon, AE (2008). Genetics for Management In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Academic Press, San Diego, p 477-483.
- Moritz C (1994) Defining 'Evolutionarily Significant Units' for conservation. *Trends in Ecology & Evolution* 9:373-375.
- Nei M (1987) Molecular evolutionary genetics, Vol. Columbia University Press, New York
- Nikaido M, Hamilton H, Makino H, Sasaki T, Takahashi K, Goto M, Kanda N, Pastene LA, Okada N (2006) Baleen whale phylogeny and past

- extensive radiation event revealed by SINE insertion analysis. *Molecular Biology and Evolution* 23:866-873.
- Noad MJ, Cato DH, Bryden MM, Jenner M-N, Jenner KCS (2000) Cultural revolution in whale songs. *Nature* 408:537.
- Olavarría C, Aguayo A, Acevedo J, Medrano L, Thiele D, Baker CS (2005) Genetic differentiation between two feeding areas of the Eastern South Pacific humpback whale population, Report SC/57/SH3 to the Scientific Committee of the International Whaling Commission. Ulsan, Korea.
- Olavarría C, Aguayo A, Acevedo J, Medrano L, Thiele D, Baker CS (2006a) Genetic differentiation between two feeding areas of the Eastern South Pacific humpback whale population: Update on SC/57/SH3, Report SC/A06/HW29 to the Inter-sessional workshop for the Comprehensive Assessment of Southern Hemisphere humpback whales Scientific Committee of the International Whaling Commission. Hobart, Australia.
- Olavarría C, Aguayo-Lobo A, Larrea A, Acevedo J (2003a) Migratory relationship between Magellan strait and Antarctic Peninsula humpback whales, Stock G, Report SH/55/SH12 to the Scientific Committee of the International Whaling Commission. Berlin, Germany.
- Olavarría C, Anderson M, Paton D, Burns D, Brasseur M, Garrigue C, Hauser N, Poole M, Caballero S, Flórez-González L, Baker CS (2006b) Eastern Australia humpback whale genetic diversity and their relationship with Breeding Stocks D, E, F and G, Report SC/58/SH22 to the Scientific Committee of the International Whaling Commission. St Kitts and Nevis.
- Olavarría C, Baker CS, Garrigue C, Poole M, Hauser N, Caballero S, Flórez-González L, Brasseur M, Bannister J, Capella J, Clapham P, Dodemont R, Donoghue M, Jenner C, Jenner M-N, Moro D, Oremus M, Paton D, Rosenbaum H, Russell K (2007) Population structure of humpback whales throughout the South Pacific and the origin of the eastern Polynesian breeding grounds. *Marine Ecology Progress Series* 330:257-268.
- Olavarría C, Baker CS, Medrano L, Aguayo A, Caballero S, Flórez-González L, Capella J, Rosenbaum HC, Garrigue C, Greaves J, Jenner M, Jenner C, Bannister JL (2000) Stock identity of Antarctic Peninsula Humpback whales inferred from mtDNA variation, Report SC/52/IA15 to the Scientific Committee of the International Whaling Commission. Adelaide, Australia.
- Olavarría C, Balbontín F, Bernal R, Baker CS (2006c) Lack of divergence in the mitochondrial cytochrome *b* gene between *Macruronus* species (Pisces: Merlucciidae) in the Southern Hemisphere. *New Zealand Journal of Marine and Freshwater Research* 40:299-304.
- Olavarría C, Childerhouse S, Gibbs N, Baker CS (2006d) Contemporary genetic diversity of New Zealand humpback whales and their genetic relationship with Breeding Stocks D, E, F and G, Report SC/A06/HW31 to the Intersessional workshop for the Comprehensive Assessment of Southern Hemisphere

humpback whales Scientific Committee of the International Whaling Commission. Hobart, Australia.

- Olavarría C, Poole M, Hauser N, Garrigue C, Caballero S, Brasseur M, Martien K, Russell K, Oremus M, Dodemont R, Flórez-González L, Capella J, Rosenbaum H, Moro D, Jenner C, Jenner MN, Bannister J, Baker CS (2003b) Population differentiation of humpback whales from far Polynesia (Group F breeding grounds) based on mitochondrial DNA sequences, Report SC/55/SH11 to the Scientific Committee of the International Whaling Commission. Berlin, Germany.
- Olavarría C, Anderson M, Paton D, Burns D, Brasseur M, Garrigue C, Hauser N, Poole M, Caballero S, Florez-Gonzalez L, & Baker CS (2006) Eastern Australia humpback whale genetic diversity and their relationship with Breeding Stocks D, E, F and G. Report SC/58/SH25 to the Intersessional workshop for the Comprehensive Assessment of Southern Hemisphere humpback whales Scientific Committee of the International Whaling Commission. Hobart, Australia.
- Omura H (1953) Biological study on humpback whales in the Antarctic whaling areas IV and V. Scientific Report of the Whales Research Institute 8:81-102.
- Palsbøll PJ (2008) Genetics In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Academic Press, San Diego, p 483-492.
- Palsbøll PJ, Allen J, Bérubé M, Clapham PJ, Feddersen TP, Hammond PS, Hudson RR, Jørgensen H, Katona S, Larsen AH, Larsen F, Lien J, Mattila DK, Sigurjonsson J, Sears R, Smith T, Sponer R, Stevick P, Øien N (1997a) Genetic tagging of humpback whales. *Nature* 388:767-769.
- Palsbøll PJ, Clapham PJ, Mattila DK, Larsen F, Sears R, Siegmund HR, Sigurjonsson J, Vasquez O, Artander P (1995) Distribution of mtDNA haplotypes in North Atlantic humpback whales: the influence of behaviour on population structure. *Marine Ecology Progress Series* 116:1-10.
- Palsbøll PJ, Larsen F, Hansen ES (1991) Sampling of skin biopsies from free-ranging large cetaceans in West Greenland: development of new biopsy tips and bolt designs. In: Hoelzel AR (ed) Genetic ecology of whales and dolphins, Vol (Special Issue13). Report of International Whaling Commission, Cambridge, p 71-79.
- Palumbi, SR & Roman J (2006) The History of Whales read from DNA. In: Estes, JA, Demaster, DP, Doak, DF, Williams, TM, and Brownell, RL (eds) Whales, Whaling and Ocean Ecosystems. University Of California Press. USA, p 102-113.
- Paterson R, Paterson P, Cato DH (1994) The status of humpback whales *Megaptera novaeangliae* in East Australia thirty years after whaling. *Biological Conservation* 70:135-142.

- Paterson RA (2001) Exploitation of humpback whales, *Megaptera novaeangliae*, in the South West Pacific and adjacent Antarctic waters during the 19th and 20th Centuries. *Memoirs of the Queensland Museum* 47:421-429.
- Paterson RA, Paterson P, Cato DH (2001) Status of humpback whales, *Megaptera novaeangliae* in east Australia at the end of the 20th century. *Memoirs of the Queensland Museum* 47:579-586.
- Pella, J.J., Masuda, M. (2001) Bayesian methods for analysis of stock mixtures from genetic characters. *Fish.Bull.* 99:151-167.
- Perry A, Baker CS, Herman LM (1990) Population characteristics of individually identified humpback whales in the central and eastern North Pacific: a summary and critique. In: Hammond PS, Mizroch SA, Donovan GP (eds) Individual recognition of cetaceans Use of photo-identification and other techniques to estimate population parameters, Vol Report of the International Whaling Commission (Special Issue 12). International Whaling Commission, Cambridge, p 307-318.
- Pomilla C, Rosenbaum HC (2005) Against the current: an inter-oceanic whale migration event. *Biology Letters* 1:476-479.
- Poole M (2006) An update on the occurrence of humpback whales (*Megaptera novaeangliae*) in French Polynesia. Report . SC/A06/58 to the Scientific Committee of the International Whaling Commission. Hobart, Australia.
- Ralls K, Mesnick SL (2008) Sexual dimorphism. In: Perrin WF, Würsig B, Thewissen JGM (eds) Encyclopedia of Marine Mammals. Academic Press, San Diego, pp. 1005-1011.
- Rasmussen K, Palacios DM, Calambokidis J, Saborio MT, Rosa LD, Secchi ER Steiger GH, Allen JM, Stone GS (2007) Southern Hemisphere humpback whales wintering off Central America: insights from water temperature into the longest mammalian migration. *Biology Letters* 3:302-305.
- Raymond M, Rousset F (1995) An exact test for population differentiation. *Evolution* 49:1280-1283.
- Reeves RR, Clapham PJ, Wetmore SE (2002) Humpback whale (*Megaptera novaeangliae*) occurrence near the Cape Verde Islands, based on American 19th century whaling records. *Journal of Cetacean Research and Management* 4:235-253
- Rice DW (1998) Marine mammals of the world: systematics and distribution, Vol 4. *Society for Marine Mammalogy*, Lawrence, KS.
- Robbins J., Dalla Rosa L., Allen JM., Mattila DK & Secchi ER (2008) Humpback whale photo-identification reveals exchange between American Samoa and the Antarctic Peninsula, and a new mammalian distance record. Document SC/60/SH5 presented at the 60th meeting of International Whaling Commission / Santiago/ Chile.

- Robbins J, Mattila DK (2006) Summary of humpback whale research at American Samoa, 2003- 2005, Report SC/58/SH5 to the Scientific Committee of the International Whaling Commission. St Kitts and Nevis. 26 May – 6 June.
- Roberts, M.A., Anderson, C.J., Stender, B., Seagars, A., Whittaker, J.D., Grandy, J.M., & Quattro J.M. (2005) Estimated contribution of Atlantic Coastal loggerhead turtle nesting populations to offshore feeding aggregations. *Conservation Genetics* 6:133-139.
- Rosenbaum H, Clapham P, Allen J, Jenner MN, Jenner C, Flórez-González L, Urbán J, Ladrón de Guevara P, Mori K, Yamaguchi M, Baker CS (1995) Geographic variation in ventral fluke pigmentation of humpback whale *Megaptera novaeangliae* populations worldwide. *Marine Ecology Progress Series* 124:1-7.
- Rosenbaum HC, Brownell-JR RL, Brown MW, Schaeff C, Portway V, White BN, Malik S, Pastene LA, Patenaude NJ, Baker CS, Goto M, Best PB, Clapham PJ, Hamilton P, Moore M, Payne R, Rowntree V, Tynan CT, Bannister JL, DeSalle R (2000) World-wide genetic differentiation of Eubalaena: questioning the number of right whale species. *Molecular Ecology* 9:1793-1802.
- Rosenburg, D. K., Overton, W. S. and Anthony, R. G. (1995). Estimation of animal abundance when capture probabilities are low and heterogeneous. *Journal of Wildlife Management* **59** 252-261.
- Sambrook J, Fritsch EF, Maniatis T (1989) Molecular cloning: A laboratory manual, Vol. Cold Spring Harbor Laboratory, Cold Spring Harbor, NY.
- Schlotterer C, Amos, B, Tautz, D (1991) Conservation of polymorphic simple sequences of cetacean species. *Nature* 354: 63-65.
- Schwarz, CJ, Seber GA (1999) Estimating Animal Abundance: Review III. *Statistical Science* 14: 427-456.
- Smith TD, Josephson E, and Reeves RR (2006) 19th Century Southern Hemisphere Humpback Whale Catches. Report SC/A06/HW53 to the Scientific Committee of the International Whaling Commission. Hobart Australia.
- SPWRC, Garrigue C, Baker CS, Constantine R, Poole M, Hauser N, Clapham P, Donoghue M, Russell K, Paton D, Mattila D (2006b) Interchange of humpback whales in Oceania (South Pacific), 1999 to 2004, Report SC/A06/HW55 to the Inter-sessional workshop for the Comprehensive Assessment of Southern Hemisphere humpback whales Scientific Committee of the International Whaling Commission. Hobart, Australia.
- SPWRC, Garrigue C, Franklin T, Russell K, Burns D, Poole M, Paton D, Hauser N, Oremus M, Constantine R, Childerhouse S, Mattila D, Gibbs N, Franklin

- W, Robbins J, Clapham P, Baker CS (2007) First assessment of interchange of humpback whales between Oceania and the east coast of Australia, Report SC/59/SH15 to the Scientific Committee of the International Whaling Commission. Anchorage, USA. 7 – 18 May.
- Steel, D., Garrigue, C., Poole, M., Hauser, N., Olavarria, C., Flórez-González, L., Constantine, R., Caballero, S., Thiele, D., Paton, D., Clapham, P., Donoghue, M., and Baker, C.S. (2008) Migratory connections between humpback whales from South Pacific breeding grounds and Antarctic feeding areas demonstrated by genotype matching. Paper SC/60/SH13. Presented to the IWC Scientific Committee, June 2008 (unpublished). 6pp.
- Stevick PT, Aguayo A, Allen J, Avila IC, Capella J, Castro C, Chater K, Engel M, Félix F, Flórez-González L, Freitas A, Hasse B, Llano M, Lodi L, Muñoz E, Olavarria C, Secchi E, Scheidat M, Siciliano S (2004) A note on the migrations of individually identified humpback whales between the Antarctic Peninsula and South America. *Journal of Cetacean Research and Management* 6:109–113.
- Stevick PT, Aguayo-Lobo A, Allen JM, Chater K, Dalla Rosa L, Olavarria C, Secchi E (2006a) Mark-recapture abundance estimates for humpback whales in the Antarctic Peninsula, Report SC/A06/HW54 to the Intersessional workshop for the Comprehensive Assessment of Southern Hemisphere humpback whales Scientific Committee of the International Whaling Commission. Hobart, Australia.
- Stevick, P.T., Palsbøll, P.J., Smith, T.D., Bravington, M.V. and Hammond, P.S. (2001) Errors in identification using natural markings: rates, sources and effects on capture-recapture estimates of abundance. *Can. J. Fish. Aquat. Sci.* 58:1861-70.
- Stone G, Flórez-González L, Katona S (1990) Whale migration record. *Nature* 346:705.
- Taylor BL (1997) Defining "population" to meet management objectives for marine mammals. In: Dizon AE, Chivers SJ, Perrin WF (eds) Molecular genetics of marine mammals. Special Publication Number 3, The Society for Marine Mammalogy, Lawrence, KS, p 49-65.
- Tønnessen JN, Johnsen AO (1982) The history of modern whaling, Vol. University of California Press, Berkeley and Los Angeles.
- Townsend CH (1935) The distribution of certain whales as shown by logbook records of American whaleships. *Zoologica* 19:1-50.
- Valsecchi E, Amos W (1996) Microsatellite markers for the study of cetacean populations. *Molecular Ecology* 5:151-156.
- Waldick, RC, Brown, NW, White, BN (1999) Characterization and isolation of microsatellite loci from the endangered North Atlantic right whale. *Molec. Ec.* 8: 1763.

- Wright S (1951) The genetic structure of populations. *Annals of Eugenics* 15:323-354.
- Wright, S. (1969) *Evolution and the Genetics of Populations Volume 2: the Theory of Gene Frequencies*, pp 294–295. Univ. of Chicago Press, Chicago.
- Zemsky VA, Berzin AA, Mikhaliyev YA, Tormosov DD (1995) Soviet Antarctic pelagic whaling after WWII: Review of actual catch data. *Report of the International Whaling Commission* 45:131-135.

Appendix A - Preliminary Assignment Tests Using Microsatellite and MtDNA Genetic Markers To Assign South Pacific Humpback Whales To Three Antarctic Areas

A.1 INTRODUCTION

Genetic markers have been useful for inferring migration connections in highly migratory species such as turtle and salmon populations (Pella & Masuda 2000). Turtles possess a strong homing instinct with females consistently returning to natal nesting regions to lay eggs. This maintains maternal lineages allowing the use of the mitochondrial DNA (mtDNA) marker in mixed-stock analysis to estimate allocations from nesting regions to foraging areas (Bolker *et al.* 2003). Assignment tests using microsatellite markers represent a useful tool for conservation and management of wild populations (Bjornstad & Reed 2001), and have been used in several salmon species to successfully assign runs back to spawning populations (Koljonen *et al.* 2005). The analyses of assignment tests utilize a genotype containing several loci of an individual and the expected probabilities of that genotype occurring in each of the potential source populations (Manel *et al.* 2005). Microsatellite markers have the ability to describe both maternal and paternal characteristics, making them unique to individuals (Frankham *et al.* 2002) providing the most direct method to determine the population of origin of target individuals (Manel *et al.* 2005). MtDNA is considered a single locus, and all maternal lineages will share the same sequence, but it cannot be used as a unique identifier (Frankham *et al.* 2002). However, mtDNA is a powerful genetic marker for studying population structure when the question involves identification of populations (Manel *et al.* 2005). Here we employ assignment tests using a combination of microsatellite and mtDNA to

infer migratory connections between humpback whale South Pacific breeding grounds and three Antarctic Areas.

A.2 METHODS

A.2.1 Microsatellite amplification and mtDNA sequencing

Microsatellites were amplified as described in Steel *et al.* (2008) including the extraction method of Sambrook *et al.* (1989) and modification for small skin samples as described in Baker *et al.* (1994). Up to 17 loci were amplified for each sample using previously published primers (GT211, GT575, GT23 (Berube *et al.* 2000) GATA417, GATA28 (Palsboll *et al.* 1997) Ev1, Ev14, Ev21, Ev37, Ev94, Ev96, Ev104 (Valsecchi and Amos 1996) 464/465 (Schlotterer *et al.* 1991) rw26, rw31, rw4-10, rw48 (Waldick *et al.* 1999)). Replicates were deleted after genotyping. Sequencing of the mitochondrial (mt) DNA control region (470bp) is described in Olavarria *et al.* (2007). The following source stocks were used in the analysis: breeding ground source stocks included Oceania regions (Cook Islands, French Polynesia, Tonga and New Caledonia) and Colombia (n = 1,174, Figure A1). Feeding area mixtures included Antarctic Area I* (n = 72) Antarctic Area V (n = 7) Antarctic Area VI (n = 28). Eastern Australia and Western Australia were excluded due to the limited number of microsatellite and haplotype data available.

A.2.2 Microsatellites Data Analyses

WHICHRUN has the advantage of using both microsatellite data and mtDNA haplotype data simultaneously in an assignment analysis. Input data for WHICHRUN assignment tests included 14 loci plus haplotype mtDNA information. Three loci were removed from the original 17 (rw26, GT575, Ev14) due to missing loci for entire populations (Tonga and Area VI).

Incorporating jack-knife iterations, WHICHRUN samples individuals one at a time and recalculates the allele frequency in the absence of each genotype before determining the most likely source population of the particular individual. Next, WHICHRUN uses the log of the odds (LOD) ratio for the two most likely source populations.

A.3 RESULTS

A.3.1 Breeding Region Classification Assignment

The assignment tests implemented in WHICHRUN (Banks & Eichert 2000) assigned an average of 47.8% of the individuals back to the correct breeding region using jack-knife iterations (Table A1). Most values ranged from 0.8-2.3 for the LOD ratio for jack-knife estimates of source stock data indicating some uncertainty in the estimate.

A.3.2 Feeding Region Mixed Stock Assignment

The assignment test from the Antarctic mixed-stocks, without the use of a Bayesian prior, assigned similarly to the SPAM analysis where haplotype data was used (Chapter 2) (Figure 2-2). A large proportion of Antarctic Area I* was assigned to Colombia (n=45), and lesser amounts to French Polynesia (n=15) and Cook Islands (n=10). Area VI assigned to all five breeding stocks, the greatest to Tonga (n=10) and French Polynesia (n=10) with lower LOD values for all samples than Area I* (<1.0) indicating some uncertainty. Area V assigned mainly to New Caledonia (n=4) with lesser amounts to Tonga (n=2) and the Cook Islands (n=1) and LOD values were generally <1.

A.4 DISCUSSION

There are two things that tend to impact the success of proper assignment; the number of loci used in the analysis and F_{ST} values between

source populations. It has been shown that a larger number of loci will influence the allocation success (Bjornstad & Reed 2001). However, even with the use of 15 loci the program only allocated about 50% of the baseline correctly suggesting the low F_{ST} values between regions as seen in the mtDNA haplotypes has a greater influence on correct assignment than the number of loci used.

It appeared the jack-knife assignment was strongest for a region having F_{ST} values that were higher between regions, and loses power when F_{ST} values are smaller between regions. Similar findings have been observed in other studies where there has been a correlation between the performance of the assignment method and the differentiation between the populations (F_{ST} values), (Maudet *et al.* 2002). Program WHICHRUN, specifically has performed well when the F_{ST} value is above 0.2 between regions, but when presented with several populations ($n>5$) and lower F_{ST} values WHICHRUN provided only intermediate accuracy (Maudet *et al.* 2002). Colombia had the highest percentage of correct assignment but also has a high F_{ST} value when compared to each region of Oceania. Colombia had the largest amount of individuals correctly assigned back to the region in the jack-knife. Contrastingly, Cook Islands had the lowest percentage of assignment, with almost as many individuals assigned back to French Polynesia, and, as seen earlier, the haplotype pairwise F_{ST} values between Cook Islands and French Polynesia were low (Chapter 2, Table 2-2).

Individual assignment tests are powerful in instances where specific population origins may not be observed within a mixed-stock context. French Polynesia, which had very little allocation in the mixed-stock program using haplotype data for allocation of populations, was more evident in the assignment tests here, although the LOD was generally low (<1.3) for those assignments.

French Polynesia was assigned to both Area VI* and Area I* revealing the first migratory connection of French Polynesia to any Antarctic feeding areas (Figure A-2). Cook Islands was also assigned to Area VI* and Area I* similar to the mixed-stock analysis (Chapter 2, Table 2-2), strengthening previous tagging studies (Hauser *et al.* in press). In addition, all genotype matches identified in Steel *et al.* (2008) were assigned correctly by WHICHRUN including Tonga from Area VI*, Colombia from Area I*, and New Caledonia from Area V. Of particular interest in Area V is the number of the individuals (n=4 out of a total n=7) assigned to New Caledonia suggesting New Caledonia is part of Area V. This is cause for concern if the Japanese government is again proposing catch allocations of humpback whales from Area V since a recent abundance estimate of New Caledonia humpbacks was estimated at less than 500 individuals (Baker *et al.* 2006).

In conclusion, assignment tests have proven to be a useful tool in conjunction with mixed-stock population analysis for the inference of migratory connections. With very little known about migratory connections from Oceania, this data provides additional information essential for management decisions including the assignment of French Polynesia from Area VI* and Area I*, and the assignment of New Caledonia from Area V. In addition, these results correlate relatively well with the mixed-stock analysis provided by the mtDNA haplotypes inferring a connection between Tonga and Area VI* and Colombia and Area I*. The addition of baseline data from the Western and Eastern Australia breeding stocks would surely add significance to this study, and work is currently in progress on the microsatellite data of these regions. The assignment of Area V to New Caledonia provides additional evidence that small breeding grounds like New Caledonia may share common feeding areas with larger breeding grounds,

like Eastern Australia where there is evidence of connections between Eastern Australia and Area V using photo-identification. This has important management implications in regards to future catch allocations.

LITERATURE CITED

- Baker, C.S., C. Garrigue, R. Constantine, B. Madon, M. Poole, N. Hauser, P. Clapham, Donoghue, K. Russell, T. O'Callahan, D. Paton, and D. Mattila. (2006) Abundance of humpback whales in Oceania (South Pacific), 1999 to 2004. Unpublished report SC/A06/HW51 for consideration the inter-sessional workshop for the comprehensive assessment of Southern Hemisphere humpback whales, Hobart, Tasmania.
- Banks, MA, Eichert, W (2000) WHICHRUN Version 3.2: a computer program for population assignment of individuals based on multilocus genotype data. *Journal of Heredity* 91: 87-89.
- Berube, MH, Jorgensen, H, McEwing R, Palsboll, PJ (2000) Polymorphic dinucleotide microsatellite loci isolated from the humpback whale, *Megaptera novaeangliae*. *Molec. Ec* 9: 2181-2183.
- Bolker, B., Okuyama, T., Bjørndal, K., Bolten, A. (2003) Sea Turtle Stock Estimation Using Genetic Markers: Accounting for sampling error of rare genotypes. *Ecological Applications* 13(3):763-775.
- Frankham R, Ballou, JD, Briscoe, DA (2002) Conservation Genetics, Vol. Cambridge University Press, Cambridge, UK.
- Hauser, N., Zerbini, A., Geyer, Y., Heide-Jorgensen, M-P. and Clapham, P. (2009) Movements of satellite-monitored humpback whales, megaptera novaeangliae, from the Cook Islands *Mar Mamm Sci* in press.
- International Whaling Commission Report on southern hemisphere humpback whales (2006) SC-58-Rep 5. Unpublished 12 pp.
- Jackson, J.A., Zerbini, A., Clapham, P., Constantine, R., Garrigue, C., Hauser, N., Poole, M.M., Baker, C.S. 2008. Progress on a two-stock catch allocation model for reconstructing population histories of east Australia and Oceania. Paper SC/60/SH14 presented to the IWC Scientific Committee, June 2008 (unpublished). 12 pp.
- Koljonen, M.L., Pella, J.J., Masuda, M. (2005) Classical individual assignments versus mixture modelling to estimate stock proportions in Atlantic salmon (*Salmo salar*) catches from DNA microsatellite data. *Can. J. of Fisheries and Aquatic Science*. 62: 2143-2158.

- Manel, S., Gaggiotti, O., and Waples, R.S. (2005) Assignment methods: matching biological questions with appropriate techniques. *Trends in Ecology and Evolution*. 20: 136-142.
- Maudet C, Miller, C, Bassano, B, Breitenmoser-Wursten, C, Gauthier, D, Obexer-Ruff, G, Michallet, J, Taberlet, P, Luikart G (2002) Microsatellite DNA and recent statistical methods in wildlife conservation management: applications in Alpine ibex. *Molec. Ec.* 11: 421-436.
- Olavarria C, Baker CS, Garrigue C, Poole M, Hauser N, Caballero S, Flórez-González L, Brasseur M, Bannister J, Capella J, Clapham P, Dodemont R, Donoghue M, Jenner C, Jenner M-N, Moro D, Oremus M, Paton D, Rosenbaum H, Russell K (2007) Population structure of humpback whales throughout the South Pacific and the origin of the eastern Polynesian breeding grounds. *Marine Ecology Progress Series* 330:257-268.
- Pella, J.J., Masuda, M. (2001) Bayesian methods for analysis of stock mixtures from genetic characters. *Fish.Bull.* 99:151-167.
- Palsbøll PJ, Allen J, Bérubé M, Clapham PJ, Feddersen TP, Hammond PS, Hudson RR, Jørgensen H, Katona S, Larsen AH, Larsen F, Lien J, Mattila DK, Sigurjonsson J, Sears R, Smith T, Sponer R, Stevick P, Øien N (1997a) Genetic tagging of humpback whales. *Nature* 388:767-769.
- Schlotterer C, Amos, B, Tautz, D (1991) Conservation of polymorphic simple sequences of cetacean species. *Nature* 354: 63-65.
- Steel, D., Garrigue, C., Poole, M., Hauser, N., Olavarria, C., Flórez-González, L., Constantine, R., Caballero, S., Thiele, D., Paton, D., Clapham, P., Donoghue, M., and Baker, C.S. 2008. Migratory connections between humpback whales from South Pacific breeding grounds and Antarctic feeding areas demonstrated by genotype matching. Paper SC/60/SH13. Presented to the IWC Scientific Committee, June 2008 (unpublished). 6pp.
- Valsecchi E, Amos W (1996) Microsatellite markers for the study of cetacean populations. *Molecular Ecology* 5:151-156.
- Waldick, RC, Brown, NW, White, BN (1999) Characterization and isolation of microsatellite loci from the endangered North Atlantic right whale. *Molec. Ec.* 8: 1763.

Table A-1. The number of individuals assigned back to each breeding region based on a 15-locus microsatellite analysis using jack-knife iterations in WHICHRUN.

	New Caledonia	Tonga	Cook Islands	French Polynesia	Colombia	n	% assigned correctly
New Caledonia	184	59	56	36	40	375	49%
Tonga	60	116	79	83	24	362	32%
Cook Islands	9	20	30	39	7	105	29%
French Polynesia	15	23	48	114	15	215	53%
Colombia	8	2	6	10	84	110	76%

Figure A-1. South Pacific humpback whales breeding grounds (Stocks D, E, F, G) and feeding areas (Area IV, V, VI* and I*). Included in the boxes is the number (n) of individuals from each region.

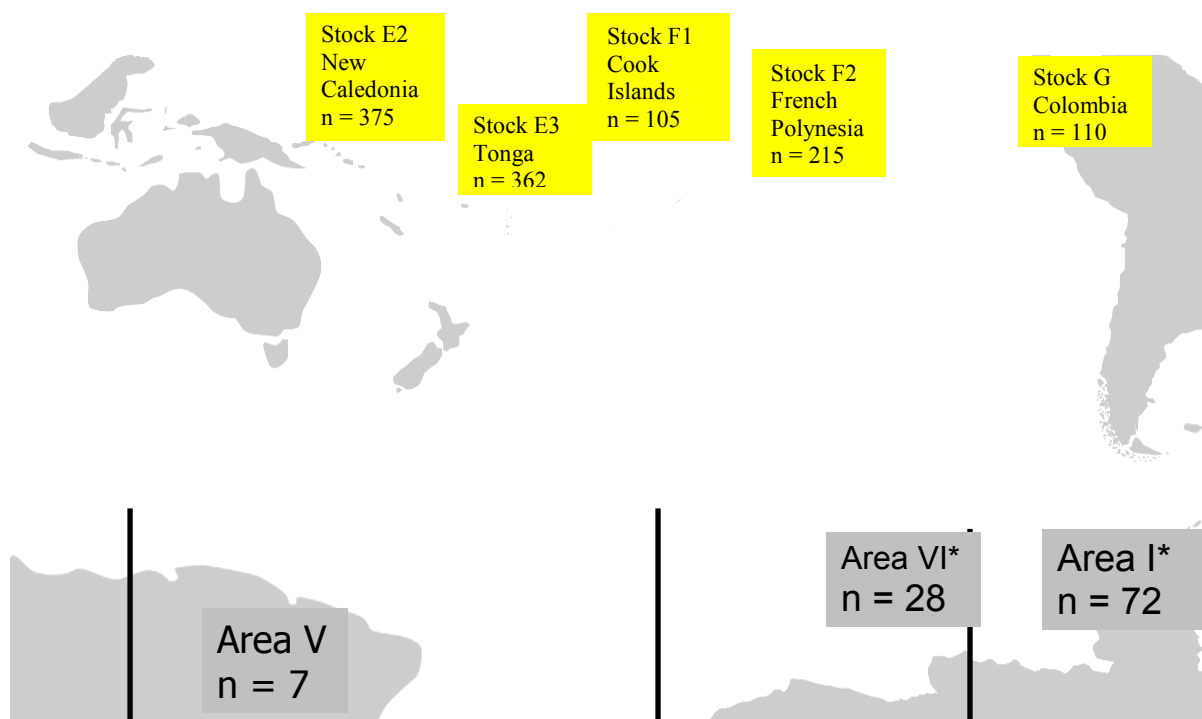
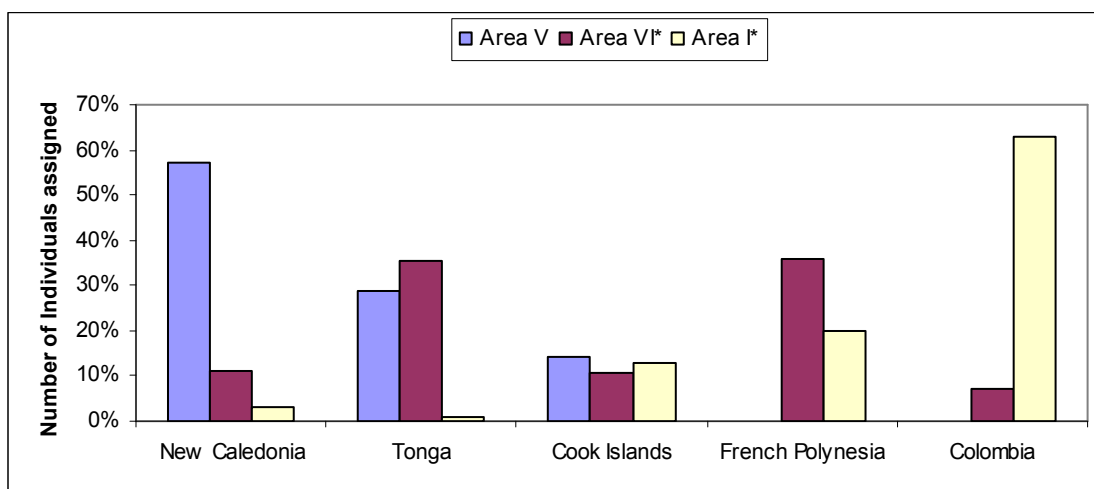


Figure A-2. The results from mixed-stock assignment tests in WHICHRUN for Antarctic Area V (n=7), Antarctic Area VI* (n=28) and Antarctic Area I* (n=72) based on 15 microsatellite loci and mtDNA haplotype data.



APPENDIX B - Supplementary Material for Chapter 2

Haplotypes of the South Pacific humpback whales.

Replicates were removed where microsatellite genotyping allowed for individual identification (Steel *et al.* unpublished). After sequencing corrections five of the original 115 haplotypes were removed (SP 51, 56, 75, 92, 103) from Olavarria *et al.* (2007) (Final n = 110)

Area I* = Area I as described in Figure 2.2

Area IV = Area IV as described in Figure 2.2

Area V = Area V as described in Figure 2.2

AreaVI* = Area VI as described in Figure 2.2

WA = Western Australia

EA = Eastern Australia

NC = New Caledonia

TG = Tonga

CI = Cook Islands

FP = French Polynesia

CO = Colombia

Hap	AreaI*	AreaIV	AreaV	AreaVI*	WA	EA	NC	TG	CI	FP	CO
SP1	8	3	0	0	16	5	8	25	24	52	2
SP2	0	0	0	0	0	4	6	1	0	0	0
SP3	0	2	0	1	0	6	7	10	1	5	0
SP4	0	0	0	0	0	0	5	1	0	0	0
SP5	0	0	0	0	0	0	0	1	0	0	0
SP6	0	0	0	0	0	0	0	0	0	9	0
SP7	0	0	0	0	3	0	0	0	0	0	0
SP8	3	0	0	0	0	0	0	0	0	0	2
SP9	0	0	0	0	0	0	0	0	0	0	1
SP10	1	0	0	0	1	5	7	3	0	0	1
SP11	0	0	2	0	0	6	9	0	0	0	0
SP12	2	0	0	1	0	0	3	7	8	3	1
SP13	0	0	0	2	0	5	12	12	1	4	0
SP14	1	2	1	2	6	5	27	22	6	22	4
SP15	0	1	1	0	2	0	1	0	0	0	0
SP16	0	0	0	0	1	0	0	0	0	0	0
SP17	0	0	0	0	0	0	12	2	0	0	0
SP18	0	0	0	1	0	0	2	0	0	0	0
SP19	2	1	0	1	3	1	0	10	3	10	0
SP20	0	0	0	0	1	0	0	0	0	0	0
SP21	0	0	0	0	1	0	0	2	0	0	0
SP22	0	0	0	0	3	0	2	7	1	0	0
SP23	0	3	0	0	4	0	0	0	0	0	0
SP24	0	0	0	1	0	0	0	1	1	4	0
SP25	0	0	0	0	1	0	0	0	0	0	1
SP26	0	0	1	0	0	14	2	6	1	1	0
SP27	0	3	0	1	6	1	8	13	1	0	0

SP28	0	0	0	0	0	0	6	0	0	0	0
SP29	0	0	0	0	0	1	7	4	0	2	0
SP30	0	1	0	0	5	0	0	0	0	0	0
SP31	0	0	0	0	0	0	0	0	0	4	0
SP32	6	0	0	0	0	0	0	0	0	0	11
SP33	0	0	0	0	0	0	5	2	0	0	4
SP34	0	0	0	0	1	0	0	0	0	0	0
SP35	0	0	0	0	1	0	0	0	0	0	0
SP36	0	2	0	0	3	0	6	0	0	0	0
SP37	0	0	0	0	0	0	0	5	1	0	0
SP38	0	1	0	0	0	1	4	7	2	0	0
SP39	0	0	0	0	0	1	0	5	0	0	0
SP40	0	0	0	0	1	0	0	0	0	0	0
SP41	0	2	0	0	2	2	4	0	0	0	0
SP42	0	2	0	2	12	0	3	7	1	2	0
SP43	0	0	0	0	0	0	0	3	2	0	2
SP44	0	0	0	0	0	0	1	0	0	0	0
SP45	0	0	0	0	7	0	1	0	0	0	0
SP46	0	0	0	0	0	4	1	1	0	0	0
SP47	0	1	0	0	1	0	0	0	0	0	0
SP48	0	0	0	0	3	0	1	0	0	0	0
SP49	0	0	0	0	1	1	1	0	0	0	0
SP50	6	0	0	0	0	0	1	6	0	1	9
SP52	6	0	0	0	8	6	18	7	4	17	5
SP53	0	0	0	0	0	0	3	0	0	0	0
SP54	0	0	0	0	0	0	1	4	0	7	1
SP55	0	0	0	0	0	0	5	0	0	0	0
SP57	0	0	0	0	3	0	0	0	0	0	0
SP58	0	0	0	0	1	0	0	0	0	0	0
SP59	0	0	0	0	1	0	1	0	0	0	0
SP60	2	0	0	0	0	0	0	0	0	0	3
SP61	2	0	0	0	0	0	0	0	0	0	1
SP62	1	0	0	0	0	0	2	18	6	14	5
SP63	2	0	0	0	0	10	5	1	0	0	2
SP64	0	0	1	0	0	0	6	2	0	0	0
SP65	0	0	0	0	0	1	3	0	0	0	0
SP66	1	0	0	0	0	0	0	0	0	0	3
SP67	0	0	0	0	3	0	0	0	0	0	0
SP68	2	0	0	1	1	5	22	8	0	0	1
SP69	0	0	0	0	0	0	1	0	0	0	0
SP70	0	1	0	0	2	0	0	1	0	0	0
SP71	0	1	0	1	9	14	11	2	0	0	0
SP72	1	0	0	3	0	1	3	17	10	23	2
SP73	0	1	1	3	2	8	22	31	8	3	1
SP74	0	0	0	2	0	0	0	5	1	2	1
SP76	0	1	0	2	8	3	7	18	1	3	0
SP77	0	0	0	0	0	0	2	0	0	0	0
SP78	0	1	0	0	1	3	5	2	0	1	0
SP79	0	0	0	0	0	0	0	0	1	0	0
SP80	0	0	0	0	2	0	0	0	0	0	0
SP81	0	1	0	0	1	0	0	0	0	0	0

SP82	0	1	0	0	1	0	0	0	0	0	0
SP83	0	0	0	1	0	0	1	5	2	0	0
SP84	0	1	0	0	1	0	0	0	0	0	0
SP85	0	0	0	0	0	3	1	0	0	0	0
SP86	0	1	0	0	2	0	0	0	0	0	0
SP87	0	0	0	0	0	5	3	0	0	0	0
SP88	0	1	0	0	6	2	14	17	3	6	0
SP89	0	0	0	0	3	1	4	2	1	8	0
SP90	13	0	0	0	0	0	0	0	0	0	28
SP91	0	1	0	1	7	1	8	4	0	2	0
SP93	0	0	0	0	3	1	7	0	0	0	0
SP94	0	1	0	0	7	1	1	3	0	0	0
SP95	0	0	0	0	0	0	2	0	0	0	0
SP96	0	0	0	0	0	4	8	1	3	3	0
SP97	0	2	0	0	3	0	1	0	0	0	0
SP98	5	0	0	0	0	0	0	0	0	0	9
SP99	0	0	0	1	0	0	15	9	3	25	0
SP100	3	0	0	0	1	0	5	15	3	11	0
SP101	0	0	0	0	0	0	0	0	0	0	4
SP102	0	0	0	0	0	12	13	7	1	1	0
SP104	0	0	0	0	0	1	1	2	0	1	0
SP105	0	0	0	0	2	0	0	0	0	0	0
SP106	0	0	0	0	0	0	0	2	0	0	0
SP107	0	0	0	0	2	3	5	0	0	0	0
SP108	0	0	0	0	0	0	1	0	0	0	0
SP109	0	1	0	0	3	0	0	0	0	0	0
SP110	0	0	0	0	1	0	0	0	0	0	0
SP111	1	0	0	0	0	0	4	4	1	0	0
SP112	0	0	0	0	0	0	1	0	0	0	0
SP113	0	0	0	0	3	0	0	0	0	0	0
SP114	0	0	0	0	0	1	3	5	0	1	0
SP115	0	0	1	0	2	8	0	0	0	0	0
Total	68	39	8	27	174	156	367	355	101	247	104

Appendix C - Supplementary Material for Chapter 3

Capture recapture photo-identification matrix

Individual codes refer to first year captured and sequence within year
i.e. FP99XX = Individual first captured in 1999, FP00XX = Individual first captured in 2000

Capture History

Each 0 or 1 represents a capture occasion

(i.e. breeding season 1999, 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007)

0 = not captured in that capture occasion

1 = captured in that capture occasion

Rurutu first sightings recoded for Program CAPTURE. The original codes are shown below in the Rurutu original ID column. All resights of Rurutu whales were in Moorea.

Usable Photos Catalogue 1999-2007

Individ.	Capture History	Rurutu original ID
FP9201	100100000	
FP9302	001000000	
FP9405	000110000	
FP9717	000001000	
FP9714	000000001	
FP9901	100000011	
FP9902	100000000	
FP9903	100000000	
FP9904	100000000	
FP9950	100000000	FP9904R
FP9905	100001000	
FP9951	100000000	FP9905R
FP9906	100000000	
FP9907	100000000	
FP9908	100000000	
FP9909	100000000	
FP9910	100000000	
FP9911	100000000	
FP9912	100000000	
FP9913	100000000	
FP9914	100000000	
FP9915	100000001	
FP9916	110000000	
FP9917	100000000	
FP9918	100000000	
FP9919	100000000	
FP9921	100000000	
FP9922	100000000	
FP9923	100000000	
FP9924	100000000	
FP9925	100000000	

FP9926	100000000	
FP9928	100000000	
FP9929	100000000	
FP9930	100000000	
FP9931	100000000	
FP9932	100000000	
FP9934	100000000	
FP9935	100000000	
FP9936	100000000	
FP9937	100000000	
FP9938	100000000	
FP9939	100000000	
FP9940	100001000	
FP9942	100000001	
FP9943	100100000	
FP9945	100000000	
FP9946	100000100	
FP9947	101000000	
FP9948	100000000	
FP9949	100000100	
FP0001	010000000	
FP0037	011001000	FP0001R
FP0003	010001000	
FP0004	010000000	
FP0008	010000000	
FP0009	010000000	
FP0010	010000000	
FP0011	010000000	
FP0012	010000000	
FP0014	010000000	
FP0015	010000000	
FP0016	010000000	
FP0017	010011000	
FP0018	010001000	
FP0019	010000000	
FP0020	010000000	
FP0022	010000000	
FP0023	010000000	
FP0024	010000000	
FP0026	010000000	
FP0027	010000000	
FP0028	010000000	
FP0029	010000000	
FP0030	010000000	
FP0031	010000000	
FP0033	010000000	
FP0034	010001010	
FP0035	010000000	
FP0036	010000000	
FP0101	001000000	
FP0128	001000000	FP0101R

FP0102 001000000	
FP0123 001001000	FP0102R
FP0103 001000000	
FP0124 001000000	FP0103R
FP0104 001000000	
FP0125 001000000	FP0104R
FP0105 001000000	
FP0126 001000000	FP0105R
FP0106 001000000	
FP0127 001000000	FP0106R
FP0107 001000000	
FP0108 001000000	
FP0110 001000000	
FP0111 001000000	
FP0112 001000000	
FP0113 001000000	
FP0114 001000000	
FP0115 001001000	
FP0116 001000010	
FP0117 001000001	
FP0118 001000000	
FP0119 001000000	
FP0120 001000000	
FP0121 001001000	
FP0122 001000000	
FP0201 000100000	
FP0202 000100000	
FP0203 000100000	
FP0242 000100000	FP0203R
FP0204 000100000	
FP0243 000100000	FP0204R
FP0205 000100000	
FP0244 000100000	FP0205R
FP0206 000100000	
FP0207 000100000	
FP0208 000110000	
FP0209 000100000	
FP0210 000100000	
FP0211 000100000	
FP0212 000100000	
FP0213 000100000	
FP0214 000100000	
FP0215 000100000	
FP0216 000100000	
FP0217 000100000	
FP0218 000101000	
FP0219 000100000	
FP0220 000100100	
FP0221 000100000	
FP0222 000110000	
FP0223 000101000	

FP0224 000100000	
FP0225 000100000	
FP0227 000100000	
FP0228 000100000	
FP0229 000100000	
FP0230 000100000	
FP0231 000100000	
FP0233 000100000	
FP0234 000100000	
FP0235 000100000	
FP0236 000100000	
FP0237 000100000	
FP0238 000100000	
FP0239 000100000	
FP0240 000100000	
FP0241 000100000	
FP0354 000010000	FP0301R
FP0302 000010000	
FP0304 000010000	
FP0355 000010000	FP0304R
FP0305 000010000	
FP0356 000010000	FP0305R
FP0306 000010000	
FP0357 000010000	FP0306R
FP0307 000010000	
FP0358 000010000	FP0307R
FP0359 000010000	FP0308R
FP0309 000010000	
FP0360 000011000	FP0309R
FP0310 000010000	
FP0361 000010000	FP0310R
FP0311 000011000	
FP0362 000010000	FP0311R
FP0312 000010000	
FP0363 000010000	FP0312R
FP0364 000010000	FP0313R
FP0314 000010000	
FP0365 000010000	FP0314R
FP0315 000010100	
FP0366 000010000	FP0315R
FP0316 000010000	
FP0367 000010000	FP0316R
FP0317 000011000	
FP0318 000010000	
FP0319 000010000	
FP0320 000011000	
FP0321 000010010	
FP0322 000010000	
FP0323 000010000	
FP0324 000010000	
FP0325 000010000	

FP0326	000011000	
FP0327	000010000	
FP0328	000010000	
FP0329	000010000	
FP0330	000010000	
FP0331	000010000	
FP0333	000010000	
FP0335	000010000	
FP0336	000010000	
FP0337	000011000	
FP0340	000010000	
FP0341	000010000	
FP0342	000010000	
FP0343	000010000	
FP0344	000010000	
FP0345	000010001	
FP0346	000010000	
FP0347	000011000	
FP0348	000010000	
FP0349	000010000	
FP0350	000010000	
FP0351	000010000	
FP0352	000010000	
FP0353	000011100	
FP0401	000001000	
FP0476	000001000	FP0402R
FP0403	000001000	
FP0404	000001000	
FP0405	000001000	
FP0406	000001000	
FP0407	000001000	
FP0477	000001000	FP0409R
FP0410	000001000	
FP0411	000001000	
FP0412	000001000	
FP0413	000001000	
FP0414	000001000	
FP0415	000001000	
FP0416	000001000	
FP0417	000001000	
FP0418	000001000	
FP0478	000001000	FP0419R
FP0420	000001000	
FP0421	000001000	
FP0422	000001000	
FP0423	000001000	
FP0425	000001000	
FP0479	000001000	FP0426R
FP0427	000001000	
FP0429	000001000	
FP0431	000001000	

FP0432 000001000	
FP0433 000001000	
FP0434 000001000	
FP0435 000001000	
FP0436 000001000	
FP0437 000001000	
FP0438 000001000	
FP0480 000001000	FP0439R
FP0442 000001000	
FP0443 000001000	
FP0444 000001000	
FP0445 000001000	
FP0446 000001000	
FP0481 000001000	FP0448R
FP0449 000001000	
FP0450 000001000	
FP0451 000001000	
FP0452 000001000	
FP0453 000001000	
FP0455 000001000	
FP0456 000001000	
FP0457 000001000	
FP0458 000001000	
FP0459 000001000	
FP0460 000001000	
FP0462 000001000	
FP0463 000001000	
FP0464 000001000	
FP0466 000001000	
FP0467 000001000	
FP0469 000001010	
FP0470 000001000	
FP0473 000001000	
FP0474 000001000	FP0475Rai
FP0475 000001010	FP0475Rai
FP0501 000000100	
FP0502 000000100	
FP0504 000000100	
FP0505 000000100	
FP0506 000000110	
FP0507 000000100	
FP0508 000000100	
FP0509 000000100	
FP0510 000000100	
FP0511 000000100	
FP0512 000000100	
FP0513 000000100	
FP0514 000000100	
FP0515 000000100	
FP0516 000000100	
FP0517 000000100	

FP0518 000000100	
FP0519 000000100	
FP0520 000000100	
FP0521 000000100	
FP0522 000000100	
FP0523 000000100	
FP0524 000000100	
FP0525 000000100	
FP0526 000000100	
FP0528 000000100	
FP0529 000000100	
FP0530 000000100	
FP0531 000000100	
FP0532 000000100	
FP0533 000000100	
FP0534 000000100	
FP0535 000000100	
FP0536 000000100	
FP0537 000000100	
FP0538 000000100	FP0538R
FP0539 000000100	FP0539R
FP0540 000000100	FP0540R
FP0541 000000100	FP0541R
FP0542 000000100	FP0542R
FP0543 000000100	FP0543R
FP0544 000000100	FP0544R
FP0545 000000100	FP0545R
FP0546 000000100	FP0546R
FP0547 000000100	FP0547R
FP0548 000000100	FP0548R
FP0549 000000100	FP0549R
FP0550 000000100	FP0550R
FP0551 000000100	FP0551R
FP0552 000000100	FP0552R
FP0553 000000100	FP0553R
FP0554 000000100	FP0554R
FP0601 000000010	
FP0602 000000010	
FP0603 000000011	
FP0604 000000010	
FP0605 000000010	
FP0606 000000011	
FP0607 000000010	
FP0608 000000010	
FP0609 000000011	
FP0610 000000010	
FP0611 000000010	
FP0612 000000010	
FP0613 000000010	
FP0615 000000010	
FP0616 000000010	

FP0617 000000010
FP0618 000000010
FP0619 000000010
FP0620 000000010
FP0621 000000010
FP0622 000000010
FP0623 000000010
FP0624 000000010
FP0625 000000010
FP0626 000000010
FP0627 000000010
FP0628 000000010
FP0629 000000010
FP0701 000000001
FP0702 000000001
FP0703 000000001
FP0705 000000001
FP0706 000000001
FP0707 000000001
FP0708 000000001
FP0709 000000001
FP0710 000000001
FP0712 000000001
FP0713 000000001
FP0714 000000001
FP0715 000000001
FP0716 000000001
FP0718 000000001
FP0719 000000001
FP0720 000000001
FP0721 000000001
FP0722 000000001
FP0723 000000001
FP0724 000000001
FP0725 000000001
FP0726 000000001
FP0727 000000001
FP0728 000000001
FP0729 000000001
FP0730 000000001
FP0731 000000001
FP0733 000000001
FP0734 000000001
FP0735 000000001
FP0736 000000001
FP0737 000000001
FP0738 000000001
FP0739 000000001
FP0740 000000001
FP0741 000000001
FP0742 000000001

FP0743 000000001
 FP0744 000000001
 FP0745 000000001
 FP0746 000000001
 FP0747 000000001
 FP0748 000000001
 FP0749 000000001
 FP0750 000000001
 FP0751 000000001
 FP0752 000000001
 FP0753 000000001
 FP0754 000000001
 FP0755 000000001
 FP0756 000000001
 FP0757 000000001
 FP0758 000000001
 FP0759 000000001
 FP0760 000000001
 FP0761 000000001
 FP0763 000000001
 FP0764 000000001
 FP0765 000000001
 FP0766 000000001

Quality Control Catalogue 1999-2007

Individ. Capture History

FP9201	100100000	
FP9302	001000000	
FP9405	000110000	
FP9717	000001000	
FP9714	000000001	
FP9901	100000011	
FP9902	100000000	
FP9950	100000000	FP9904R
FP9905	100001000	
FP9951	100000000	FP9905R
FP9906	100000000	
FP9907	100000000	
FP9908	100000000	
FP9909	100000000	
FP9910	100000000	
FP9911	100000000	
FP9912	100000000	
FP9913	100000000	
FP9914	100000000	
FP9915	100000001	
FP9923	100000000	
FP9924	100000000	
FP9925	100000000	
FP9926	100000000	

FP9932 100000000	
FP9937 100000000	
FP9942 100000001	
FP9940 100001000	
FP9947 101000000	
FP9949 100000100	
FP0037 011001000	FP0001R
FP0009 010000000	
FP0011 010000000	
FP0012 010000000	
FP0015 010000000	
FP0017 010011000	
FP0018 010001000	
FP0026 010000000	
FP0027 010000000	
FP0028 010000000	
FP0029 010000000	
FP0031 010000000	
FP0033 010000000	
FP0034 010001010	
FP0036 010000000	
FP0102 001000000	
FP0123 001001000	FP0102R
FP0103 001000000	
FP0124 001000000	FP0103R
FP0104 001000000	
FP0125 001000000	FP0104R
FP0105 001000000	
FP0126 001000000	FP0105R
FP0106 001000000	
FP0127 001000000	FP0106R
FP0111 001000000	
FP0112 001000000	
FP0114 001000000	
FP0115 001001000	
FP0116 001000010	
FP0117 001000001	
FP0118 001000000	
FP0119 001000000	
FP0121 001001000	
FP0122 001000000	
FP0201 000100000	
FP0202 000100000	
FP0203 000100000	
FP0204 000100000	
FP0244 000100000	FP0205R
FP0208 000110000	
FP0209 000100000	
FP0210 000100000	
FP0212 000100000	
FP0213 000100000	

FP0215 000100000	
FP0217 000100000	
FP0218 000101000	
FP0219 000100000	
FP0220 000100100	
FP0221 000100000	
FP0222 000110000	
FP0223 000101000	
FP0224 000100000	
FP0225 000100000	
FP0228 000100000	
FP0229 000100000	
FP0230 000100000	
FP0231 000100000	
FP0234 000100000	
FP0235 000100000	
FP0236 000100000	
FP0237 000100000	
FP0238 000100000	
FP0239 000100000	
FP0240 000100000	
FP0241 000100000	
FP0302 000010000	
FP0304 000010000	
FP0355 000010000	FP0304R
FP0356 000010000	FP0305R
FP0306 000010000	
FP0357 000010000	FP0306R
FP0307 000010000	
FP0360 000011000	FP0309R
FP0361 000010000	FP0310R
FP0311 000011000	
FP0362 000010000	FP0311R
FP0312 000010000	
FP0363 000010000	FP0312R
FP0313 000010000	
FP0315 000010100	
FP0316 000010000	
FP0367 000010000	FP0316R
FP0317 000011000	
FP0319 000010000	
FP0321 000010010	
FP0322 000010000	
FP0323 000010000	
FP0324 000010000	
FP0326 000011000	
FP0327 000010000	
FP0328 000010000	
FP0330 000010000	
FP0331 000010000	
FP0333 000010000	

FP0335	000010000	
FP0336	000010000	
FP0337	000011000	
FP0341	000010000	
FP0342	000010000	
FP0343	000010000	
FP0344	000010000	
FP0345	000010001	
FP0346	000010000	
FP0347	000011000	
FP0349	000010000	
FP0350	000010000	
FP0351	000010000	
FP0352	000010000	
FP0353	000011100	
FP0403	000001000	
FP0405	000001000	
FP0406	000001000	
FP0407	000001000	
FP0410	000001000	
FP0411	000001000	
FP0412	000001000	
FP0416	000001000	
FP0417	000001000	
FP0478	000001000	FP0419R
FP0420	000001000	
FP0421	000001000	
FP0422	000001000	
FP0423	000001000	
FP0425	000001000	
FP0431	000001000	
FP0432	000001000	
FP0434	000001000	
FP0480	000001000	FP0439R
FP0442	000001000	
FP0443	000001000	
FP0445	000001000	
FP0449	000001000	
FP0450	000001000	
FP0451	000001000	
FP0452	000001000	
FP0453	000001000	
FP0481	000001000	FP0448R
FP0457	000001000	
FP0459	000001000	
FP0460	000001000	
FP0462	000001000	
FP0463	000001000	
FP0464	000001000	
FP0466	000001000	
FP0467	000001000	

FP0469 000001010	
FP0470 000001000	
FP0474 000001000	FP0474Rai
FP0475 000001010	FP0475Rai
FP0502 000000100	
FP0504 000000100	
FP0506 000000110	
FP0509 000000100	
FP0510 000000100	
FP0512 000000100	
FP0513 000000100	
FP0517 000000100	
FP0520 000000100	
FP0527 000000100	
FP0529 000000100	
FP0531 000000100	
FP0533 000000100	
FP0535 000000100	
FP0536 000000100	
FP0540 000000100	FP0540R
FP0541 000000100	FP0541R
FP0543 000000100	FP0543R
FP0551 000000100	FP0551R
FP0554 000000100	FP0554R
FP0601 000000010	
FP0602 000000010	
FP0603 000000011	
FP0604 000000010	
FP0606 000000011	
FP0607 000000010	
FP0609 000000011	
FP0610 000000010	
FP0612 000000010	
FP0613 000000010	
FP0615 000000010	
FP0617 000000010	
FP0619 000000010	
FP0620 000000010	
FP0621 000000010	
FP0624 000000010	
FP0625 000000010	
FP0626 000000010	
FP0627 000000010	
FP0629 000000010	
FP0701 000000001	
FP0702 000000001	
FP0703 000000001	
FP0706 000000001	
FP0707 000000001	
FP0708 000000001	
FP0710 000000001	

FP0711 000000001
FP0719 000000001
FP0720 000000001
FP0723 000000001
FP0724 000000001
FP0726 000000001
FP0727 000000001
FP0728 000000001
FP0731 000000001
FP0735 000000001
FP0736 000000001
FP0737 000000001
FP0738 000000001
FP0739 000000001
FP0740 000000001
FP0742 000000001
FP0744 000000001
FP0745 000000001
FP0746 000000001
FP0747 000000001
FP0748 000000001
FP0749 000000001
FP0750 000000001
FP0751 000000001
FP0752 000000001
FP0753 000000001
FP0754 000000001
FP0755 000000001
FP0756 000000001
FP0757 000000001
FP0758 000000001
FP0760 000000001
FP0761 000000001
FP0763 000000001
FP0764 000000001
FP0766 000000001

APPENDIX D – Additional Supplementary Material for Chapter 3.

Results from all models as calculated in Program CAPTURE, Program JOLLY and the Schnabel estimate for French Polynesia humpback whales.

Usable Photos						Quality Control				
	N	SE	CV	95% CI	Model Selection	N	SE	CV	95% CI	Model Selection
Schnabel 1999-2007	1,679	254	0.15	1,181-2,177	--	825	132	0.16	566-1,084	--
Closed Population Program CAPTURE Results 1999-2007										
M(o)	1858	241	0.13	1462-2,435	0.13	878	115	0.13	691-1,149	0.13
M(h) jackknife	1513	77	0.05	1,372-1,675	0.0	882	61	0.07	773-1,014	0.0
M(b)	1641	1458	0.89	613-8,149	0.09	942	913	0.97	213-2,462	0.09
M(tb)	2283	3161	1.38	610-18,667	0.34	1028	899	0.87	388-5,016	0.34
M _{th} Chao	2,046	318	0.16	1,532-2,798	0.80	949	154	0.16	708-1,321	0.66
Darroch's M(t)	1,824	235	0.13	1,437-2,389	1.0	861	112	0.13	678-1,124	1.0
Closed Population Program CAPTURE Results 2003-2007										
M(o)	1747	354	0.20	1,202-2,619	0.13	826	166	0.20	577-1,276	0.13
M(h) jackknife	953	466	0.49	483-2,571	0.0	692	127	0.18	280-872	0.0
M(b)	2178	493	0.23	1,431-3,413	0.09	492	206	0.42	280-1,206	0.09
M(tb)	1696	361	0.21	1,147-2,596	0.34	864	1491	1.73	239-9,357	0.39
M _{th} Chao	1,849	439	0.16	1,197-2,970	0.73	853	206	0.24	556-1,392	0.72
Darroch's M(t)	1,724	112	0.13	678-1,124	1.0	803	160	0.20	561-1,203	1.0
Open Population Program JOLLY Results 1999-2007										
Program Jolly	1,225	500	0.40	246-2,203	--	564	509	0.90	0-1,587	--
Survival Rate Φ	0.82	0.17	--	--	--	0.78	0.15	--	--	--