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ESCORTING OF MOTHER-CALF PAIRS OF HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) IN THE COLOMBIAN PACIFIC DURING THE BREEDING SEASON

by

Natalia Botero Acosta

A Dissertation
Submitted to the Graduate School,
the College of Education and Psychology,
and the Department of Psychology
at The University of Southern Mississippi
in Partial Fulfillment of the Requirements
for the Degree of Doctor of Philosophy

December 2017

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December 2017

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ABSTRACT

ESCORTING OF MOTHER-CALF PAIRS OF HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) IN THE COLOMBIAN PACIFIC DURING THE BREEDING SEASON

by Natalia Botero Acosta

December 2017

Humpback whales (*Megaptera novaeangliae*) belonging to the “breeding G-stock” annually migrate from the Antarctic Peninsula and southern Chile to the southeastern Pacific to reproduce. Associations between mother-calf pairs and escorts were examined in the Gulf of Tribugá, northern Colombian Pacific, using photo-identification and behavioral/spatial sampling. Research hypotheses included: 1. The association between cows and escorts is short-lived, consistent with a male reproductive strategy, 2. The presence of escort(s) elicits a behavioral response from mother-calf pairs and, 3. The patterns of spatial distribution reflect the spatial segregation of maternal females. Groups were classified as mother-calf pairs (Mc), mother, calf and escort (McE), and mother, calf and multiple escorts (McME). Sightings were made in 2010 and between 2013 and 2016. Photo-identification procedures included comparisons of caudal and dorsal fins. For each group, coordinates were processed in ArcMap v10.3, extracting depth and distance to the coast. Speed data was calculated using Basecamp v4.6. Tracks were classified as traveling or milling based on directionality and trajectory. Spatial variables were processed with multivariate and factorial analyses of variance. Chi-squared tests compared behavioral frequencies across group types. Groups with calves (n=108) represented 20.7% of all sightings. While a total of 15 re-sightings were recorded, they were limited to changes in group composition or separate encounters with either the cow or the escort(s). Escorted pairs spent significantly more time traveling and executing surface-active and social behaviors. Additionally, they spent less time diving and resting when compared to unescorted pairs ($\chi^2_8 > 15.51$, $p < 0.05$). The multivariate analysis indicated no significant differences in depth and distance to the coastline between group types $F(4, 208) = 0.564$, $p > 0.05$. Similarly, the factorial ANOVA indicated that traveling speeds were not significantly different when compared across date or group/track types $F(3, 61) = 0.860$, $p > 0.05$. In conclusion, in the Gulf of Tribugá, associations between cows and escorts seem to be transitory, consistent with a male mating strategy. Since the habitat structure appears to lessen the effectiveness of the spatial segregation strategy for maternal females, research effort continuity is vital to understand key aspects of the behavior and habitat use of humpback whales.

ACKNOWLEDGMENTS

I would like to thank my advisor Dr. Stan Kuczaj, for his encouragement on the early stages of this dissertation and other research projects on which I worked as a member of the Marine Mammal Behavior and Cognition Laboratory at Southern Miss. I would also like to thank Dr. Fernando Félix. Sometimes it is hard to believe it had been ten years already since I was your intern in Ecuador. It has been a tremendous honor to work with you. To Drs. David Echavarria and Donald Sacco, I extend all my gratitude for their support. Finally, I thank Dr. Frank Moore and Dr. Richard Mohn, for their guidance with this project and their patience with my numerous questions and concerns.

Many thanks to all my friends and colleagues from Macuáticos Colombia Foundation. Macuáticos has been one of the best learning experiences I have had and I want to thank everyone that has been involved in creating and maintaining this dream.

I want to extend my greatest gratitude to the local communities and the community counsels in the Gulf of Tribugá. Because of your hospitality and generosity, I think of Chocó as my second home. It is thanks to the research and environmental education efforts that you have all supported, that I can contribute to overcoming the information gaps that have hindered the progress of marine mammal science in Colombia; and for that I feel extremely grateful. To my field family, Genaro Moreno, Cruzmélida Martínez, Esperanza Lemus, and Fausto Moreno: I have no means of telling you how much your support and assistance has meant for me.

Thanks to Cristian Moreno, Miguel Ramos, Angelo Mosquera, Harrison Murillo, Bayron Manyoma, and Emel Martínez for their assistance with fieldwork. I will always treasure all the great moments we shared along the research vessel.

A special message of gratefulness to Juliana López, Andrés Cañas, Carolina López, Carolina Ávila, Rocío Lancheros, Katherine Arévalo, Alejandra Vergara, Christina Perazio, Maria Camila Medina, Andrea Caicedo, Alejandra Neira, Cristian Bedoya, Nadya Ramirez, Maria Zapetis and Dr. Héctor Guzmán for your assistance in the field. This project was truly a team effort so I can only hope you all know how much I appreciate the fact that you were part of it.

Many thanks to all members of the Laboratory of Molecular Ecology of Aquatic Vertebrates (LEMVA) at Los Andes University, especially Dalia Barragán, Dr. Federico Riet and Dr. Susana Caballero for their fieldwork assistance, particularly with the processing and analysis of tissue samples.

A heartfelt thank you to my friends and colleagues at the Marine Mammal Behavior and Cognition Lab, including our honorary member Mitch Brown. Your encouragement and support over these years have been extremely important for me. A special recognition for Riley Macgregor and Alexandra Walker for their assistance with photo-identification comparisons. A million thank you for the million times you went through the fluke shots.

To Carlos Ortiz, Ana Fernandez, and Nohelia Farías my gratitude for your assistance with the spatial distribution analyses.

I would like to thank all whale watching operators including Posada Palo de Agua, El Cantil Ecolodge, Nautilos Ecolodge, Posada La Joviseña, Ecohotel Punta Brava, Turquí Buceo & Ecolodge, and Ecolodge El Almejal for supporting the integration of scientific research and environmental education.

Finally, I would like to thank Cetacean Society International, Rufford Small Grants for Nature Conservancy, Idea Wild, The Society for Marine Mammalogy and Columbus Zoo for providing the funding that allowed the completion of this and other research initiatives in the Gulf of Tribugá. The Doctoral Fellowship granted by Colciencias allowed me to maintain and nurture research connections in Colombia and for that I will be eternally grateful.

DEDICATION

To my family-

You are the greatest support system someone could ask for. Thank you for ALWAYS being there for me, for encouraging me, believing in me, and loving me unconditionally. I love you.

To my advisor, Dr. Stan Kuczaj-

After almost five years as your student, I can say with confidence that I have met few people as generous and funny as you. I do not think I could have ever thanked you enough for your support and encouragement with my work in Colombia. I will always treasure the moments I shared with you. You are, and will always be, greatly missed.

To the local communities in the Gulf of Tribugá-

With great joy I can say that I am a better biologist and a better person thanks to all the wonderful experiences I have lived in Chocó. Even the hard times have been softened by the fortune of having the support and encouragement of so many wonderful people. Thank you for allowing me to do what I love most and for letting me be a part of your lives.

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LIST OF ABBREVIATIONS

ANOVA	Analysis of variance
MANOVA	Multivariate analysis of variance
Mc	Mother-calf pair
McE	Mother, calf and escort group
McME	Mother, calf and multiple escorts group

CHAPTER I - INTRODUCTION

A marked preference for coastal waters, as well as the ability to identify individuals based on the coloration patterns of their caudal fins, have made humpback whales the most well studied baleen whale species (Clapham, 2000). In fact, several long-term programs have been active for over 25 years on both feeding and breeding grounds (e.g. Clapham, 1993; Glockner-Ferrari & Ferrari, 1985; Perry, Baker, & Herman, 1990). Nonetheless, despite such intensive research effort, many aspects of the life history and reproductive ecology of the species remain poorly studied. For example, little is known about the associations of mother-calf pairs with other whales, often referred to as escorts (Clapham, Palsbøll, Mattila, & Vasquez, 1992; Glockner & Venus, 1983; Herman & Antinoja, 1977; Herman & Tavolga, 1980). Two main hypotheses have been proposed to explain the role of escorts when joining a mother-calf pair. One hypothesis states that escorts offer protection from male harassment and predation (Chittleborough, 1953, 1958; Herman & Antinoja, 1977; Herman & Tavolga, 1980; Pitman et al., 2015). The alternative hypothesis proposes that escorts are looking to mate with the female in case of a post-partum ovulation (Craig, Herman, Pack, & Waterman, 2014; Félix & Botero-Acosta, 2011; Herman & Tavolga, 1980; Smultea, 1994). If, in fact, escorts do mate with cows, this association could also be interpreted as evidence of mate guarding (Clapham, 1996). Photo-identification comparisons as well as behavioral/spatial sampling allowed for the generation and testing of predictions regarding the function of this association, which greatly increases our current understanding of male and female mating strategies.

CHAPTER II – REVIEW OF RELATED LITERATURE

Behavioral Ecology of Humpback Whales

Humpback whales (*Megaptera novaeangliae*) are a cosmopolitan species (Clapham & Mead, 1999). Different populations, which are believed to be geographically and reproductively isolated (Johnson & Wolman, 1984), occupy every major ocean around the world. For the Southern Hemisphere, the International Whaling Commission recognizes seven breeding stocks (A-G, IWC, 1998). After feeding in the Antarctic Peninsula and southern Chile during the austral summer, whales of the breeding stock "G" migrate to coastal waters of Peru, Ecuador, Colombia, Panama and Costa Rica to breed during the winter months (Félix & Haase, 2001; Flórez-González, 1991; Pacheco, Silva, & Alcorta, 2009; Rasmussen & Palacios, 2013).

According to whaling records, and remote biopsy efforts, the migration to and from the breeding grounds is segregated by the reproductive condition of individuals (Brown & Corkeron, 1995; Brown, Corkeron, Hale, Schultz, & Bryden, 1995; Chittleborough, 1965; Craig & Herman, 1997; Dawbin, 1966, 1997; Nishiwaki, 1959). Lactating females, accompanied by their yearlings, would be the first to arrive to the breeding grounds, followed by juveniles and adults of both sexes. Pregnant females are typically the last ones to leave the feeding grounds. The southward migration presumably follows the inverse order. Females that weaned their yearlings would be the first to leave, followed by immature whales. While most of the mature males presumably remain on the breeding grounds to exploit additional mating opportunities, newly pregnant females leave shortly after conception. Lactating females are thought to be the last ones to the leave the breeding grounds (Brown et al., 1995; Chittleborough, 1965; Dawbin, 1966, 1997; Nishiwaki, 1959).

It was traditionally assumed that all individuals within a population migrated between feeding and breeding grounds. Nonetheless, evidence indicates that due to the energetic demands of migration and reproduction, some animals, particularly adult females and juveniles of both sexes, may not migrate annually (Lockyer, 1984). Instead, these individuals would remain relatively close to the feeding grounds during the winter months (Brown & Corkeron, 1995; Brown et al., 1995; Craig & Herman, 1997). As a result, sex ratio is skewed towards males during the migration and the time spent on the breeding grounds (Brown & Corkeron, 1995; Brown et al., 1995; Clapham, 1996; Clapham et al., 1992; Félix & Botero-Acosta, 2012).

Humpback whales do not typically feed while on the breeding grounds. Only a few reports describe scarce occurrences of feeding activity during the winter months (e.g. Gendrom & Urbán-Ramirez, 1993). Instead, they rely on fat reserves generated during the feeding season (Chittleborough, 1965; Dawbin, 1966; Nishiwaki, 1959). Predation risk on the breeding grounds tends to be mild, at least for adults (Clapham, 2000; Flórez-González, Capella, & Rosembaum, 1994; Naessig & Lanyon, 2004; Pitman et al., 2015). Therefore, sexual selection appears to be the main selective pressure behind the generation, and maintenance, of behavioral strategies that maximize reproductive benefits (Brown & Corkeron, 1995; Cerchio, Jacobsen, Cholewiak, Falcone, & Merriwether, 2005; Clapham, 1996).

Researchers have long agreed that humpback whales do not conform to a monogamous mating system. Instead, authors have proposed polygamy, polygyny, promiscuity, and even lek aggregations as a better fit (Baker & Herman, 1984; Brownell & Ralls, 1986; Cerchio et al., 2005; Clapham, 1993, 1996; Clapham & Palsbøll, 1997; Clutton-Brock, 1989; Darling, 1983, 2001; Emlen & Oring, 1977; Herman & Tavolga, 1980; Mobley & Herman, 1985). These assumptions are based on behavioral observations that include: 1. Short lived associations between males and females (Andriolo et al., 2014; Darling, 1983; Mobley & Herman, 1985), 2. Intense competition for access to receptive females within mating groups (Baker & Herman, 1984; Félix & Novillo, 2015; Tyack & Whitehead, 1982), 3. Sexual proportions biased towards males on the breeding grounds (Brown & Corkeron, 1995; Brown et al., 1995; Clapham, 1996), and 4. Interactions between males mediated by acoustic and behavioral displays (Darling & Bérubé, 2001; Darling, Gibson, & Silber, 1983)

Copulation has not been conclusively reported in the scientific literature despite approximately 25+ years of research effort (Nishiwaki & Hayashi, 1950). A photograph taken by Jason Edward, constitutes the first reliable description of copulation in humpback whales (Holland, 2012). It was only through genetic analyses that some insight into the patterns of reproductive behavior of humpback whales has been gained. Clapham & Palsbøll (1997) reported that three females wintering in the Gulf of Maine were serially promiscuous across multiple seasons (Clapham & Palsbøll, 1997). Furthermore, according to Cerchio and colleagues (2005), the majority of males sampled at the Revillagigedo Archipelago, had no paternity assignments. Conversely, a few males sired at least three calves. Since most successful males fathered only one calf, reproductive skew appeared not to be severe, which is consistent with mild polygyny (Cerchio et al., 2005).

The Social Structure of Humpback Whales

Similar to what has been suggested for most Mysticetes, the social structure of humpback whales is often characterized as a fission-fusion society (Clapham, 1993, 2000). Group membership appears to be highly unstable, on both feeding and breeding grounds; and with the exception of mothers and calves, long-term associations appear to be rare (Andriolo et al., 2014; Baker & Herman, 1984; Baraff & Weinrich, 1993; Clapham, 1996; Helweg & Herman, 1994; Mobley & Herman, 1985; Szabo & Duffus, 2008; Whitehead, 1983). Groups of humpback whales are often small, with most observations including single animals and pairs. Nonetheless, larger aggregations occasionally occur in the context of cooperative foraging, or in relation to male intra-sexual competition for access to receptive females during the breeding season (Baker & Herman, 1984; Clapham, 1993; Clapham et al., 1992; Félix & Novillo, 2015; Mobley & Herman, 1985; Tyack & Whitehead, 1982; Weinrich, 1991; Weinrich & Kuhlberg, 1991; Whitehead, 1983).

Although males are not involved in parental care, occasionally adult and/or juvenile individuals, known as escorts, can temporarily associate with a mother and her calf (Glockner & Venus, 1983; Herman & Antinoja, 1977; Herman & Tavolga, 1980). Underwater observations of the genital region, and DNA sampling, have indicated that escorts are almost exclusively males (Clapham et al., 1992; Glockner-Ferrari & Ferrari, 1985; Glockner & Venus, 1983). The only known exceptions include two females, one juvenile and one adult, identified as escorts (Andriolo et al., 2014; Glockner-Ferrari & Ferrari, 1985). Despite the relative high frequency of escorting behavior on the breeding grounds, the conclusions on the role of escorts in these kinds of associations are still speculative (Clapham, 1996; Darling, 2001; Herman & Tavolga, 1980; Mobley & Herman, 1985).

One hypothesis states that the association with a male escort is beneficial for the cow and her calf because it offers protection from male harassment and predation attacks (Brown et al., 1995; Chittleborough, 1953, 1958; Glockner & Venus, 1983; Herman & Antinoja, 1977; Herman & Tavolga, 1980; Pitman et al., 2015). For example, Chittleborough (1953) and Pitman and colleagues (2015) described instances in which escorts repelled killer whales by interposing themselves between the calf and the orcas, vocalizing and slapping their fluke and pectoral fins on the water. Furthermore, Glockner & Venus (1983) reported an escort guarding the calf until it could station itself with its mother, further suggesting a protective role.

An alternative hypothesis proposes that escorts are either looking to mate with the female in case of a post-partum ovulation or mate guarding after copulation has occurred (Andriolo et al., 2014; Baker & Herman, 1984; Cerchio et al., 2005; Craig, 2001; Craig et al., 2014; Darling et al., 1983; Félix & Botero-Acosta, 2011; Glockner-Ferrari & Ferrari, 1985; Herman & Tavolga, 1980; Mobley & Herman, 1985; Smultea, 1994). A key observation supporting this hypothesis is that by the end of the season, newly pregnant females have started the migration back to the feeding grounds, so the proportion of receptive females on the breeding grounds decreases. In this context, joining a mother and calf pair would be an adaptive behavior for males since it would allow them to maximize breeding opportunities (Chu & Nieukirk, 1988; Craig, Herman, & Pack, 2002; Félix & Botero-Acosta, 2011; Glockner-Ferrari & Ferrari, 1985; Mackintosh, 1972; Mobley & Herman, 1985; Smultea, 1994).

If indeed the escort seeks a mating opportunity, the association would ideally last until the female became receptive, or until another female was detected. Nonetheless, if copulation has occurred, a prolonged association might be expected, as a form of mate guarding (Brown & Corkeron, 1995; Félix & Botero-Acosta, 2011). In fact, escorts commonly direct behaviors that follow a hierarchical scale of intensity in an attempt to defend their position next to the cow. Displays include interceptions, bubble trails, underwater blows, head lunges, charges, fluke and peduncle slaps, and tail slashes (Baker & Herman, 1984; Chu & Nieukirk, 1988; Darling et al., 1983; Glockner-Ferrari & Ferrari, 1985; Glockner & Venus, 1983; Mattila, Clapham, Katona, & Stone, 1989; Mobley & Herman, 1985; Tyack, 1981; Tyack & Whitehead, 1982). Furthermore, escorts and challengers are commonly seen with bloody or raw patches of skin, demonstrating the potential intensity of this competition (Baker & Herman, 1984; Darling et al., 1983; Herman & Tavolga, 1980; Mattila et al., 1989; Tyack & Whitehead, 1982).

Through photo-identification matching, several authors have suggested that male-female pairs associate for short periods of time only, from a few hours up to a few days (Baker & Herman, 1984; Darling et al., 1983; Félix & Botero-Acosta, 2011; Mobley & Herman, 1985; Tyack & Whitehead, 1982). Such a brief association period suggests that allomaternal behavior is probably not the main function of the cow-escort association (Baker & Herman, 1984; Mobley & Herman, 1985). Andriolo and colleagues (2014) provided support for such estimates by tagging two sets of mother and escort while associating. The first pair remained in close proximity for at least 5 days from the moment of tagging. A similar pattern was observed for the second dyad, which associated for at least four days.

The duration of this association is relevant because it has been reported that the presence of escort(s) can cause a significant change on the behavior of the mother-calf pair (Cartwright & Sullivan, 2009; Helweg & Herman, 1994). Upon escort affiliation, the female and her calf typically increase their traveling speed, and consequently their energetic expenditure, and reduce the time spent resting and nursing (Baker & Herman, 1984; Cartwright & Sullivan, 2009; Craig et al., 2014; Videsen, Bejder, & Madsen, 2015). Occasionally, multiple males join a mother-calf pair, forming a competitive group. In this context, males frequently exhibit a high level of surface activity and some degree of antagonism within their interactions (Baker & Herman, 1984; Clapham et al., 1992; Félix & Novillo, 2015). As a result, the calf is placed at greater risk of injury or separation from the mother (Baker & Herman, 1984; Cartwright & Sullivan, 2009; Craig et al., 2014; Pack, Herman, Craig, Spitz, & Deakos, 2002; Smultea, 1994).

Habitat Use of Humpback Whales

Anecdotal observations, whaling records, and research reports generally describe humpback whales as a predominantly coastal species (Craig, 2001; Dawbin, 1966; Ersts & Rosenbaum, 2003; Glockner-Ferrari & Ferrari, 1985; Mackintosh, 1972). Conversely, modern techniques such as satellite tagging have indicated that individuals occasionally occupy oceanic waters during migration, when foraging, and even while on the breeding grounds (Dalla Rosa, Secchi, Maia, Zerbini, & Heide-Jørgensen, 2008; Félix & Guzmán, 2014; Guzman & Félix, 2017; Lagerquist, Mate, Ortega-Ortiz, Winsor, & Urbán-Ramirez, 2008; Rosenbaum, Maxwell, Kershaw, & Mate, 2014; Zerbini et al., 2006, 2011). Overall, humpback whales seem to prefer waters less than 200m in depth, irrespective of the distance to the coastline (Garrigue, Clapham, Geyer, Kennedy, &

Zerbini, 2015; Glockner-Ferrari & Ferrari, 1985; Herman & Antinoja, 1977). Observations of high densities of whales in offshore waters, further suggest that depth, and possibly bottom topography, might be more important than distance to shore (Cartwright et al., 2012; Craig, 2001; Garrigue et al., 2015; Guzman & Félix, 2017; Smultea, 1994).

Within the breeding grounds, humpback whales tend to exhibit a heterogeneous spatial distribution, according to the age class and reproductive state of individuals (Andriolo et al., 2014; Craig, 2001; Craig & Herman, 2000; Craig et al., 2014; Ersts & Rosenbaum, 2003; Felix & Haase, 2005; Smultea, 1994). While mother and calf pairs are typically found in shallow, coastal waters; most of the adult males and juveniles of both sexes are usually found in deeper, more exposed waters (Craig, 2001; Craig et al., 2014; Ersts & Rosenbaum, 2003; Félix & Botero-Acosta, 2011; Felix & Haase, 2005; Glockner-Ferrari & Ferrari, 1985; Herman & Antinoja, 1977; Herman & Tavolga, 1980; Martins et al., 2001; Oviedo & Solís, 2008; Sanders, Barrios-Santiago, & Appeldoorn, 2005; Smultea, 1994; Whitehead & Moore, 1982).

Although this pattern has been consistently reported in different breeding areas around the world, the factors that motivate this segregation have not been thoroughly examined. Some authors have suggested that it might occur in response to ecological pressures typical of breeding areas, such as predation risk for calves and prevention of male harassment. Additional factors including conservation of energy and preference for calm, protected waters are also presumed to be important for mother-calf pairs (Cartwright et al., 2012; Cartwright & Sullivan, 2009; Corkeron & Connor, 1999; Craig, 2001; Craig et al., 2014; Flórez-González et al., 1994; Pitman et al., 2015; Smultea, 1994).

In order to fully understand the selective pressures affecting the habitat use of humpback whales during the breeding season, it is necessary to contextualize known patterns to the spatial and environmental features of each location. For example, Cartwright and colleagues (2012) noted that in breeding areas characterized by a narrow continental shelf, female-calf pairs are often found close to the coastline, where the shallowest waters were available (Cartwright et al., 2012; Ersts & Rosenbaum, 2003; Oviedo & Solís, 2008; Smultea, 1994). Conversely, with a broad continental shelf, water depth and distance to shore increase gradually. In this scenario, cows typically cover a much greater area, and can be found several kilometers off the coast (Félix & Botero-Acosta, 2011; Martins et al., 2001).

The study of the patterns of habitat use and their connection with properties of the social structure is an important task for the conservation of humpback whales (Flórez-González et al., 2007). Mother and calf pairs are especially susceptible to anthropogenic impacts due to their preference for shallow, coastal waters. Conservation threats include water pollution, vessel collisions, harassment from whale watching boats, and incidental mortality due to entanglement (Avila, Correa, & Parsons, 2015; Félix, 2007; Félix, Muñoz, Falconí, Botero, & Haase, 2011; Flórez-González et al., 2007; Guzman, Gomez, Guevara, & Kleivane, 2013).

Current Study

The current investigation employed photo-identification techniques and behavioral/spatial sampling to study the stability and function of the association between cows and escorts. Such an integrative strategy allowed for a knowledgeable evaluation of the two main hypotheses concerning the role of an escort when joining a mother and calf pair: a protective role vs. an opportunistic mating strategy. The following hypotheses were formulated to study the spatial, temporal, and behavioral aspects of this association: 1. The association between cows and escorts is short-lived, consistent with a male reproductive strategy, 2. The presence of escort(s) elicits a behavioral response from mother-calf pairs and, 3. The patterns of spatial distribution reflect the spatial segregation of maternal females.

CHAPTER III - METHODOLOGY

Study Area

The Gulf of Tribugá is located in the Chocó province, in the northern Colombian Pacific coast (Figure 1). The area, comprised of several small bays, limits with the locality of El Valle, municipality of Bahía Solano (6°06'N, 77°25'W) to the north, and with Cape Corrientes, municipality of Nuquí (6°06'N, 77°25'W) to the south (Díaz, 2002). The main logistic station for the current project was Coquí (5°36'N, 77°21'W), a small fishing community located southwest within the Gulf of Tribugá.

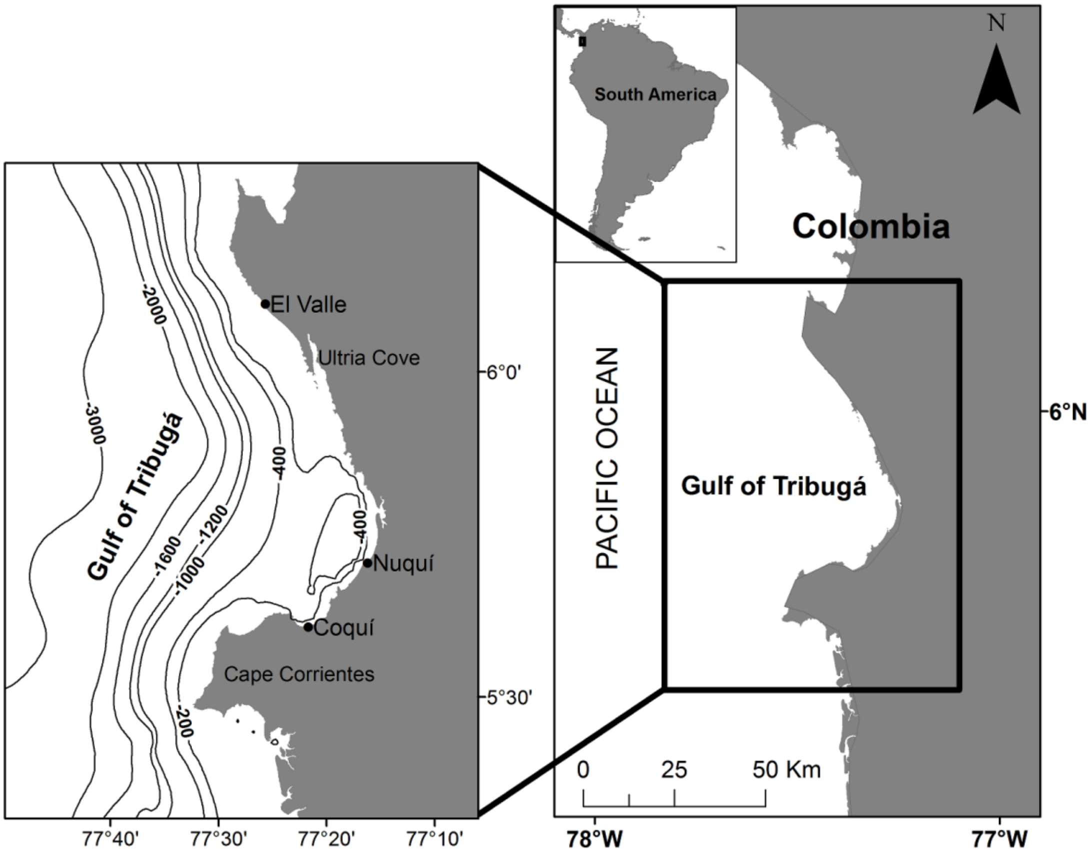


Figure 1. Study area.

Several marine currents affect the north of Colombian Pacific, including the North Equatorial current, the North Equatorial countercurrent, the Panamanian Gulf current, and the Colombian current. Considering the interaction of these currents, and the freshwater input from the continent, coastal waters tend to be turbid, relatively warm (22-28°C), and of medium-low salinities: ≤ 33.5ppt in oceanic waters and around 20ppt near the coast (Cantera, 1993; Díaz, 1998). Tides are characterized by a semidiurnal macro-tidal regime of up to 5 meters, with two daily high and low tides (Díaz, 2002; Jaramillo & Bayona, 2000).

The study area is located within the zone of influence of the Intertropical Convergence Zone. As a consequence, weather is characterized by slow winds and high pluviosity (Eslava, 1993). The rainy period extends from May to November, while the dry season starts around December and ends in April. The mean pluviosity for the zone is approximately 8,000 mm/year (Jaramillo & Bayona, 2000; Vargas-Ángel, 2003). Relative humidity is always high, with average values of 80-90% saturation. Air temperature on the coast is fairly constant with annual means between 25 and 27°C (Cantera, 1993; Díaz, 1998; Eslava, 1993).

The Gulf of Tribugá is characterized by a narrow and sloped continental shelf, which causes the 300m isobaths to be located a few kilometers from the coast (Galvis & Mojica, 1993). Most of the territory is flat or slightly wavy, although Coquí and Cugucho hills stand out with heights up to 500 m.a.s.l. As a result of the high precipitations, most of the local rivers are short and abundant (Cantera, 1993; Díaz, 1998). Within the littoral and neritic ecosystems of the Gulf of Tribugá, there is great variability of habitats, including mangrove forests, muddy flats, sand bottoms, rocky substrates, cliffs and coral reefs (Cantera & Contreras, 1993; Díaz, 1998; Jaramillo & Bayona, 2000).

Field Methods

Between 2013 and 2016, boat trips typically occurred daily or every other day throughout the southeastern Pacific humpback whale breeding season (June-October). Additionally, 15 surveys made as part of inventory completed in 2010 were considered (Botero-Acosta et al., unpublished data). Within that study, 10km transects, with different orientation to the coastline, were completed in different time periods, including July/August. Both, coastal and oceanic waters were considered. In contrast, 2013-2016 boat trips were conducted exclusively within coastal waters and consisted of free-search along north and south routes.

A small (6-7m long) fiberglass boat, with capacity for approximately four researchers, was used to follow the whales. Members of the research team had different roles on board, including tissue collection, photo-identification, and field notebook/ethogram. A hand-held GPS (Garmin 62S) recorded the entire track followed by the research vessel. GPS waypoints were also taken to geo-reference the start and end of each encounter.

After detection, group size and composition were assessed. In the context of this investigation, a group was defined as all whales within a radius of 100m that moved in the same direction and displayed a similar breathing pattern (Félix & Botero-Acosta, 2011). In order to determine age class, a relative size criterion was used, differentiating between: 1. Adults (≥ 10m in length); 2. Juveniles (6-10m in length); and 3. Calves (< 6m and in close association with an adult, Félix & Botero-Acosta, 2011). Following age class determination, groups were classified as mother-calf pairs (Mc), mother, calf and escort (McE), and mother, calf and multiple escorts (McME). Escorts were defined as the individuals of unknown sex that associate with a mother-calf pair.

Behavioral frequencies were assessed using a combination of instantaneous and frequency sampling (Altmann, 1974). Events (brief behavioral patterns) and states (behavioral patterns of relatively long duration) were considered. While behavioral events were recorded continuously, behavioral states were assessed every minute. Whenever the identity of the individual executing an event was identified, an additional notation was made on the ethogram data sheet. The operational definitions of behavioral states and events can be found on Tables 1 and 2, respectively. Diving times, travel path, and weather/oceanographic conditions were also recorded on standardized data sheets.

Table 1

Operational definitions for humpback whale behavioral states.

Behavioral State	**Definition**
Surface Active	A whale executes aerial displays that involve the use of its extremities or its entire body and often produce percussion sounds.
Social	A whale interacts with other whale(s) as part of parental care, affiliative, reproductive and/or competitive behavior.
Travel	A whale displaces horizontally over the water surface, sometimes adopting specific body postures.
Social Sounds	A whale produces sounds while at the surface. Sounds are detectable without the use of any acoustic equipment.
Respiration	A whale breathes or emits air through its mouth or blowhole.
Rest	A whale stays immobile at the surface. Any displacement is limited to movements up and down the water column to breathe.
Diving/Not Found	A whale is not visible at the surface.

Note. Definitions adapted from (Darling, 2001; Frankel et al., 1995).

Table 2

Operational definitions for humpback whale behavioral events.

Behavioral State	**Behavioral Event**	**Definition**
Surface Activity	Breaching	A whale leaps from the water, spinning in the air before re-entry.
	Belly Flop	A whale leaps partially out of the water and lands on its belly.
	Fluke Slap	A whale slaps its fluke on the water surface. It can occur in a horizontal position, slapping the ventral surface; or belly-up, slapping the dorsal surface.
	Flippering	A whale raises a flipper into the air and slaps it down on the surface of the water.
	Tail Slash	A whale lashes its fluke and/or peduncle. It can occur with flukes on a horizontal or vertical plane.
	Spy Hop	A whale raises its head vertically out of the water while stationary with flippers outstretched, and without open mouth or extending throat pleats.
Social	S Posture	A whale travels with its back arched and head above the surface.
	Chasing	Rapid and persistent pursuit of another whale.
	Head Lunge	Whale lunges forward with most of its head coming out of the water.
	Tactile	A whale briefly contacts (touches) another whale.
	Block	One whale blocks the path of another with its body.
	Strike/Collision	One whale intentionally hits another with its flukes or any other body appendage.
	Head Slap	A whale leaps partially out of the water and strikes the ventral side of its head forcefully on the surface.
Travel	Fluke In	A whale surfaces and then dives down under the water without raising its fluke out of the surface of the water.

Table 2 (continued).

	Fluke Out	A whale surfaces and then dives down raising its fluke up in the air and out of the water.
	Side Swim	A whale is at the surface with one fluke lobe and one pectoral fin visible above or close to the surface.
	Belly up	A whale turns ventral side to surface, often with pectoral fins extended and exposing the ventral side of its flukes.
	Roll	A whale transitions from a belly-up to a horizontal position, at times slapping flippers on surface.
Sounds	Trumpeting	A whale vocalizes on the surface with a prolonged low trumpet-like or foghorn-like sound emitted from the blowhole.
	Snoring	A whale vocalizes on the surface with a snoring-like sound.
	Chuffing	A whale emits loud exhalations creating a puffing sound.
Respiration	Breath	A whale surfaces and takes a breath, observable with a spout of water vapor coming out of the blowhole.
	Bubble trail	A whale releases a controlled stream of bubbles from its blowhole, leaving a long line of bubbles behind it.
	Bubble burst	A whale releases a blast of air from its blowhole below the surface of the water, usually just prior to surfacing.

Photographs were taken with DSLR Cameras (Canon EOS Rebel and Nikon D5000/ D7100) equipped with 70-300mm zoom lenses. Identification of individual whales was based on the coloration patterns, scars, and trailing edge of the ventral side of the flukes (Katona & Whitehead, 1981) as well as the shape, scars, rake marks, and barnacles visible on the dorsal fins (Félix & Botero-Acosta, 2011).

Data Analysis

Behavioral Data

Behavioral states and events were summarized as Excel® contingency tables. After each boat trip, tables were updated. Pearson chi-squared tests were completed to examine the presumed variation of behavioral frequencies between group types. In order to increase statistical power, additional chi-squared tests were completed collapsing McE and McME groups. Results were only reported when they differed from those comparing all group types. Calculating, and interpreting, Cramer's V coefficient achieved a measure of effect size. Standardized coefficients complemented statistically significant results. Whenever the assumption of expected values ≥5 was violated, Pearson chi squared test was substituted by Fisher's Exact test, much more tolerant to small sample sizes. All statistical procedures were completed on SPSS v21 with a minimum significance level of $\alpha = 0.05$.

Spatial Distribution Data

After every boat trip, waypoints and tracks were downloaded from the GPS unit using BaseCamp v4.6 (Garmin®). Coordinates were transformed from a degree, minute, and second format to decimal coordinates by applying the following formula: $D + m/60 + s/3600$. An Excel® database, later converted to the text separated by comma format (.csv), was created to store the initial coordinate for each sighting, differentiating between group types. Information on Colombia's administrative areas was downloaded as an ESRI personal geo-database accessible from the GADM database of global administrative areas (GADM v2.8). A global topography layer (1kmx1km) was downloaded from the ERDDAP database, maintained by NOAA, to extract water depth measurements for the geo-referenced positions of groups with calves (Becker et al., 2009). This layer was first downloaded as a text file with an esriAscii extension. The text file was then converted to a raster data set using the conversion tools (Ascii to Raster) available on the ArcToolBox Set on ArcMap. After importing, all layers adopted the Bogota_UTM_Zone_18N projection.

Survey effort was described creating a polygon grid data layer on ArcMap. First, an excel database containing a series of points automatically taken by the GPS outside of humpback whale sightings was converted to a CSV format and then added to the data frame. A date field as well as unique track and point identifiers were used to facilitate conversion of the point series into a track line on ArcMap v10.3.1. Then, the shapefile containing the outline of Colombia's administrative area was included. The polygon grid layer was created following a series of transformations between raster, point, and polygon file formats. Then, the parts of the polygon that fell on land were removed using a combination of the union tool and the select by location feature. By employing the Intersect tool, the length of survey tracks falling on each polygon grid cell was calculated. Finally, the symbology settings were edited to display survey effort on a graduated scale (Macleod, 2013).

Bathymetry data was extracted for each point using the Extraction tool (Extract values to points) available on the ArcToolBox Set. Some groups, sighted on extremely shallow waters, provided erroneous results as ArcMap interpreted them as falling on land. A nautical chart published by the General Marine Direction (DIMAR) was used as an auxiliary tool to estimate depth for such records. The distance of whale groups to the coastline was calculated using the Near tool available on the Analyst toolbox. In order to evaluate potential differences in the habitat use patterns between group types, water depth and distance to the coastline were examined with a multivariate analysis of variance (MANOVA). As an exploratory measure to increase statistical power, a separate MANOVA was conducted collapsing McE and McME groups. All statistical procedures were completed on SPSS v21 with a significance level of $\alpha = 0.05$.

Speed data was calculated using Basecamp v4.6. The software provided information on the distance covered while following the group, which was then divided by the duration of the encounter. Sighting tracks were visually classified as either traveling or milling. Straight track lines that went on a N→S or S→N direction were indicative of traveling behavior; while milling tracks were characteristically convoluted, with numerous turns and changes of directionality. Speed data was processed with a factorial analysis of variance, where group type, date and track type were used as independent variables. In order to increase statistical power, McE and McME groups were collapsed. Similarly, given concerns over reduced sample size, June and July observations were joined. All statistical procedures were completed on SPSS v21 with a significance level of $\alpha = 0.05$.

Photo-Identification Data

Photographs were processed after each boat trip, creating separate folders for each encounter. First, water and blurry/unfocused shots were deleted. Then, dorsal fins and flukes were extracted, and processed, using Photoshop CS6®. For both types of images, lighting and contrast were edited using the "Levels" tool.

The best photos depicting each individual dorsal fin (both left and right side were used when available) were cropped and then copied into a new file to confirm group size estimates made during sightings. This composite image was named according to the following sequence: D_boat trip number + sighting ID_year (e.g. D_7A_2016). Considering the "limited" shape variability, and the instability of rake marks and other temporary markers (e.g. barnacles), dorsal fins were not considered for inter-seasonal photo-identification comparisons. However, since cows do not usually execute fluke out behaviors before deep dives (Cerchio, 2003; Garrigue, Greaves, & Chambelant, 2001; Rice, Carlson, Chu, Dolphin, & Whitehead, 1987), dorsal fins were used for intra-seasonal photo-identification comparisons of groups with calves. Finally, when an entire fluke-out sequence was photographed, dorsal fins were also included in the fluke's photo-identification record.

Flukes were initially assigned a temporary code as follows: C(order of appearance)_boat trip number + sighting ID_year (e.g. C1_7B_2016). In order to detect intra-seasonal matches, all flukes photographed during a specific sampling period were compared against each other. When a match was detected, the best quality photo was selected for future comparisons. After intra-annual reviews were completed, flukes were compared with photos taken on previous years. After each comparison round, flukes were given a code (BGT_XXXX) before being added to the photo-identification catalog. The catalog's metadata included a special notation for flukes baring signs of predation by killer whales. Considering that the coloration patterns of calves' flukes often change as they mature (Cerchio, 2003), these photographs were assigned a code, and added to the catalog, but treated separately.

The author (NB) processed photographs from the 2010-2015 period. Two members of the Marine Mammal Behavior and Cognition Laboratory, Riley McGregor and Alexandra Walker, assisted with 2016 comparisons. Training consisted on matching 20% of pre-2016 material, requiring a minimum 80% agreement. Both assistants achieved 100% reliability. After this, all remaining photographs were divided equally.

CHAPTER IV – RESULTS

Survey Effort

Survey effort was quite variable during the study period, mostly due to logistical and financial constraints. A total of 212 boat trips were completed, spending 1,120.9 hours at sea and traveling for a total of 12,769.8 Kilometers. Details on the survey effort for each year can be found on Table 3.

Table 3

Survey effort in the Gulf of Tribugá 2010-2016.

	2010					
Item	June	July	August	September	October	Total
Boat Trips	--	4	11	--	--	15
Distance (km)	--	461.1	1061.6	--	--	1,522.7
Time (h)	--	29.9	70.4	--	--	100.3
Groups	--	7	33	--	--	40

	2013					
Item	June	July	August	September	October	Total
Boat Trips	7	13	14	12	--	46
Distance (km)	633	915	789.3	639.3	--	2,976.6
Time (h)	53.5	100.6	82.8	48.5	--	285.4
Groups	9	53	45	28	--	135

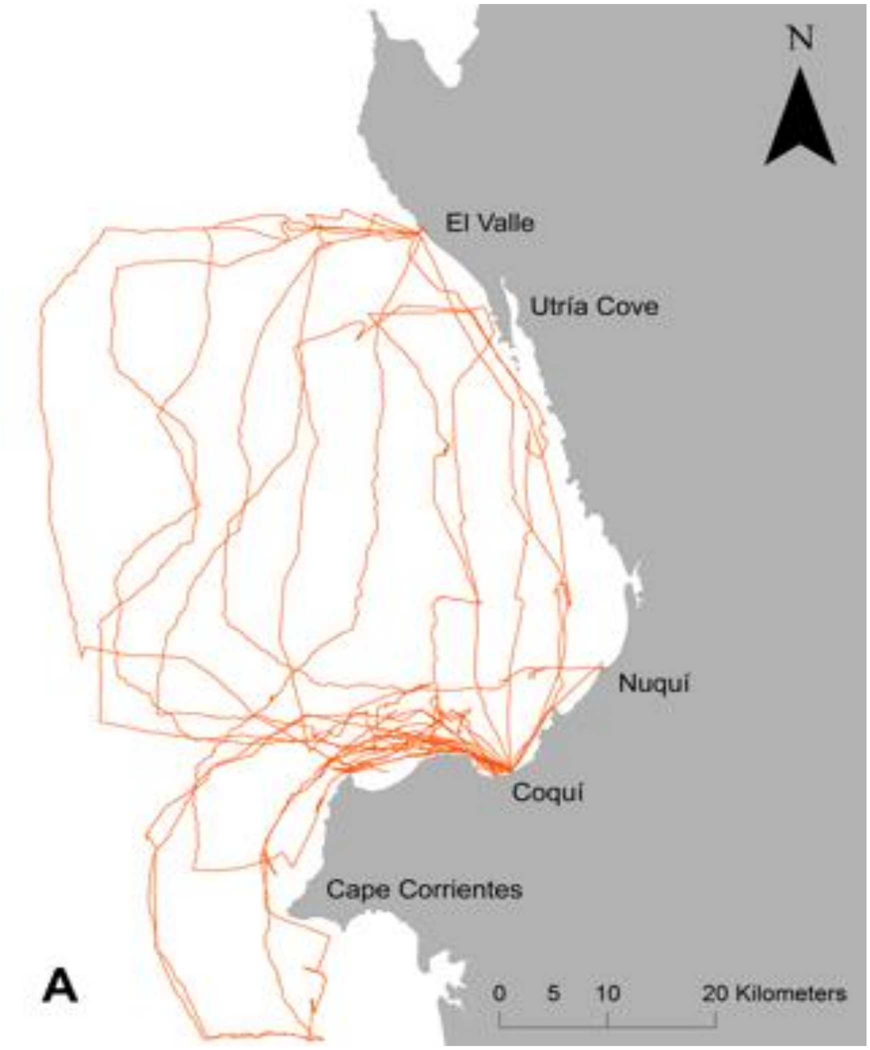
	2014					
Item	June	July	August	September	October	Total
Boat Trips	--	6	25	14	5	50
Distance (km)	--	194	792.1	561.6	270.2	1,817.9
Time (h)	--	23.3	81.8	52.1	21.2	178.4
Groups	--	14	45	23	8	90

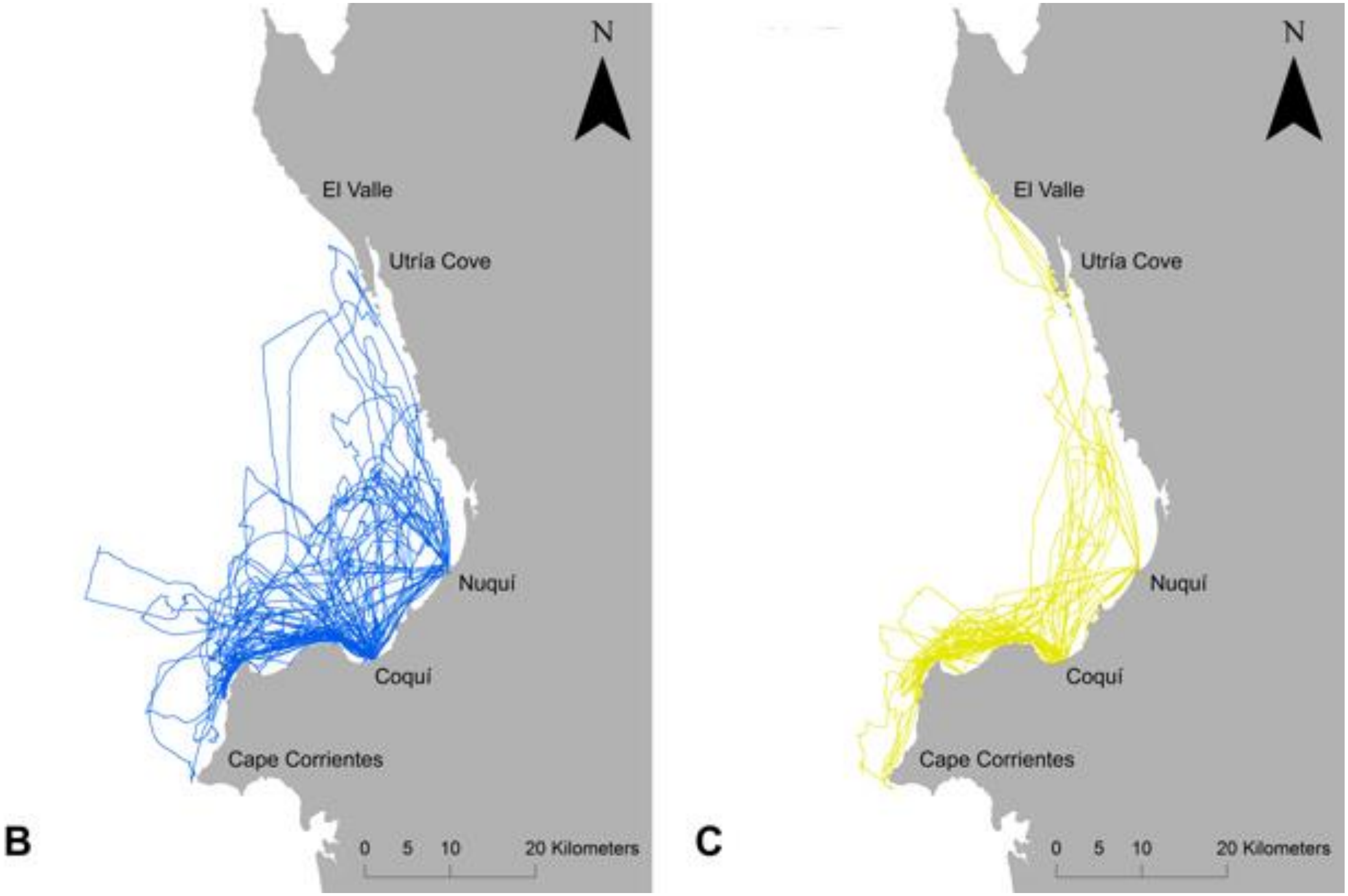
	2015					
Item	June	July	August	September	October	Total
Boat Trips	--	--	4	20	7	31
Distance (km)	--	--	--	1,208.9	327.5	1,536.4
Time (h)	--	--	--	100.9	32.2	133.1
Groups	--	--	11	39	14	64

Table 3 (Continued)

	2016					
Item	June	July	August	September	October	Total
Boat Trips	1	22	24	20	3	70
Distance (km)	82.5	1,567.7	1,589.6	1,475.1	201.3	4,916.2
Time (h)	7.05	143.3	137.3	120.1	16.03	423.78
Groups	2	63	71	49	8	191

With the exception of 2010, where some transects covered oceanic waters approximately 50km away from the coastline, most boat trips completed between 2013 and 2016 focused primarily on coastal waters in the Gulf of Tribugá (Figure 2).

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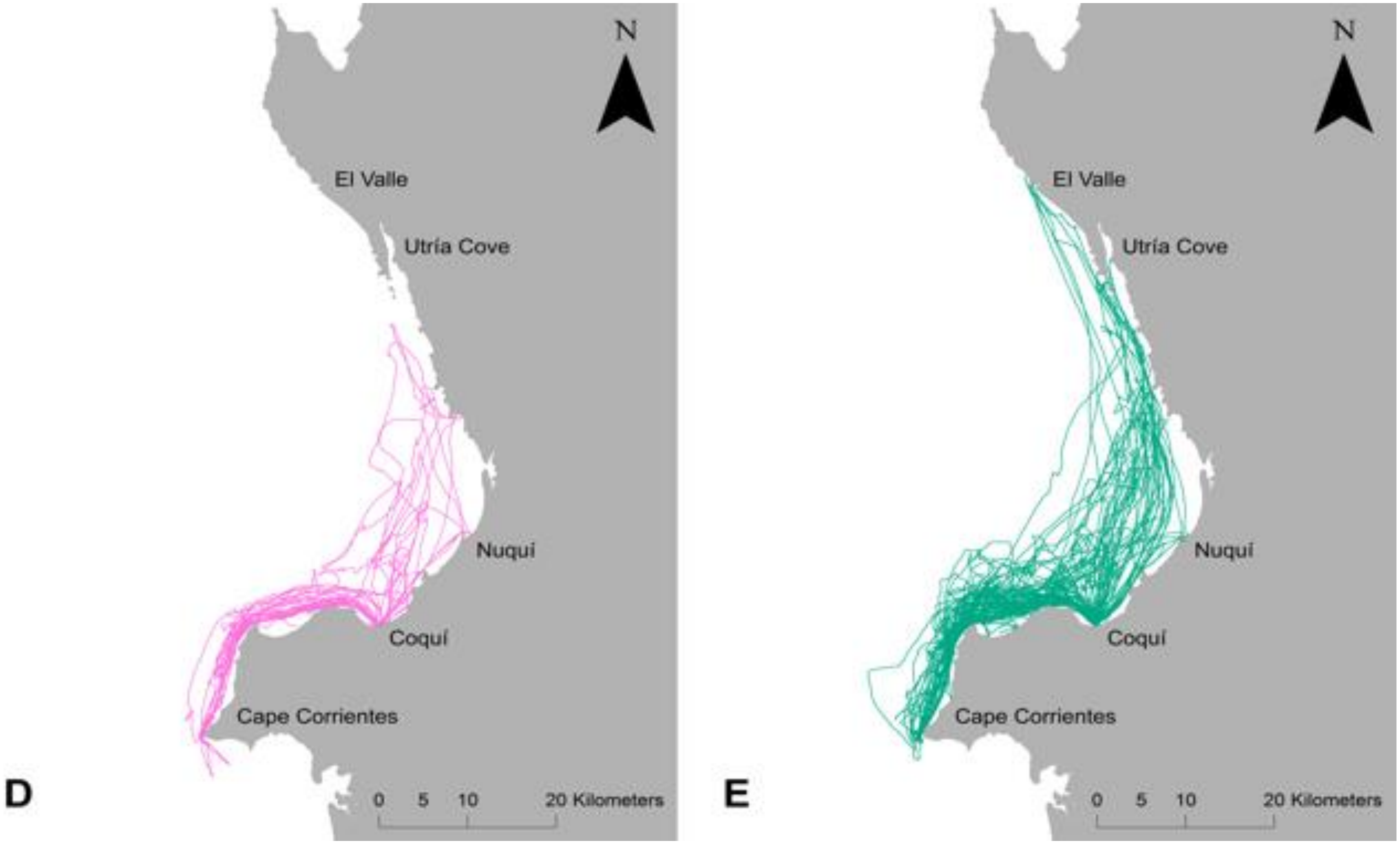


Figure 2. Boat Trip Surveys.

Note: A) 2010; B) 2013; C) 2014; D) 2015, E) 2016

Given the location of the main logistic base (Coquí), there was a degree of sampling bias in favor of the southern portion of the Gulf. In spite of this, nearly all coastal areas within the 300m isobaths were sampled. A graphic representation of survey effort can be found in Figure 3.

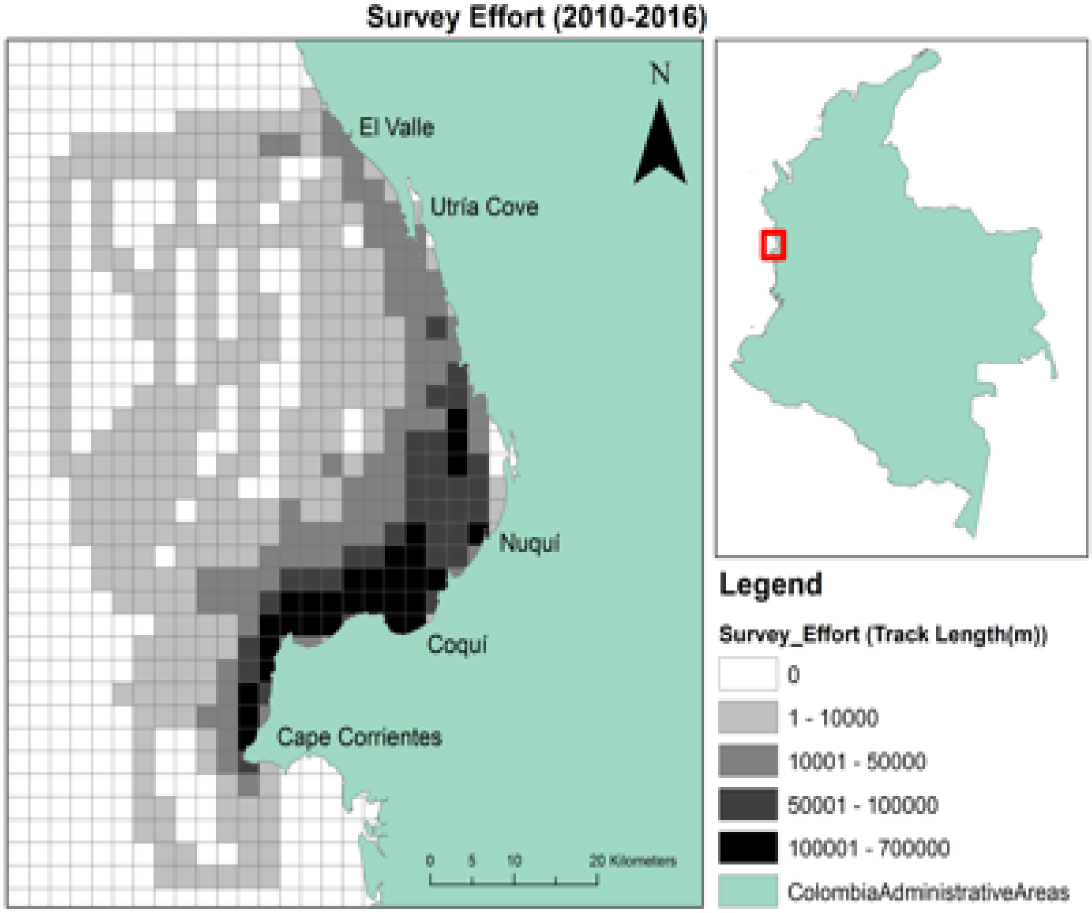


Figure 3. Survey Effort 2010-2016.

In 2010 and between 2013 and 2016, groups with calves (n= 108) represented 20.7% of all groups registered in the Gulf of Tribugá. The most common group type was the mother-calf pair (Mc, n= 66), followed by groups with a single escort (McE, n=28) and, then by groups that included multiple escorts (McME, n=14). The average group size for groups with multiple escorts was 4.8 (range: 4-7).

Behavioral Frequencies

Behavioral data was recorded for sightings made between 2013 and 2016. However, in those years, such information was unavailable for nine groups. Therefore, behavioral frequencies were assessed for a total of 91 groups. Observed frequencies of each behavioral state are available in Table 4.

Table 4

Observed Frequencies of Humpback Whale Behavioral States

Group Type	Diving	Rest	Respiration	Social	Social Sounds	Surface Active	Travel
Mc	849	82	0	1	0	20	415
	(0.62)	(0.06)	(0.00)	(<0.01)	(0.00)	(0.01)	(0.30)
McE	308	3	0	6	0	47	265
	(0.49)	(<0.01)	(0.00)	(0.01)	(0.00)	(0.07)	(0.42)
McME	137	4	0	37	0	42	172
	(0.35)	(0.01)	(0.00)	(0.09)	(0.00)	(0.11)	(0.44)

Note: Observed frequencies located on top while proportions are included in parenthesis.

The Pearson chi-squared test indicated that group type had a significant effect on the observed behavioral states ($\chi^2_8 = 337.41$, $p<0.001$). Cramer's V (0.266) indicated this corresponded to a medium size effect, highly significant ($p<0.001$).

Standardized residuals revealed significant differences between group types for most behavioral state categories. With the exception of diving and social/agonistic behaviors, where there were significant differences between Mc pairs and McME but not with McE groups, escorted and unescorted mother-calf pairs showed opposite patterns of behavior. While Mc pairs spent significantly more time resting than expected, the reverse pattern was found for McE and McME groups. Furthermore, while escorted groups spent significantly more time than expected traveling and executing surface-active behaviors the opposite was true for Mc pairs (Table 5).

Table 5

Standardized Residuals for the Behavioral States Comparison

Group Type	Diving	Rest	Social	Surface-Active	Travel
Mc	**4.0**	**4.4**	**-4.8**	**-5.4**	**-3.3**
McE	-1.8	**-4.2**	-1.6	**3.4**	**2.7**
McME	**-5.2**	**-2.8**	**11.1**	**5.7**	**2.7**

Note: Values ± 1.96 are significant at $p < 0.05$, Values ± 2.58 are significant at $p < 0.01$, and Values ± 3.29 are significant at $p < 0.001$. Statistically significant values are bolded.

Regarding surface-active behaviors, the follow-up chi-squared test determined that group type had a significant effect on the observed behavioral frequencies (χ^2_{10}= 60.40, p<0.001). Cramer's V (0.224) indicated this corresponded to a medium size effect, highly significant (p<0.001). Observed frequencies for surface-active events are available in Table 6.

Table 6

Observed Frequencies of Humpback Whale Surface Active Events

Group Type	Breach	Belly Flop	Fluke Slap	Flippering	Tail Slash	Spy Hop
Mc	45 (0.46)	21 (0.22)	9 (0.09)	11 (0.11)	1 (0.01)	10 (0.10)
McE	50 (0.21)	66 (0.28)	13 (0.06)	62 (0.26)	34 (0.14)	10 (0.04)
McME	61 (0.23)	87 (0.32)	35 (0.13)	49 (0.18)	16 (0.06)	21 (0.08)

Note: Observed frequencies located on top while proportions are included in parenthesis.

The standardized residuals revealed significant differences between Mc pairs and McE groups. Conversely, the behavioral frequencies for McME groups were in close agreement with the expected values. While Mc pairs executed significantly more breaches than expected, McE groups executed significantly less fluke slaps. Pectoral fin slaps and tail slashes showed opposite patters for Mc pairs and McE groups: While the observed frequencies for Mc pairs were significantly lower in comparison with expected values, the opposite was true for McE groups. Belly flop was the only event in which none of the group types deviated from the expected frequencies (Table 7). When McE and McME groups were collapsed no significant differences were found in the frequencies of surface-active behaviors.

Table 7

Standardized Residuals for the Surface-Active Events Comparison

Group Type	Belly Flop	Breach	Fluke Slap	Flippering	Tail Slash	Spy Hop
Mc	-1.3	**4.0**	-0.1	**-2.0**	**-2.5**	1.3
McE	-0.2	-1.4	**-2.0**	**2.1**	**3.1**	-1.5
McME	1.0	-1.1	1.9	-0.8	-1.4	0.6

Note: Values ± 1.96 are significant at $p < 0.05$, Values ± 2.58 are significant at $p < 0.01$, and Values ± 3.29 are significant at $p < 0.001$. Statistically significant values are bolded.

An additional chi-squared test determined that group type had a significant effect on the observed frequencies of travel behaviors ($\chi^2_6 = 51.7$, $p<0.001$). Cramer's V (0.191) indicated this corresponded to a small size effect, yet highly significant ($p<0.001$). Observed frequencies for travel events are available in Table 8.

Table 8

Observed Frequencies of Humpback Whale Travel Events

Group Type	Side Swim	Ventral Swim	Rolling	Fluke In	Fluke Out
Mc	16 (0.07)	0 (0.00)	3 (0.01)	190 (0.79)	32 (0.13)
McE	33 (0.14)	8 (0.04)	0 (0.00)	121 (0.53)	66 (0.29)
McME	30 (0.12)	16 (0.07)	0 (0.00)	136 (0.56)	59 (0.24)

Note: Observed frequencies located on top while proportions are included in parenthesis.

The standardized residuals revealed that the observed frequencies of Mc pairs concentrated most statistical differences. Mc pairs executed significantly less fluke out dives, and side/ventral swims. Conversely, they executed significantly more fluke in dives. While McE groups completed significantly more fluke out dives, McME groups displayed a similar trend regarding ventral swims (Table 9). When McE and McME groups were collapsed, only side swim frequencies were not significantly different from the expected values. Escorted groups combined the tendencies exhibited by each group separately regarding fluke out and ventral swim. Additionally, they showed a combined effect for fluke in dives, which was executed less often than what was expected.

Table 9

Standardized Residuals for the Travel Events Comparison

Group Type	Fluke In	Fluke Out	Side Swim	Ventral Swim
Mc	**3.2**	**-2.9**	**-2.1**	**-2.8**
McE	-1.9	**2.2**	1.5	0.1
McME	-1.3	0.7	0.6	**2.7**

Note: Values ± 1.96 are significant at $p < 0.05$, Values ± 2.58 are significant at $p < 0.01$, and Values ± 3.29 are significant at $p < 0.001$. Statistically significant values are bolded.

Considering some of the expected frequencies were ≤ 5, social events were examined with a Fisher's Exact Test. Results indicated that group type had a significant effect on the observed frequencies (FET= 71.8, $p<0.01$). Cramer's V (0.451) indicated this corresponded to a large size effect, highly significant ($p<0.001$). Observed frequencies for travel events are available in Table 10.

Table 10

Observed Proportions of Humpback Whale Social Events

Group Type	Block	Chase	Head Lunge	Rub/ Tactile	S Posture	Strike
Mc	0 (0.00)	0 (0.00)	5 (0.10)	46 (0.90)	0 (0.00)	0 (0.00)
McE	0 (0.00)	8 (0.33)	2 (0.08)	10 (0.42)	4 (0.17)	0 (0.00)
McME	8 (0.08)	31 (0.31)	24 (0.24)	26 (0.26)	5 (0.05)	7 (0.07)

Note: Observed frequencies located on top while proportions are included in parenthesis.

The standardized residuals revealed Mc pairs engaged in significantly higher frequencies of rub/tactile behavior. The opposite was observed for McME groups. Mc pairs were never observed chasing each other, and consequently the observed frequencies were significantly lower than expected just by chance. Finally, McE groups executed significantly more S postures than expected (Table 11). When McE and McME groups were collapsed, the frequencies of rub/tactile behaviors were still significantly lower than expected. Additionally, escorted groups exhibited chasing behaviors more often than what was expected just by chance.

Table 11

Standardized Residuals for the Social Events Comparison

Group Type	Block	Chase	Head Lunge	Rub/Tactile	S Posture	Strike
Mc	-1.5	**-3.4**	-1.3	**4.6**	-1.6	-1.4
McE	-1.0	1.2	-1.1	-0.4	**2.5**	-1.0
McME	1.6	1.8	1.5	**-3.1**	-0.1	1.5

Note: Values ± 1.96 are significant at $p < 0.05$, Values ± 2.58 are significant at $p < 0.01$, and Values ± 3.29 are significant at $p < 0.001$. Statistically significant values are bolded.

Respiration events violated the expected frequencies assumption, so they were also examined with a Fisher's Exact Test. This analysis showed that group type had a significant effect on the observed behavioral frequencies (FET= 105.4, p<0.001). Cramer's V (0.113) indicated this corresponded to a small size effect, yet highly significant (p<0.001). Observed frequencies are available in Table 12.

Table 12

Observed Frequencies of Humpback Whale Respiration Events

Group Type	Breath	Bubble Burst	Bubble Trail
Mc	2020 (0.99)	5 (<0.01)	0 (0.00)
McE	1281 (0.99)	5 (<0.01)	1 (<0.01)
McME	1317 (0.95)	56 (0.04)	10 (<0.01)

Note: Observed frequencies located on top while proportions are included in parenthesis.

Differences concentrated on bubble behaviors, as breath frequencies for all groups were consistent with the expected values. Mc pairs and McE groups showed the same pattern with bubble burst and bubble trail frequencies that were lower than what was expected by chance. Conversely, observed frequencies for both event types were significantly higher than expected for McME groups (Table 13). While the statistical significance of bubble burst frequencies remained when McE and McME groups were collapsed, this was not the case for bubble trail events.

Table 13

Standardized Residuals for the Respiration Events Comparison

Group Type	Breath	Bubble Burst	Bubble Trail
Mc	0.6	**-4.4**	**-2.2**
McE	0.4	**-3.1**	-1.2
McME	-1.2	**8.3**	**3.8**

Note: Values ± 1.96 are significant at $p < 0.05$, Values ± 2.58 are significant at $p < 0.01$, and Values ± 3.29 are significant at $p < 0.001$. Statistically significant values are bolded.

Social sounds, examined with a Fisher's Exact Test, did not yield significant results (FET= 5.9, p=0.176). Observed frequencies are available in Table 14.

Table 14

Observed Frequencies of Humpback Whale Social Sound Events

Group Type	Trumpeting	Puff	Snoring
Mc	2	1	0
	(0.67)	(0.33)	(0.00)
McE	1	5	8
	(0.07)	(0.36)	(0.57)
McME	2	5	9
	(0.13)	(0.31)	(0.56)

Note: Observed frequencies located on top while proportions are included in parenthesis.

When McE and McME groups were collapsed there was a significant effect of group type over the frequency of social sounds (FET=5.8, $p<0.05$). Specifically, the frequency of trumpeting sounds for Mc pairs was significantly lower when compared with expected values (Table 15).

Table 15

Standardized Residuals for the Social Sounds Comparison

Group Type	Trumpeting	Puff	Snoring
Mc	2.3	**0.0**	**-1.2**
McE+	-0.7	**0.0**	0.4

Note: Values ± 1.96 are significant at $p < 0.05$, Values ± 2.58 are significant at $p < 0.01$, and Values ± 3.29 are significant at $p < 0.001$. Statistically significant values are bolded.

Spatial Distribution

Overall, all groups that included a calf were recorded fairly close to the coastline. While several sightings were made well beyond the 300m isobaths, on average, sightings concentrated along water depths of 200m or less. Figure 4 depicts the location of all sightings. A summary of the information on depth and distance to the coastline, extracted for each sighting, can be consulted on Table 16.

Table 16

Depth and distance to the coast for groups with calves

Variable	Mc	McE	McME
Depth (m)	Range: 2-510 $\bar{x}$ = 163.33 SD= 157.3 n= 66	Range: 7-429 $\bar{x}$ = 168.64 SD= 153.2 n= 28	Range: 9-544 $\bar{x}$ = 163.93 SD= 146.8 n= 14
Distance to coast (km)	Range: 0.24-7.89 $\bar{x}$ = 1.74 SD= 1.6 n= 66	Range: 0.20-6.18 $\bar{x}$ = 2.15 SD= 1.6 n= 28	Range: 0.63-9.22 $\bar{x}$ = 2.02 SD= 2.2 n= 14

As part of the multivariate analysis of variance (MANOVA), the null hypothesis of variance-covariance equality and the assumption of homogeneity of variance for both dependent variables were examined, through Box's and Levene's Tests respectively. Since both statistics were not significant ($p>0.05$), it was concluded that both assumptions had been met (Field, 2009). No significant differences in depth and distance to the coastline between group types were detected $F(4, 208) = 0.564$, $p>0.05$.

A total of 28 groups were excluded from the speed analysis because of GPS malfunction, incomplete track information, or because the observation time was <15 minutes, increasing the potential for misclassification. In this way, a total of 77 tracks were processed: 22 classified as milling and 55 as traveling. Three additional tracks were placed in the "Other" category. Details of the track classification can be consulted in Table 17 and figure 5.

Table 17

Transect classification

Variable		N
Group Type	Mc	45
	McE	23
	McME	9
Date	June	2
	July	9
	August	27
	September	26
	October	13
Track Type	Traveling	55
	Milling	22

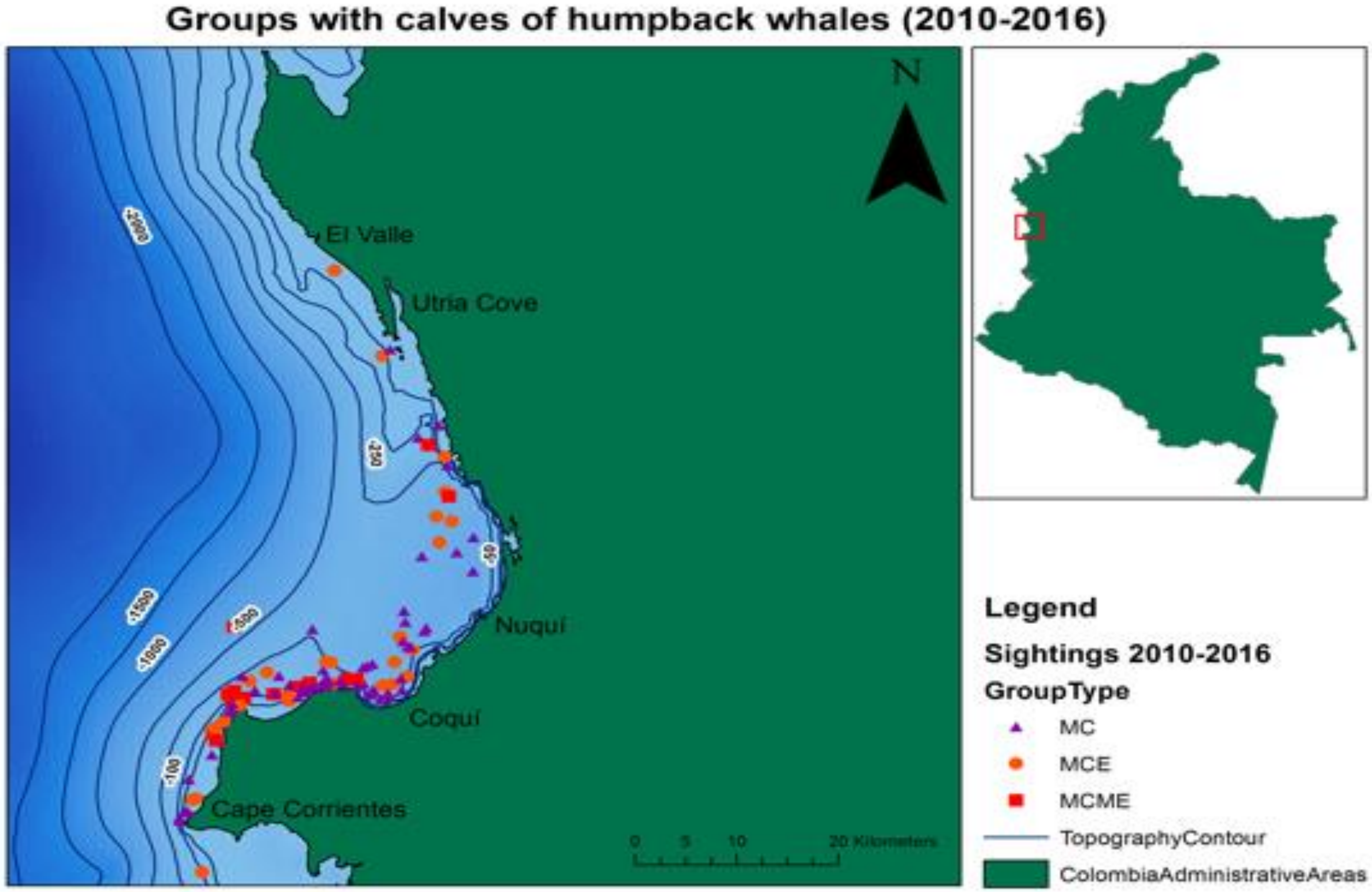


Figure 4. Groups with calves of humpback whales in the Gulf of Tribugá (2010-2016).

Speed data showed little variation among group types. While the average traveling speed increased with the affiliation of a single escort, McME groups displayed a slower traveling speed than Mc pairs and McE groups (Table 18).

Table 18

Speed data for groups with calves

Variable	Mc	McE	McME
Speed (km/h)	Range: 0,76-22.40 $\bar{x}$ = 6.28 SD= 3.48 Median: 6.18	Range: 3.98-20.80 $\bar{x}$ = 6.79 SD= 3.13 Median: 6.38	Range: 2.46-11.50 $\bar{x}$ = 6.04 SD= 2.45 Median: 6.46

A factorial analysis of variance also included a Levene's Tests. In this case the F statistics was significant ($p<0.001$), so it was concluded that the assumption of homogeneity of variance was violated (Field, 2009). The omnibus test indicated that there were no significant differences in speed across date and group/transect types $F(3, 61) = 0.860$, $p>0.05$.

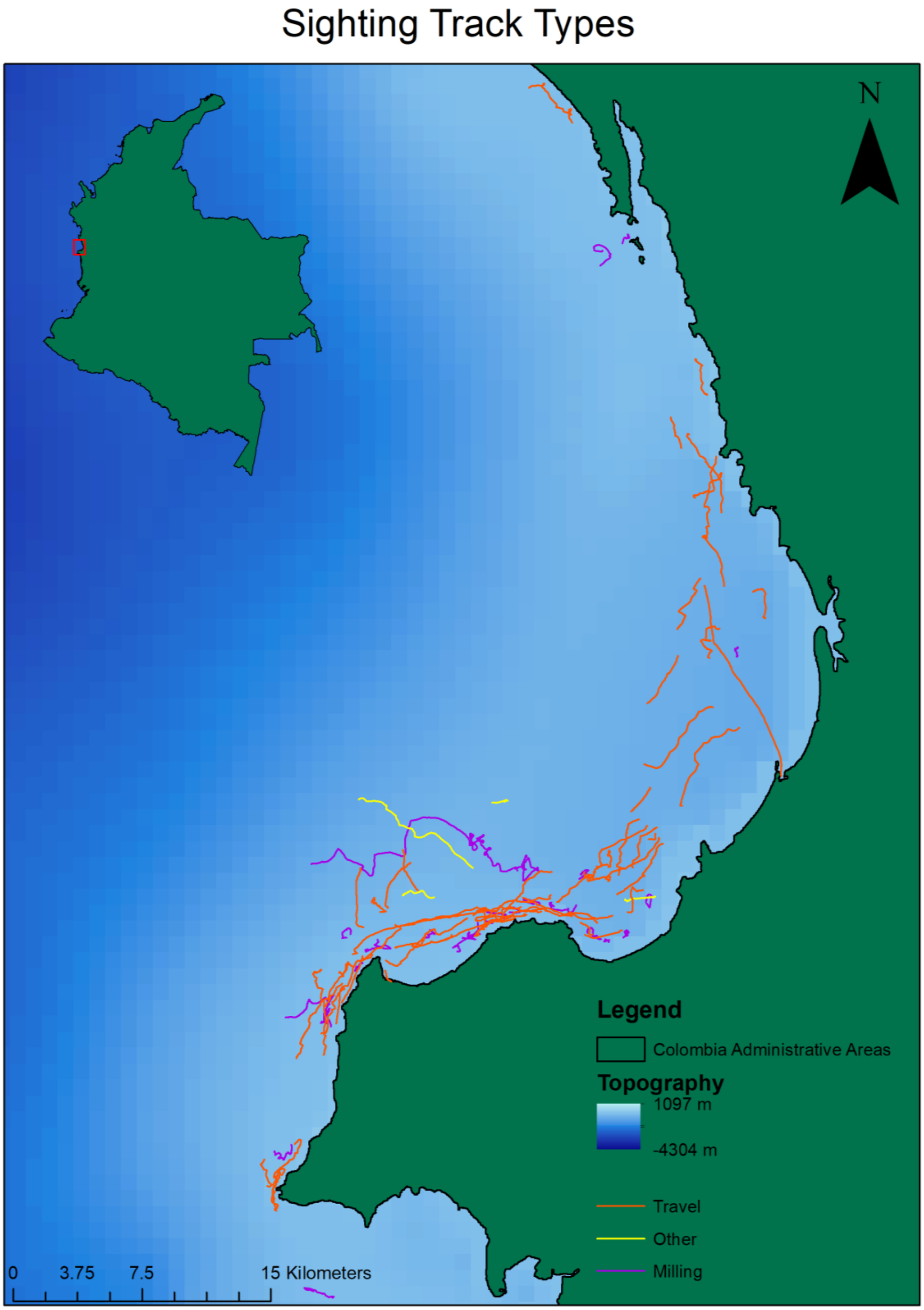


Figure 5. Sighting track types.

Photo-Identification

Between 2010 and 2016, a total of 543 whales were identified in the Gulf of Tribugá, based on the coloration patterns, scars, and trailing edge of the ventral side of their flukes. Of these, 60 were photographed within groups that included a calf. Of these flukes, some were traced back to the mother (n=14), the calf (n=16), or the escort(s, n=24). Dorsal fin composite pictures were available for 92.6% of groups with calves. A total of 15 resightings were made involving individuals identified as members of a group that included a calf (Figures 6 and 7). Of those, 11 were made within the same season (6 dorsal fin matches and 5 fluke matches), while the remaining involved sightings made on separate years (based exclusively on fluke comparisons, Table 19).

Table 19

Resightings of humpback whales in groups with calves

Match Type	First Sighting	Role	Second Sighting	Role
Flukes	17/07/2013	Escort	03/09/2016	Escort
Dorsal fins	19/08/2013	McE	19/08/2013	McME
Dorsal fins	26/08/2013	Mc	26/08/2013	Mc
Flukes	22/07/2014	Adult dyad	29/09/2016	Mother
Dorsal fins	27/08/2015	McE	01/10/2015	Mc
Flukes	27/08/2015	Adult trio	03/10/2016	Mother
Dorsal fins	01/10/2015	Mc	01/10/2015	McE
Flukes	01/10/2015	Competitive group	01/10/2015	Escort
Flukes	01/10/2015	Escort	27/08/2016	Escort
Flukes	21/07/2016	Competitive group	03/09/2016	Escort
Flukes	23/07/2016	Competitive group	11/09/2016	Escort
Flukes	08/08/2016	Escort	08/08/2016	Competitive group
Dorsal fins	24/08/2016	Mc	24/08/2016	McE
Flukes	07/09/2016	Competitive group	11/09/2016	Escort
Dorsal fins	10/09/2016	Mc	11/09/2016	McME

The majority of dorsal fin resightings involved photos taken on the same day, as some whales were encountered more than once. Sighting intervals for the two remaining cases spanned over 2 and 35 days, respectively. Dorsal fin matches informed about changes on group structure. One cow remained unescorted between sightings, which were made with a 6-hour difference. An additional Mc pair went from unescorted to escorted between sightings that spanned over one and a half hours. One Mc pair was seen accompanied by two escorts and unescorted the next day. Furthermore, an escorted cow gained an additional escort, two hours after the first sighting.

One particular resighting record was quite informative on the stability of cow-escort associations. The first sighting, made on August 27th of 2015, consisted of a MCE group. Then, on October 1st at 10:04 a.m. the mother and her calf were seen again, this time unescorted. This pair was seen once again later that day (1:41 p.m.), this time escorted by an individual identified as a member of a competitive group earlier that day. In turn, the escort was also resighted in 2016, when, once again, it was identified as the escort of a Mc pair. The 2016 sighting was noteworthy because the escort disaffiliation was detected after 27 minutes of observation, when the escort made a sudden turn and completed two fluke out dives, traveling on the opposite direction at a fast pace.

Fluke matches were biased in favor of escorts. Two whales identified as mothers in 2016, were seen in previous years (2014 and 2015) as members of an adult pair and trio respectively. Four individuals identified as escorts of a Mc pair were first seen as members of competitive groups. The opposite was true for an additional individual. Finally, two whales were identified as escorts on two separate years (2013/2016 and 2015/2016).

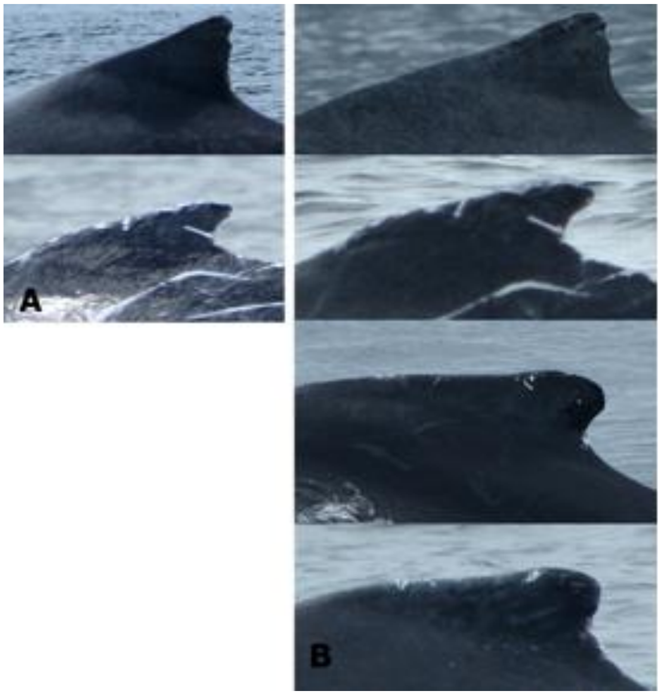


Figure 6. Photo-identification match based on dorsal fin photographs.

Note: A) Initial sighting on September 10th, 2016, B) Second sighting on September 11th, 2016.

Figure 7. Photo-identification match based on fluke photographs.

Note: A) Initial sighting on October 1st, 2015, B) Second sighting on September 11th, 2016.

CHAPTER V – DISCUSSION

Behavioral Frequencies

Humpback whale behavior in lower latitudes is heavily influenced by the occurrence of breeding and nursing activities. While males attempt to maximize reproductive encounters, female efforts are directed toward balancing resource investment with respect to mating and/or calving (Clapham, 1996, 2000). In the current study, this assumption was applied to the Gulf of Tribugá, revealing that the presence of escorts did significantly change the behavior of maternal females.

Although resting and diving dominated the behavior of Mc pairs, the presence of a single escort was associated with an increase in time spent traveling and executing surface-active displays. Maternal females accompanied by multiple escorts exhibited such trends as well, while additionally showing a reduction in diving and an increase in social behaviors. Overall, these results indicate that escorts basically shift the behavioral patterns of Mc pairs, transitioning from low to high-energy displays.

These patterns coincide with studies conducted in other breeding areas around the world (Cartwright & Sullivan, 2009; Félix, 2004; Jones, 2010). Observations from Australia, Hawaii, and the West Indies have described mother-calf behavior as being characterized by prolonged periods of slow travel and resting (Darling, 2001). While most sources report that the affiliation of a single escort has a relatively mild effect on mother-calf behavior, the presence of multiple escorts has been shown to elicit a more have a more substantial behavioral response. This is likely caused by the principal escort's attempts to defend its position next to the mother by increasing speed, agonistic interactions, and surface-active behaviors (Darling, 2001). Similarly, Jones (2010) reported that escorted Mc pairs in Hawaii spent significantly more time traveling, and less time resting, when compared to unescorted pairs. Likewise, in Ecuador, Mc pairs showed greater surface activity when one or more escorts were present (Félix, 2004).

Humpback whales are known for executing a variety of surface-active behaviors, in contexts as diverse as social excitement, aggression, and courtship (Darling, 2001; Félix, 2004; Félix & Botero-Acosta, 2011; Flórez-González et al., 2007). The current study found that group structure had a significant effect on the occurrence of surface-activity. Differences between group types were evident in all categories except belly flops. While for Mc pairs breach frequencies were significantly higher than expected, McE groups executed significantly more pectoral fin slaps and tail slashed and less fluke slaps than expected. Interestingly, the observed frequencies exhibited by McME groups did not significantly deviate from the expected frequencies.

When accompanied exclusively by their mothers, calves concentrated most of the surface activity. Therefore, it is suggested that in the Gulf of Tribugá the execution of surface-active behaviors by calves is the result of muscular/behavioral development and play. The apparent predisposition of calves to engage in surface activity has also been reported in several breeding grounds (Ávila, 2006; Darling, 2001; Dunlop, Cato, & Noad, 2008; Félix, 2004; Flórez-González et al., 2007; Jones, 2010; Zoidis, Lomac-Macnair, Chomos-Betz, Day, & Mcfarland, 2014). For example, in Málaga Bay, Avila (2006) reported that calves showed higher rates of surface-active displays when compared to adults. This pattern was not limited to breach, but also referred to fluke slaps and belly flops. The author interpreted this as a normal step within the behavioral development of calves.

When the frequencies McE and McME groups were pooled, no significant differences were found. This suggests that surface-active behaviors contributed, to some extent, to the differential role fulfilled by a single vs. multiple escorts when associating with Mc pairs. Within McE groups, pectoral fin slaps and tail slashes were significantly more frequent. Interestingly, both displays have only a modest acoustic potential. In this case, surface activity could be diffusing some of the tension that builds up as a result of the escort's affiliation. If differences would have concentrated on behaviors with a greater acoustic potential (e.g. breach or fluke slap) the conclusion could have been that either the cow or the escort were trying to attract other whales dispersed in the area (Félix, 2004; Félix & Botero-Acosta, 2012; Frankel, Clark, Herman, & Gabriele, 1995). This pattern suggests that in the Gulf of Tribugá, single escorts would be trying to avoid competitors. Whether this means that maternal females were not receptive at the time of the association is unknown, since there was no mechanism available to estimate the occurrence of post-partum ovulations. Jones (2010) interpreted surface activity within McE groups as a mechanism intended to coerce maternal females. Alternatively, pectoral fin slaps and tail slashes could represented efforts made by the cow to reject the presence of the escort (Félix, 2004; Félix & Botero-Acosta, 2012).

Travel events evidenced additional differences in the behavioral patterns of escorted and unescorted mother-calf pairs. Mc pairs exhibited significantly higher frequencies for fluke-in dives but lower frequencies for fluke-out dives. Conversely, McE groups executed significantly more fluke out dives than expected. Considering the close bond that exists between a female and her calf, and the differences in the calf's diving capacity when compared to adults, it logically follows that females would not execute fluke out dives frequently, as this behavior is associated with deep, long dives. While mothers may not surface as often as calves, they do tend to remain close to them, lingering stationary only a few meters below the surface (Cartwright & Sullivan, 2009; Darling, 2001; Glockner-Ferrari & Ferrari, 1985). The observed increase in the frequency of fluke out dives in McE groups is probably caused by the presence of the escort.

For Mc pairs, opposite trends were seen regarding side and ventral swims. While side swims were executed with a significantly lower frequency, ventral swims were performed significantly more than expected. Similarly, McME groups engaged in higher frequencies of ventral swimming. While ventral swimming is often associated with female mating avoidance (Darling, 2001; Jones, 2010; Swartz, 1986), its frequent occurrence within Mc pairs is not consistent with such role and probably more related to calf behavior. According to underwater behaviors observed in Hawaii, calves often roll and swim belly up, probably as part of play and even anti-predatory behavior (Cartwright & Sullivan, 2009; Darling, 2001; Zoidis et al., 2014). Conversely, maternal females more likely perform most of the ventral swimming events within McME groups, probably to repel mating advances (Baker & Herman, 1984; Darling, 2001).

Social events are a key component of humpback whale interactions within the breeding grounds. In the Gulf of Tribugá, despite small sample size limitations for some categories, social interactions reflected maternal care and intra-sexual competition. Events within Mc pairs were limited to rub/tactile interactions between the cow and her calf. Due to reduced visibility, underwater observations are rare in the Gulf of Tribugá. Nonetheless, it was possible to witness several instances of tactile behavior during rest periods, often involving subtle lifts of the calf by the mother's rostrum. Similar observations have been made in Hawaii (Darling, 2001; Glockner-Ferrari & Ferrari, 1985) and Colombia (Ávila, 2006). A significantly high frequency of tactile behavior was also observed for McME groups. In this case, the behavior is probably not affiliative in nature, but instead has an agonistic connotation. McME groups often display aggressive behaviors, as secondary escorts challenge the position of the main escort next to the cow and her calf (Félix, 2004; Flórez-González et al., 2007; Jones, 2010). Many of these interactions (hits, tail slashes, rear body throws) involve physical contact between the animals (Baker & Herman, 1984; Darling, 2001; Tyack & Whitehead, 1982).

The observed frequencies of the S-posture, a behavior in which a humpback whale arches the caudal peduncle, lowers its fluke, raises its rostrum and spreads its pectoral fins, were significantly higher for McE groups. In all instances, calves executed the behavior, presumably directing it at the escort. According to Helweg and colleagues (1992) the behavior might be implicitly aggressive. Nonetheless, the authors considered that when executed by calves, s-postures probably indicated a stressful state or increased arousal (Helweg, Bauer, & Herman, 1992). Considering some of the behavioral impacts previously discussed, the association of escorts could result stressful for calves. It is important to note that the observed frequencies are probably an underestimation because of the reduced visibility in the Gulf of Tribugá.

Bubble events were indicative of noteworthy differences in the behavior of mother-calf pairs when escorted by a single vs. multiple individuals. Unescorted maternal females and McE groups showed a similar pattern regarding bubble production. For Mc pairs, the observed frequencies of bubble bursts and bubble trails were significantly lower than what would be expected just by chance. A similar pattern was found for bubble burst frequencies within McE groups. On the contrary, McME groups executed significantly higher frequencies of both displays. Given those opposite behavioral trends, when McE and McME groups were collapsed, the frequencies of bubble trail events no longer reached statistical significance.

Within breeding grounds, bubble displays presumably work as a threat display between escorts. Such function is consistent with the observations made in the Gulf of Tribugá. Furthermore, while identification of the animal producing bubbles was constrained by the intensity of social interactions and the limited visibility, the fact that it was only within McME groups that the observed frequencies of bubble events reached statistical significance, suggest that they would be produced predominantly by the main escort, as an attempt to obstruct the challenges to its position next to the maternal female. Similar observations have been made in other breeding areas (Baker & Herman, 1984; Darling, 2001; Tyack & Whitehead, 1982). For example, on the West Indies, over 60% of bubble streams were produced by the main escort, versus 7% that were assigned to the secondary escorts (Tyack & Whitehead, 1982).

Significant differences were only detected for social sounds when McE and McME groups were collapsed. In this case, trumpeting frequencies were significantly lower for Mc pairs. While some form of social sound was detected in all group types, statistical analyses were greatly limited by the small sample sizes recorded in the Gulf of Tribugá, so these results should be interpreted with caution. Observations made in other breeding areas show that while social sounds are rare for Mc pairs, they are commonly produced within competitive groups. In this way, it has been suggested that social sounds demonstrate aggression when multiple males are trying to establish social dominance (Darling, 2001; Dunlop et al., 2008; Stimpert, 2010). Furthermore, Silber (1986) reported that an increase in vocalization was often associated with group affiliations, suggesting they could constitute a threat display directed at individuals joining the group and challenging the proximity of the main escort respect to the female (Silber, 1986).

Spatial Distribution

Within breeding grounds, researchers consistently describe humpback whales as a predominantly coastal species, with most sightings concentrating around the 200m isobaths (Bruce, Albright, & Sheehan, 2014; Ersts & Rosenbaum, 2003; Felix & Haase, 2005; Glockner-Ferrari & Ferrari, 1985; Martins et al., 2001; Mattila, Clapham, Vasquez, & Bowman, 1994; Oviedo & Solís, 2008; Pacheco et al., 2009; Sanders et al., 2005). Furthermore, as mother-calf pairs are often distributed over the shallowest areas, their patterns of habitat use appear to reflect some degree of spatial segregation (Cartwright et al., 2012; Craig & Herman, 2000; Craig et al., 2014; Félix & Botero-Acosta, 2011; Smultea, 1994).

The spatial distribution of mother-calf pairs (escorted and unescorted) exhibited considerable variability regarding depth and distance to shore in the Gulf of Tribugá. Sightings were made in extremely shallow locations (depth ≤5m) as well in oceanic waters (depth >500m). Regarding distance to shore, groups were encountered between 0.2 and 9.2 kilometers from the coastline. A multivariate analysis of variance compared depth and distance to the coast between group types, but found no significant differences. The lack of spatial segregation by group type in the study area suggests a lack of differential habitat use between age classes. It appears that the morphology of the Gulf, characterized by a narrow continental shelf, restricts the distribution of groups with calves to a “corridor” delimited by the 500m isobaths.

The depth ranges reported in the current study seem closer to what has been reported for oceanic islands. Overall, researchers have documented that groups with calves are restricted to waters between 12-60m deep. Nonetheless, Guzman & Félix (2017) reported Mc pairs in depths of over 2000m based on maternal females tagged off Las Perlas (Panamá) and Salinas (Ecuador). On the other hand, reported distances from the coastline are more variable, with values ranging between 0.4 to 18 km from the coast (Bruce et al., 2014; Cartwright et al., 2012; Craig et al., 2014; Ersts & Rosenbaum, 2003; Félix & Botero-Acosta, 2011; Felix & Haase, 2005; Flórez-González et al., 2007; Glockner-Ferrari & Ferrari, 1985; Lowe, 2012; Mackay, Würsig, Bacon, & Selwyn, 2016; Martins et al., 2001; Oña, Garland, & Denkinger, 2017; Oviedo & Solís, 2008; Pacheco et al., 2009; Sanders et al., 2005). The pattern that emerges implies that habitat use in groups with calves is highly dependent of habitat physiography. Overall, in locations characterized by a narrow continental shelf (like the Gulf of Tribugá), groups will be found considerably closer to the coast, as depth increments abruptly. Conversely, when the continental shelf is broad and water depth increases gradually, groups with calves typically distribute over a more extended area, up to 20 km off the coast (Cartwright et al., 2012; Ersts & Rosenbaum, 2003; Félix & Botero-Acosta, 2011; Oviedo & Solís, 2008; Smultea, 1994).

Traditionally, researchers have interpreted the distribution patterns of maternal females as a strategy to avoid male harassment, save energy and/or prevent predation (Cartwright et al., 2012; Craig & Herman, 2000; Craig et al., 2014; Ersts & Rosenbaum, 2003; Félix & Botero-Acosta, 2011; Smultea, 1994; Whitehead & Moore, 1982). Nonetheless, within breeding areas, predation risk for calves seems to be mild, so the contribution of this factor might be more limited than originally thought. In coastal waters of the Gulf of Tribugá, only one verified killer whale sighting was made during the study period, so the presence of the species in the area would be occasional at best. For other breeding locations within the southeastern Pacific, evidence of killer whale attacks to humpback whale calves also appears to be scarce, with only two published records (Flórez-González et al., 1994; Scheidat, Castro, & Denkinger, 2000). Nonetheless, approximately 8% of whales sighted in the Gulf bared marks of killer whale attacks. It is possible that the recovery that has been reported for this population means the frequency of these attacks will also increase. As killer whales appear to attack mainly calves, predation might become a greater predictor of mother-calf pairs along the southeastern Pacific in the coming years.

According to Whitehead & Moore (1982) mother-calf pairs in the West Indies were frequently found in the calm waters associated with coral reefs. The authors reported little predation potential in the more exposed, rougher, portions of the study area, so they suggested that the preference for calm waters was probably a strategy to reduce energy expenditure for the calves. The argument made was that calves would experience a higher energy drain while swimming in rough waters. Furthermore, calm waters would also facilitate the occurrence of nursing bouts. Nonetheless, it was suggested that maternal females would occasionally induce calves to occupy rougher waters, as a kind of “training” for the migration back to the feeding grounds.

Alternatively, it has been suggested that the segregation of mother-calf pairs is motivated by avoidance of male harassment. Since it is presumed that shallow waters reduce the maneuverability of males within the water column, depth would be a major constraint for the association of multiple male escorts (Ersts & Rosenbaum, 2003; Félix & Botero-Acosta, 2011; Smultea, 1994). Nonetheless, Ersts and Rosembaum (2003) proposed that escorts could overrule this maternal strategy by taking advantage of transition periods, when mother-calf pairs would occupy areas of greater depth while in transit between two shallow locations. If this is the case, female social maturity and maternal experience could explain why some maternal females manage to remain unescorted despite exploiting deep waters.

Considering the spatial structure of the Gulf of Tribugá, it was possible that the efficacy of the maternal segregation strategy could be reduced. Nonetheless, the proportion of unescorted mother-calf pairs (66.1%), which greatly outnumbered the proportion of escorted mother-calf pairs (38.9%), is very similar to those reported for other breeding grounds including Ecuador (Félix & Botero-Acosta, 2011; Félix & Haase, 2001), Puerto Rico (Mackay et al., 2016), and the Dominican Republic (Mattila et al., 1994). Conversely, in Hawaii, between 60 and 85% of maternal females were escorted by at least one individual (Cartwright et al., 2012; Craig et al., 2002; Smultea, 1994).

Clapham and colleagues (1992) proposed differences in the rates of post-partum ovulation rates between populations could be responsible for the observed discrepancies. Conversely, Félix & Botero-Acosta (2011) proposed that differences in spatial structure between locations could be a more likely explanation. Although the exact cause may remain a mystery so far, it is clear that different populations are using different behavioral strategies. While maternal females in Hawaii might be prone to accept the affiliation of a single escort, in the southeastern Pacific females with a calf could be relying on the acoustic detection of song, social sounds or sounds associated with the execution of surface-active behaviors to avoid escort affiliation. Some experimental support for such behavioral avoidance came from Jones (2010) and a series of playback experiments conducted in Hawaiian breeding grounds. According to the author, Mc pairs consistently moved away from devices that reproduced sounds recorded in groups with multiple males.

Traveling speeds in the Gulf of Tribugá exhibited little differentiation among group types. While median values showed a slight increase on median speed values as the number of escorts increased, average values for McME groups were actually lower than those of Mc pairs and MCE groups. Furthermore, the great majority of sighting tracks reflected a traveling pattern, with only a fraction engaging in a more convoluted displacement, characterized as milling. It appears that in addition to the lack of spatial segregation evidenced by the noticeable overlapping of sightings of Mc pairs and McE/McME groups; humpback whales uniformly adopt fast traveling when passing the Gulf of Tribugá. Conversely, Cartwright & Sullivan (2009) reported a gradual increase in traveling speed as group composition changed from Mc pairs to McME groups. It is possible this is precisely the strategy of Mc pairs employ to remain unescorted even after entering deeper waters, where male maneuverability is presumed to be better. Alternatively, the observed speed values can be related to boat avoidance behavior. Surface-active behavior, changes in travel path, and increasing speed/diving times have all been cited as evidence of behavioral response resulting from vessel activity (Avila et al., 2015; Scheidat, Castro, Gonzalez, & Williams, 2004; Stamation, Croft, Shaughnessy, Waples, & Briggs, 2010). Considering that whale watching in the Gulf of Tribugá is still incipient (Zapetis, Samuelson, Botero-Acosta, & Kuczaj, 2017) humpback whales, Mc pairs in particular, could be responding by traveling fast upon vessel approach and/or presence.

Photo-Identification

Individual humpback whales have been identified by the coloration patterns, and trailing edge, of their flukes for over 30 years (Katona & Whitehead, 1981). This methodology has been tremendously successful, as photo-identification catalogs inform on life history patterns, population structure, and foraging behavior among others (Herman et al., 2011). In the Gulf of Tribugá, after five seasons of research, a total of 551 of whales were identified, 60 within groups that included a calf. Resighting data was available for a total of 14 of those 60 whales, comprising 15 separate events. Such matches provided two important pieces of information: 1.) They offered a glimpse into the flexibility of the social roles adopted by individually identified whales; 2.) They informed on the stability of group structures of interest.

Only two whales, sexed as females because of the presence of a calf, were resighted. This low resighting frequency is expected, as cows rarely execute fluke out dives (Cerchio, 2003; Garrigue et al., 2001; Rice et al., 1987). Before being identified as mothers, both females associated with one and two other adults, respectively. Unfortunately, information on the sex of those associates is not available.

In one case, the initial sighting occurred so early in the season (July 22nd) that it could correspond to the influx of receptive females that arrives on the breeding grounds along with mature males. Furthermore, the GPS track indicates that during the entire encounter, the adult dyad maintained a northern traveling direction, which provides some support to the claim that at the time of the sighting, the mother could have been arriving to the Gulf of Tribugá as a receptive female. Nonetheless, since the following sighting was made two years later, the relevance of its first record in relation to its 2016 status as a mother is quite limited.

In contrast, the second cow was observed in consecutive years, so the initial sighting is a considerably more informative for interpreting its status the following year. This female was first seen on August 28th, 2015. While the GPS track for this boat survey was not available, the field notebook records indicate that the group maintained a southern traveling direction for the entire duration of the sighting. It has been previously reported that newly pregnant females quickly return to the feeding grounds after mating has occurred, which could explain the travel direction. The two adults associating with this female could have been engaging in mate guarding behavior or waiting on the association of additional males to form a competitive group. Unfortunately, since our observation period extended for 30 minutes only, and with no possibility to prove that either associate is the father of the calf she was caring for in 2016, both scenarios remain highly speculative.

In Hawaii, comprehensive analyses of the resighting histories of known females have revealed some degree of variability in the social roles adopted by females while in the breeding grounds (Herman et al., 2011; Jones, 2010). Females can be seen alone, as the member of a dyad, accompanied by a dependent calf or yearling, associated with escort(s), or as the nuclear animal within a competitive group. Additionally, there were distinctive patterns in the frequency in which different females adopted such social roles. For example, Herman and colleagues (2011) reported that while female No. 479 was never identified as a mother, female No. 75 was always seen with a dependent calf.

In the Gulf of Tribugá, there is evidence that some whales consistently choose to associate with a mother and calf pair. Two individuals photographed in 2016, had been classified as escorts in previous years (2013 and 2015, respectively). Since the current study did not involve sexing whales in the field, there are some interpretation constraints. Nonetheless, considering that escorts have been reliably identified as males in many breeding locations around the world (Baker & Herman, 1984; Flórez-González, 1991; Glockner & Venus, 1983), it is safe to assume that those identified as escorts in the northern Colombian Pacific, were males as well. The fact that some males repeatedly act as escorts of a mother-calf pair, suggest that such social role is beneficial, and therefore, worth pursuing (Herman et al., 2011). Such benefit was difficult to quantify until Cerchio (2003) indicated that up to 20% of paternity assignments in the Revillagigedo Islands corresponded to males identified as escorts.

Similar resighting patterns have been reported in Hawaii (Baker & Herman, 1984; Glockner-Ferrari & Ferrari, 1990). For example, Baker and Herman (1984) reported that whale No. 13 was seen 10 times during the study period (1979-1981), and identified as the main escort to a mother-calf pair in all but one of those sightings. Furthermore, the associated mother-calf pair was the same in only two of those records, when sightings spanned over a three-hour period. In this way, this particular male escorted a total of eight different cows. Likewise, whale No. 49 accumulated four sightings during the study period, always as an escort of a mother-calf pair. Glockner-Ferrari and Ferrari

(1990) reported similar results. Whales No. 6010 and No. 1148 were seen over two and three different breeding seasons respectively, always as escorts. Similarly, Mobley & Herman (1985) reported three cases in which individually identified males were classified as escorts on two separate sightings.

For the current study, a total of five individuals identified as escorts were also classified as members of competitive groups. For the majority (n=4) of those records, the involvement in a competitive group preceded the association with a mother-calf pair, while the opposite was true for the remaining case. The apparent equivalence of these two roles further implies that they could be similarly profitable for males. Resighting data from other breeding locations supports this conclusion. In Hawaii, Baker & Herman (1984), reported that whale No. 22, sighted 12 times over a year period, adopted multiple mating strategies including escorting a mother-calf pair, competing for proximity to the nuclear animal within a competitive group, and singing while escorting. Similarly, according to Glockner-Ferrari and Ferrari (1985), whale No. 1601, observed over10 different breeding seasons, was seen as the escort of a mother-calf pair as well as the member of two competitive groups, in preceding and subsequent sightings. Moreover, Mobley and Herman (1985) also described a resighting in Hawaii, in which a male was first observed as the escort of a mother-calf pair before being sighted as a member of a competitive group.

Additional evidence has been provided by a recent comprehensive analysis of the resighting history of Hawaiian humpback whales (Herman et al., 2011). A total of 27 individually identified males were observed at least on 10 separate occasions over more than 30 years of research. All these males were observed fulfilling different social roles, including member of an adult pair, singer, escort to a female with no dependent calf, and escort of a mother-calf pair. The authors concluded the majority of individuals adopted all the roles at some point of their resighting history. Nonetheless, the precise frequencies for each role differed between individuals. Most males were identified as an escort to a mother-calf pair or a member of a competitive group. All the remaining social roles were recorded with a similar frequency.

In the Gulf of Tribugá changes in group composition were detected only for a small number of groups with calves, with most groups gaining members. Over short periods of time, three unescorted cows attracted at least one escort. Moreover, a group of mother, calf, and escort gained an additional member between sightings. Interestingly, three out of four affiliations occurred in mid August and mid September, when whale abundance is presumably still high in the Colombian Pacific (Flórez-González et al., 2007). The fact that most changes in group structure were affiliations; and more importantly, that those affiliations occurred at a time where most receptive females were presumably still in the breeding grounds, could suggest that the attractiveness of maternal females might not be as limited as once thought. Alternatively, given the passive nature of their behavior, escorts could be interested in affiliating with Mc pairs to rest and recover from demanding social and agonistic interactions like those occurring within competitive groups.

Only one disaffiliation was noticeable when processing the resighting data. An escorted cow, encountered in late August was resighted one month after, this time unescorted. Given the lack of data between the two records, it is impossible to estimate how long were the cow and escort associated for. The same female was seen once again, escorted by a different whale. This time, sightings were separated only by three hours. The second escort joined the mother-calf pair at a point in the breeding season (early October) that would be consistent with a post-partum ovulation by the mother and a low abundance of receptive females without a calf. The escort was resighted the following year, when it separated from a mother-calf pair after 27 minutes of observation. Although it is not possible to estimate how long were the cow and the escort associated for before the research vessel encountered them, the observed separation is consistent with the presumed sequence of events following the association of an escort with a mother-calf pair. Escorts are believed to affiliate with a cow until they can detect whether or not the female might be experiencing a post-partum ovulation (Mobley & Herman, 1985). The sudden disaffiliation of the escort could have resulted from detecting that the female was not ovulating or after noticing a female with a greater reproductive potential. Similarly, Jones (2010) reported that less than 3% of escorted Mc pairs split during the observation period (Jones, 2010).

While only one mother-calf pair was observed with different escorts as part of two separate sightings, such events seem to be fairly common. For example, Baker & Herman (1984) reported frequent changes in the identity of the main escort of three mother-calf pairs. Whale No. 71 was seen with two different escorts, while whales No. 75 and No. 62 had three and four different escorts respectively. Similarly, Mobley & Herman (1985) indicated that a single cow attracted a total of four escorts over a 93-minute observation. Furthermore, they concluded that only one of five mother-calf pairs was seen with the same escorts over two sightings that spanned over 3.5 hours. For the remaining females, escorts were always different between encounters. Likewise, female

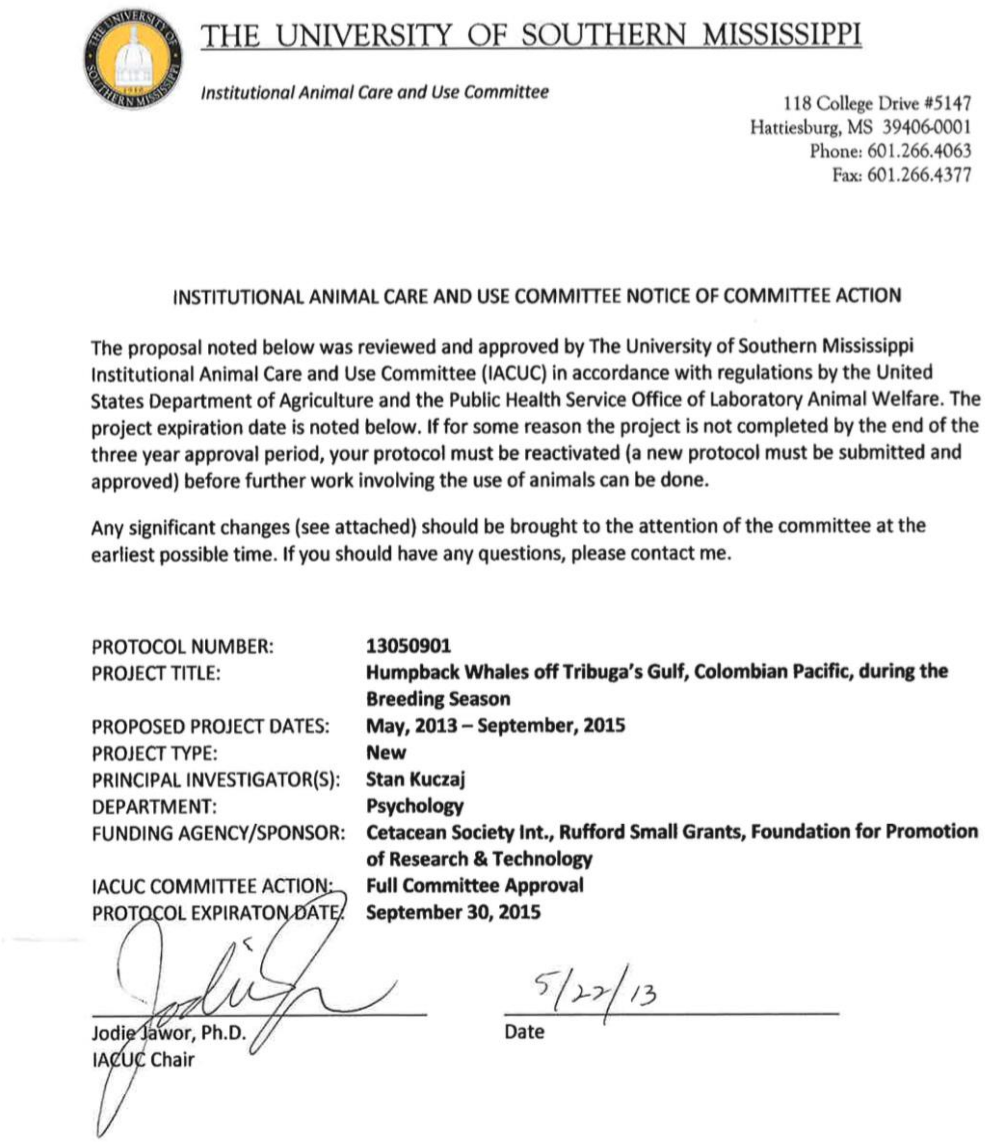
No. 3208, observed by Glockner-Ferrari & Ferrari (1985), was seen 12 times over the course of their study, always escorted. No resightings regarding any of the whales associating with this female were detected. Finally, Jones (2010) reported that 78.6% of identified associates of resighted mother-calf pairs were different.

Out of all resightings recorded in the Gulf of Tribugá, only one group remained with the same composition that was noticed when first detected. A single mother-calf pair remained unescorted six hours after its initial sighting. Interestingly, this sighting occurred in late August, at the time when other groups with calves predominantly gained escorts. Data from different localities in Colombia, Ecuador and Peru, suggest that in the Southeastern Pacific, the majority of groups with calves would be unescorted (Ávila, 2006; Félix & Botero-Acosta, 2011; Pacheco et al., 2009). In contrast, multiple studies have reported that the vast majority groups with calves encountered in Hawaiian waters are accompanied by at least one escort (Baker & Herman, 1984; Jones, 2010; Mobley & Herman, 1985). The cause of this discrepancy could be due exclusively to differences in habitat structure, but further research is needed, especially in the Southeastern Pacific.

Concluding Remarks: The Role of Escorts

Escorting of mother-calf pairs is a common phenomenon for humpback whales along their breeding grounds. Despite the many contributions made by numerous researchers over the world, to some degree, the role of escorts when joining mother-calf pairs remains uncertain. The current study examined the association of maternal females and escorts through three different techniques: photo-identification, behavioral sampling and spatial distribution monitoring. While there were only a few resightings of whales identified as members of groups that included a calf, photo-identification techniques provided no evidence of long-term association between cows and escorts. Nonetheless, a few instances of repeated observations of individually identified whales suggest that participation within competitive groups and escorting of maternal females are interchangeable mating strategies for males. Furthermore, in the Gulf of Tribugá, there was an evident behavioral response from the cow and her calf resulting from escort affiliation. Overall, escorted mother-calf pairs increased traveling, reduced resting and engaged in higher frequencies of social and surface activity. Finally, the spatial component of the analysis revealed no differences in habitat use patterns between group types, suggesting that the social status of maternal females is not determined solely by depth. The available data suggests that the physiography of the Gulf of Tribugá masks the spatial segregation strategy used by maternal females at breeding grounds. Future studies should focus on techniques that allow a more precise estimation of the duration of the association between cows and escorts. Satellite tagging, a methodology that allows for continuous monitoring of an individual's position for periods of time that do not have a methodological equivalent on boat surveys, is certainly be an optimal technique. Ideally, satellite tagging should be complemented by remote biopsy. Tissue samples obtained with this methodology would allow the determination of sex and the estimation of genetic relatedness, two critical pieces of information to determine the role of escorts when joining a mother-calf pair. Additionally, future initiatives should examine the possibility of determining whether the cow is ovulating post-partum through the completion of hormonal testing. Tissue samples collected through remote biopsy usually contain a portion of the whale's bubbler, a tissue that allows for extraction of sex steroids, which can be informative on the reproductive status of the cow. Behavioral studies would greatly benefit from the habit of determining social roles when evaluating the frequency of behavioral events. For such purpose, the enforcement of a buffer period before the onset of behavioral observations could be extremely useful. Future spatial analyses should consider additional variables such as sea surface temperature and bottom topography, which will likely improve the predictive power of statistical comparisons. Furthermore, considering sample size differences, it is important to focalize future research efforts in the monitoring of traveling speeds in the Gulf of Tribugá, as the patterns evidenced so far suggest its potential role as a transit area. Finally, a key spot within the Gulf of Tribugá, Utria Cove National Park, should be surveyed more extensively as it includes some of the shallowest waters available. A detailed examination of this location will likely benefit the current level of comprehension of the patterns of spatial distribution of groups with calves in the Gulf of Tribugá.

APPENDIX A – IACUC Approval Letter 2013



THE UNIVERSITY OF SOUTHERN MISSISSIPPI

Institutional Animal Care and Use Committee

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INSTITUTIONAL ANIMAL CARE AND USE COMMITTEE NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the three year approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

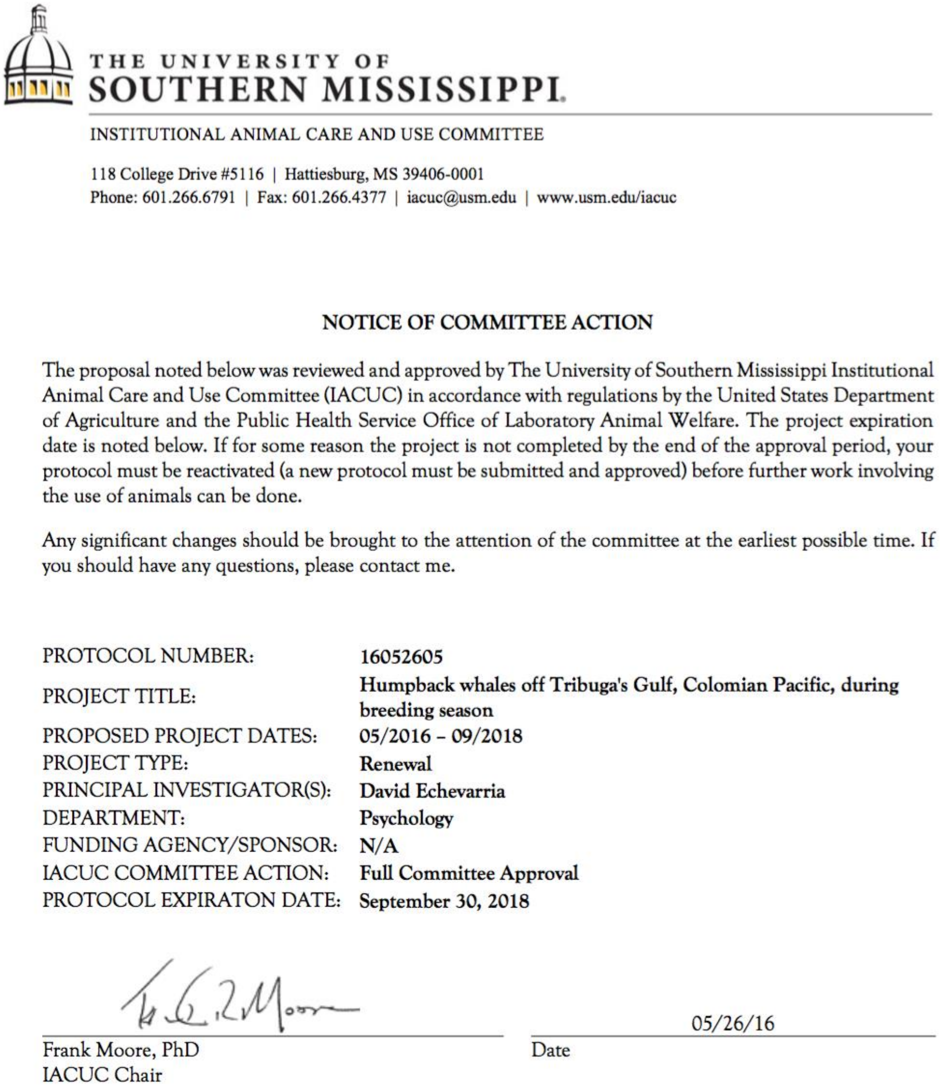
Any significant changes (see attached) should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER:	**13050901**
PROJECT TITLE:	**Humpback Whales off Tribuga's Gulf, Colombian Pacific, during the Breeding Season**
PROPOSED PROJECT DATES:	**May, 2013 – September, 2015**
PROJECT TYPE:	**New**
PRINCIPAL INVESTIGATOR(S):	**Stan Kuczaj**
DEPARTMENT:	**Psychology**
FUNDING AGENCY/SPONSOR:	**Cetacean Society Int., Rufford Small Grants, Foundation for Promotion of Research & Technology**
IACUC COMMITTEE ACTION:	**Full Committee Approval**
PROTOCOL EXPIRATON DATE:	**September 30, 2015**

Jodie Jawor, Ph.D.
IACUC Chair

5/22/13
Date

APPENDIX B – IACUC Approval Letter 2016



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NOTICE OF COMMITTEE ACTION

The proposal noted below was reviewed and approved by The University of Southern Mississippi Institutional Animal Care and Use Committee (IACUC) in accordance with regulations by the United States Department of Agriculture and the Public Health Service Office of Laboratory Animal Welfare. The project expiration date is noted below. If for some reason the project is not completed by the end of the approval period, your protocol must be reactivated (a new protocol must be submitted and approved) before further work involving the use of animals can be done.

Any significant changes should be brought to the attention of the committee at the earliest possible time. If you should have any questions, please contact me.

PROTOCOL NUMBER:	**16052605**
PROJECT TITLE:	**Humpback whales off Tribuga's Gulf, Colomian Pacific, during breeding season**
PROPOSED PROJECT DATES:	**05/2016 – 09/2018**
PROJECT TYPE:	**Renewal**
PRINCIPAL INVESTIGATOR(S):	**David Echevarria**
DEPARTMENT:	**Psychology**
FUNDING AGENCY/SPONSOR:	**N/A**
IACUC COMMITTEE ACTION:	**Full Committee Approval**
PROTOCOL EXPIRATON DATE:	**September 30, 2018**

Frank Moore, PhD
IACUC Chair

05/26/16
Date

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