

Fundamentals of Sperm Whale Societies:  
Care for Calves

By

Shane Gero

Submitted in partial fulfilment of the requirements for the  
Degree of Masters of Science in Biology

At

Dalhousie University  
Halifax, Nova Scotia  
December 2005

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*Your file* *Votre référence*  
*ISBN: 978-0-494-16575-1*  
*Our file* *Notre référence*  
*ISBN: 978-0-494-16575-1*

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To the one it took me away from...

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## **ABSTRACT**

The matrilineal society of the sperm whale functions to provide protection for calves at the surface while mothers make deep dives for food. Sperm whale females do have a system of babysitting, but details are unknown. This study aimed to elucidate the behaviour involved in sperm whale allocares, in particular who babysits whose calf; whether or not suckling from a non-parent occurs; and to describe sperm whale suckling behaviour. Using photo-identification and behavioural calf-follows, I examined patterns of adult-infant interaction for 22 sperm whale calves in the Sargasso and Caribbean Seas. In the Caribbean, a preferred babysitter provided most of the allocares but did not nurse the calf; whereas in the Sargasso, multiple nursing escorts provided care for the young. Furthermore, I found that peduncle dives by calves under adults, surface behaviour previously thought to indicate suckling, are laterally asymmetrical and may not always indicate milk acquisition through the mouth.

## **LIST OF ABBREVIATIONS AND SYMBOLS USED**

COA.....	COEFFICIENT OF ASSOCIATION
GLM.....	GENERAL LINEAR MODEL
GOS.....	"THE GROUP OF SEVEN" SOCIAL UNIT
HWI.....	HALF WEIGHT INDEX
IFAW.....	INTERNATIONAL FUND FOR ANIMAL WELFARE
NAMSC.....	NORTH AMERICAN SPERM WHALE CATALOGUE

## ACKNOWLEDGEMENTS

First and foremost, I would like to thank Hal for his guidance, support, and overall genius. They say that leaders sometimes resemble the conductor of a marching band. The leader is the one who is out in front of the band waving a large golden baton, in the big hat, with the whistle, and demanding that the rest follow. I have always believed that the better, more effective leaders are ones that more resemble the bass drummer. The drummer maintains the beat of the march with consistent support of the whole band using the deepest bass tones and drives the rest of the instruments forward from behind. These types of leaders allow the band to make their own decisions as to where to go but keep them on track in the hopes that they will follow their beat. Drummers are not interested in the show of the baton twirling band conductors; they are more interested in creating good music and developing the band as a cohesive unit. Thank you, Hal, for being the drummer for us all. You and Lindy have created a familial lab environment where all of your students feel comfortable to discuss opinions, ideas, and objections. You truly care about your students, their decisions, and their futures; and invest the time needed when problems arise.

My supervisory committee, Marty Leonard and Don Bowen, who suffered through both my ATC and defence, provided me with important input after each. Paul Bentzen, the chair, and Ian McLaren, the external examiner, from my ATC also gave valuable insight during the question periods. I thank Denise Herzing for acting as external examiner at my defense and Robert Scheibling for chairing the spectacle.

To *Balaena* and her crews, I paraphrase Capt. Malcolm Reynolds who said, Do you know what keeps a boat afloat? Love. You can know all the math in the universe, but

take a boat out on the ocean that you don't love and she won't keep you up just as sure as the world turns. Love keeps her up when she ought to fall down and tells you she's hurting before she keens. Love makes her home. The many hours at sea could not have been endured without the friendships forged with the crew members and with *Balaena* herself. Ricardo Antunes, Sherry Hudson, Erica Johnson, Marianne "the Queen of Vinyl" Marcoux, Hilary "Limp-wristed" Moors, Tyler Shultz, and Leslie "Lester" Thorne to whom I owe many laughs and good meals. An ever indebted thanks to the three skippers: Hal, Luke Rendell, and Meaghan Jankowski, to whom I owe my life and days of smooth sailing...well...on most days. I am particularly grateful for Luke's guidance through the disasters of the first field season and the successes of the Promised Land.

All the members of the Whitehead Lab over the years: Andrea, Derek, Hilary, Jana, Joe, Katie, Lars, Luke, Mandy, Marcoux, Marie, Meaghan, Merel, Tonya, Tyler, and Ross. All of you have offered me different parts of who I am and I thank you for those. I look forward to the days when we get to work together again. In particular, I would like to thank Lars, for supporting me, offering me opportunities of a lifetime, being a good friend and teaching me the ways of the Danish Dreamboat, even though I lost the GPS and never got that bathymetry done. I hope the future holds more opportunities for us to work together and to play cards.

I have spent six and a half years in the biology department here at Dal. Countless faces have helped me through many challenges which have lead to both defeats and successes. I enjoyed my time at Biobeer, Bioween, Bioball, and any other events that could stand the "Bio" prefix. I have appreciated the friendship of all those in the

department and the LSC over my years here, in particular, those who rejoiced with me over academic, athletic, and personal victories at the Gradhouse.

At a personal level, none of this would have been possible without the support of my family, my roommates, and Erica. Mom, Dad, Joanne, Martin, Sasha, Chantelle and Granny thank you for the words of advice and encouragement either via email, MSN, or Sunday afternoon phone calls. To the Stoop, thanks for putting up with my subleters and my incessant complaining about science. E, it's done! No more early morning trips to the airport.

The project was supported by operating and equipment grants to H.W. from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Whale and Dolphin Conservation Society, to Luke Rendell from the U.K. Natural Environment Research Council and I was supported during the course of this study by an NSERC Postgraduate Scholarship (PGS-M). Research in Dominica was carried out under a scientific research permit (SCR 013/05-02) provided by the Ministry of Agriculture and Environment of the Commonwealth of Dominica

Finally, I thank the following for contributing financially, in kind, or in thought to me or my work over the last few years: Marie Auger-Méthé, Hilary Moors, and Lindy Weilgart provided useful comments on early drafts of this thesis; Dr. Dan Engelhaupt for his genetic expertise and Ron Burns at Northwoods DNA Inc. for completing much of the genetic lab work; Paul Brodie for his expert opinion on the anatomical likelihood of nasal suckling and his kind words of encouragement in regards to bringing forward a hypothesis which at first seems outlandish; Jennifer Milne from the Map and Geospatial Information Collection at the Killam Memorial Library for creating the GIS map; Vivien

Hannon from Digital Media Services for her help cleaning up the underwater photographs; Evasion Tropicale for giving me a reason to discover a better field site; Cedric Million for living with the crazy Canadians; Carole Carlson for providing me with my original contacts to being this work and offering support when the contacts couldn't be contacted; IFAW for continuing to curate the NAMSC catalogue; Jonathan Gordon for offering to contribute the data from his previous work which he completed with many others from IFAW; members of the Read Lab at the Duke University Marine Laboratory; Andrew Amour and the staff at the Anchorage Hotel for their kind support; and the crews of the various whale watching groups in Dominica for their cooperation; the Lett Fund and the Dalhousie Faculty of Graduate Studies for providing me with much needed funding to present this work at the 16<sup>th</sup> Biennial Conference on the Biology of Marine Mammals; the 'Group of Seven' who decided to participate actively in this research project without whom much of this thesis would be hearsay and conjecture; and finally to you the reader...yes, you the one reading this now...for actually opening this and caring about what I have done.

## **CHAPTER ONE :**

### **GENERAL INTRODUCTION**



The sperm whale, *Physeter macrocephalus*, is truly an animal of extremes. They are the largest of all odontocetes or toothed whales and, of all mammals, they dive the deepest, remain submerged the longest, and possess the largest brain in the world (Rice 1989). The sperm whale is also the most sexually dimorphic species among cetaceans with females reaching lengths of 12 metres and weighing up to 24 tons, and males can reach up to 18 metres and 57 tons (Rice 1989). Their distribution is cosmopolitan with males being found from ice-edge to equator in both hemispheres. The females have a more confined distribution, remaining primarily in tropical and sub-tropical waters (Rice 1989). *Physeter macrocephalus* forages at depth, consuming mainly medium and large sized squid, however their diet may also include octopus, fish, and crustaceans (Rice 1989; Whitehead 2003). Sperm whales consume about as much biomass per year as the global human marine fisheries, making them a significant element of their oceanic habitat (Clarke 1977; Whitehead 2003).

Historically, much of the research on sperm whales used dead animals collected during major hunts, which were significant from the 18<sup>th</sup> Century until the 1980's (Gosho et al. 1984). Recent work has focused on studying living sperm whales in their natural habitat (summarized in Whitehead 2003). It is important to note here that while hunts are currently ongoing in the name of science, studies which are both productive and progressive can be completed by means which inflict a minimal impact on the lives of these animals. During fieldwork for this thesis I used only non-invasive research techniques.

I will begin this thesis with an introduction to theories fundamental to my work and this thesis. Beginning with a summary of the conceptual framework within which I

study cetacean societies, I will discuss factors affecting group formation in mammals, sperm whale social structure, the evolution of sociality in sperm whales, and finally the gaps in our knowledge and my research objectives.

## **STUDYING CETACEAN SOCIAL STRUCTURE**

A society can be defined as a set of conspecifics that interact more regularly with one another than with members of other societies (Struhsaker 1969; Kappeler and van Schaik 2002). Studying the society in which a species lives often gives insight into the behaviour and ecology of the species, as well as into the dynamics of the population under study (Whitehead 1997). A society is composed of three interrelated components: (1) the social organization, which characterises society's demographics by describing the size, age composition, sexual composition and spatiotemporal cohesion of a society; (2) the mating system, which describes both the behavioural and genetic aspects of the reproductive interactions within the system; and (3) the social structure, which refers to the patterning of social interactions and relationships among dyads of society members (Kappeler and van Schaik 2002). According to Hinde's (1976) framework, the type and patterning of social interactions between a pair of individuals defines their social relationships and the pattern of dyadic relationships can then be used to characterise the social structure of a society. Thus, to study social structure, one must collect detailed data on the interactions between individuals over time (Hinde 1976).

As cetaceans spend the majority of their time underwater, social interactions are often difficult to observe, let alone quantify (Whitehead 1997; Mann 1999; Whitehead et al. 2000). In this case, it becomes important to develop some measure of interaction without directly observing the interactions themselves. Quantifying the spatio-temporal

proximity of individuals can be used as such a measure of interaction. The spatio-temporal group, or a set of individuals in the same place and time, acts as a proxy for interaction and can be used to define association (Whitehead 1997; Whitehead and Dufault 1999; Whitehead et al. 2000). Thus, to understand cetacean social structure it is critical to investigate factors that may determine group formation.

## **GROUP FORMATION**

Protection from predation and improved resource acquisition are widely accepted as principal factors promoting group formation in mammals (Alexander 1974; Wrangham and Rubenstein 1986; Connor 2000). For cetaceans, the acquisition or protection of resources are thought not to be major factors influencing group formation in most cases, since both the cetaceans themselves and their prey have large ranges and are highly mobile (Connor 2000). It is believed that predation pressure is the primary factor affecting group formation in cetaceans (Connor 2000). By living in groups, individuals decrease their chance of being preyed upon through increased vigilance, protection by mobbing, predator confusion or through dilution (Connor 2000).

Among sperm whales, the sexes have very different social lives presumably due to differences in the factors driving group formation. Males live a much more solitary life, remaining alone or in ephemeral “bachelor groups” when not breeding, and roving individually between groups of females during breeding season. In contrast, females live in small stable groupings, called *units*, of approximately 14 individuals (Whitehead 2003).

## FEMALE AND IMMATURE SOCIAL STRUCTURE

The social structure of the female and immature sperm whales is hierarchically organized into several levels based on differing spatial and temporal scales (Whitehead and Weilgart 2000). As the nomenclature is quite confused in the literature, Appendix 1 has been included in which relevant terms (italicized in this chapter) have been defined. Overall, associations among female and immature sperm whales are of two types: 1) casual acquaintances, whales which are associated for only a few days, and 2) constant companions, whales which are associated with an individual over long periods of time across years (Christal et al. 1998; Whitehead 1999; Whitehead and Weilgart 2000). Constant companions are members of an individual's social *unit* and can be considered permanent associates. *Unit* members are often, but not always, matrilineally related (Richard et al. 1996; Lyrholm and Gyllensten 1998; Whitehead and Weilgart 2000; Mesnick 2001; Mesnick et al. 2003). Individuals show preferential association patterns for *unit* members, but not for particular individuals within a given *unit* (Christal and Whitehead 2001). Conversely, casual acquaintances are members of another social *unit* with which the first is grouped (Christal et al. 1998).

A *group* tends to be the assemblage that is most commonly observed while in the field. On average, *groups* contain about 20 individuals and are made up of one to three *units* that associate for hours to days (Whitehead and Kahn 1992; Christal et al. 1998; Whitehead 2003).

There are larger scales of clustering, including *aggregations* which have temporary membership of around 40 individuals and span 10-20 km. Even larger are *concentrations*, which contain 1000 animals or more and span geographic areas of a few

hundred kilometres. At these larger scales, assemblages are thought to mimic the patchy distribution of prey rather than be affiliative social groupings (Whitehead et al. 1991; Whitehead and Weilgart 2000; Whitehead 2003).

### **CARE AS AN EVOLUTIONARY FORCE**

Protection of young through babysitting is a likely candidate as a major evolutionary force driving sperm whale sociality (Best 1979; Gordon 1987; Arnborn and Whitehead 1989; Whitehead 1996; Whitehead 2003). In contrast to the generally-accepted paradigm for primates, for whom intraspecific resource competition is considered the force driving the development of long-term bonds (Wrangham 1980); Whitehead (1996, 2003) suggests that in sperm whales the communal defence of the calves from predators has led to the formation of social units and the strong bonds between sometimes unrelated females. Unlike most of their terrestrial mammalian counterparts, the pelagic sperm whales have no refuges in which to hide from predators (Whitehead 2003). A permanent set of companions would grant members greater vigilance and a better ability to fight off predators (Whitehead 2003); however, the absence of social structure in adult male sperm whales suggests that sociality offers little improvement in adult survivorship. Thus, it is likely the evolution of a babysitting system and possibly the communal care for calves that was a driving force towards sociality.

### **GAPS IN OUR KNOWLEDGE AND RESEARCH OUTLINE**

The obvious limitations of working with a marine species, especially deep-diving ones, have slowed advances in our knowledge of sperm whales in many regards. In comparison to a terrestrial counterpart, the elephant, we have only recently begun to understand sperm whale behaviour. The elephant shares many similarities with the sperm

whale in terms of brain and physical size, complex social organization, and ecological success (Weilgart et al. 1996). Unlike in elephants, in which our knowledge is quite comprehensive on small-scale behaviour, communication, movement, and social interactions between individuals (summarized in Payne 2003), in sperm whales, most of our understanding stems from long-term multi-year data sets collected over large spatial and temporal scales (Whitehead 2003). Small-scale research focusing on the interactions between individuals is needed to elucidate the details of mate selection, contextual use of vocalizations, and of particular interest in this thesis, care for calves.

Very little directed study has been carried out on calf care in sperm whales, despite its importance. Calf survival not only perpetuates sperm whale society, but may have been at its foundation. The principal aim of my study was to learn the details of calf behaviour (Chapter II) and the practices involved in calf care within sperm whale social groups (Chapter III). Each of following two chapters is organized as an independent paper in which I address questions that are associated with each of these objectives. I conclude with a short discussion that unites these works and touches on some limitations and recommendations for future research.

## **CHAPTER TWO :**

### Suckling Behaviour of Sperm Whale Calves

## INTRODUCTION

The majority of animal societies revolve around the production and care of offspring and are characterized by both, the mating system of the species and the nature and quality of care provided to their young. Eusocial insects are characterized by the number of adults living together and the presence of distinct castes, one of which is usually dedicated to the care of the offspring (Brockmann 1991). Avian societies vary on a continuum from territorial, pair-breeding species in which one or both parents provide care to flock-living, communal breeding species in which both parents and alloparents provide for the offspring (Emlen 1991). Reptiles (Shine 1988), amphibians (Crump 1994), and fishes (Balon 1984) often provide very little or no care for their offspring and as such do not have intricate social structures. Different strategies have been adopted in different situations and by different species, but in all cases, the production and care of offspring are central to the social interactions among members of complex societies. The proxy by which we measure fitness of animal groups, offspring are the focus of all animal social organizations.

Among mammals, the social organization of many species has at its base the mother-offspring unit, as mothers provide the bulk of parental care by virtue of the nursing relationship (Kleiman and Malcolm 1981; Klopfer 1981; Clutton-Brock 1991; Reeve and Shellman 1997). While some mammals wean their offspring abruptly after birth, others nurse their young for years and maintain contact between generations over a lifetime (Klopfer 1981).

Sperm whales, *Physeter macrocephalus*, live in matrilineal social units consisting of females and their descendant offspring. The principal function of these units seems to



be to provide protection for calves while mothers make lengthy foraging dives at depth (Best et al. 1984; Gordon 1987; Arnborn and Whitehead 1989; Whitehead 1996). Much of our knowledge about social units of sperm whales has been derived from studies that focus mothers and their adult associates. Detailed studies of the other half of the mother-offspring unit, the calf, are lacking (Whitehead 2003).

Generally speaking, sperm whale calves have three important behaviours to perform on a daily basis: breathing, swimming, and suckling. As Whitehead (2003) points out, calves do not have difficulty breathing even immediately after birth, but are unable to make prolonged dives with older individuals in the social unit. Quite soon after birth, sperm whale calves are proficient swimmers (Weilgart and Whitehead 1986) and manage to keep up with the foraging adults below presumably by following the sounds of their echolocation clicks (Gordon 1987). Suckling is more of an enigma. The predominantly accepted theory which is supported by both nineteenth-century whalers and modern observations by snorkellers suggest that the nipple is held in the gape of the calf's jaw (Beale 1839; Best et al. 1984; Gordon 1991). However, Best et al. (1984) cite an observation by Bennett (1840) who describes an adult female rolling onto her side with her pectoral fin above water and a calf suckling with its blowhole above water from the exposed nipple.

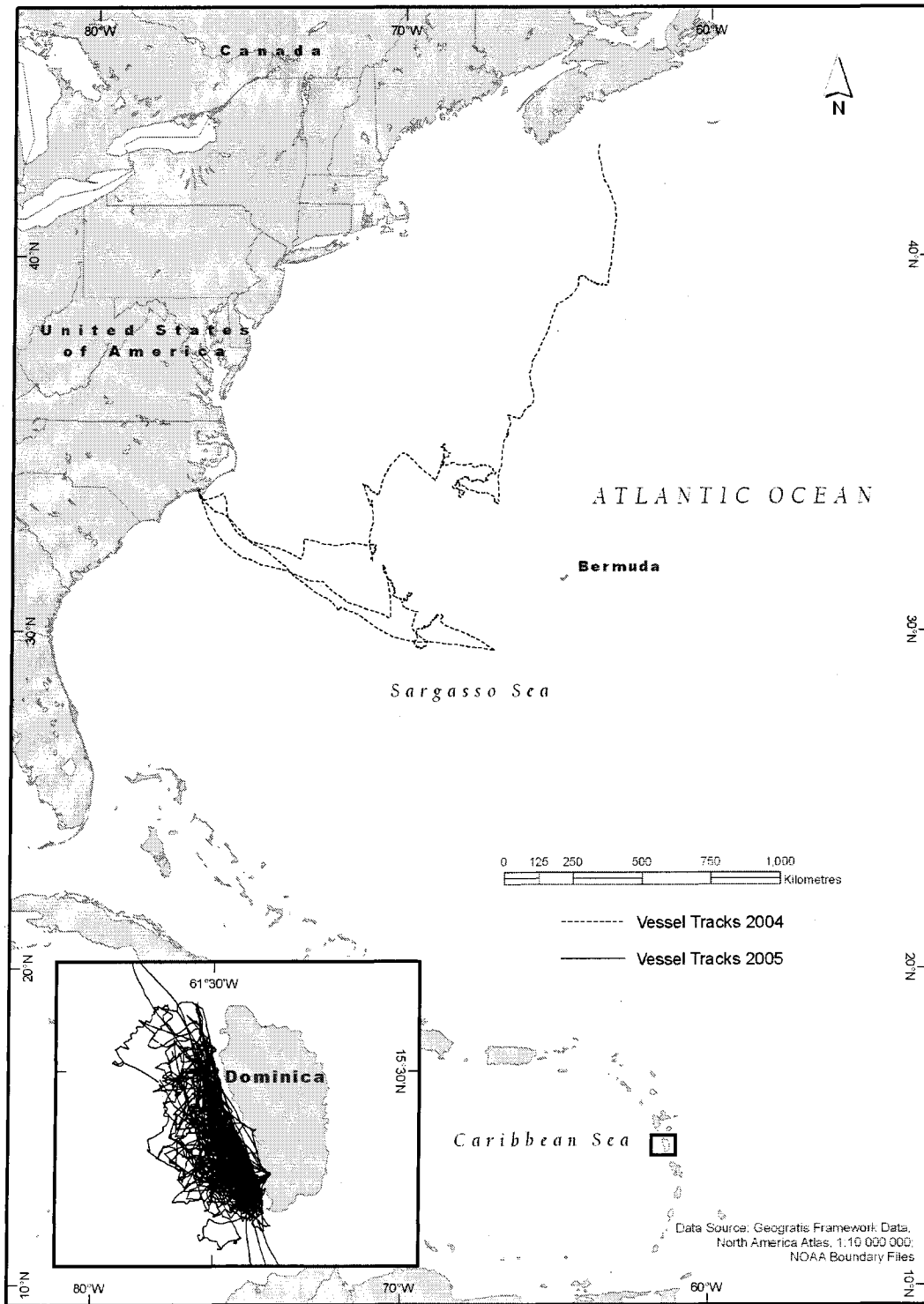
Given the lack of comprehensive descriptions of calf behaviour, and in particular behaviours relating to suckling, this study was undertaken to describe calf suckling behaviour in detail and to act as a basis from which to develop a more complete ethogram of infant sperm whale behaviour.

## **METHODS**

### **FIELD METHODS**

Groups of female and immature sperm whales were located and followed both acoustically, using a directional and towed hydrophone, and visually, by observers on a dedicated 13 m. auxiliary sailing vessel (Whitehead and Gordon 1986). Small sailing vessels are preferred for this type of research due to their economy while not jeopardizing data collection (Gordon et al. 2005). Fieldwork was split between two study areas (Figure 2-1). The first (May 5 – June 20, 2004; 38 days effort) was located in international waters between Bermuda and the east coast of the United States in the Sargasso Sea. The 2005 fieldwork (January 14 – April 13, 2005; 58 days effort) was completed off the leeward shore of the Commonwealth of Dominica in an area that covered approximately 2000km<sup>2</sup> along the entire west coast of the island, in waters sheltered from trade winds. Three-week trips were carried out during the offshore fieldwork in the Sargasso Sea, but, with the proximity of the study area to port, data were collected during 6-10 day trips off Dominica. “Encounters” with sperm whale groups were defined as uninterrupted time periods during which sperm whales were either seen or heard and lasted from 1 to 6 days.

During daylight hours, individuals resting at the surface were approached and photographs were taken to identify individuals. During our approach, priority was given to taking dorsal fin pictures of the calves from alongside the animals, before moving behind the animals in order to photograph distinct markings on the trailing edge of their



**Figure 2-1: GIS map of vessel track showing the north-western Atlantic. The vessel track for the 2004 fieldwork in the Sargasso Sea is shown by a dashed line on the background map. Vessel track for the 2005 fieldwork off of the Commonwealth of Dominica is shown as a solid line in the enlarged insert of the island of Dominica.**

flukes as adult individuals initiated deep dives (Arnbom 1987). Sloughed skin samples, for genetic determination of relatedness, were collected in the slicks of individuals after identification (Whitehead et al. 1990; Amos et al. 1992; Richard et al. 1996; Richard et al. 1996). During the 2004 field season, photographs were taken using a Canon EOS Elan II SLR camera with a Canon EF fixed 300mm lens and Ilford HP5 400 black and white film. For the 2005 field season, a Canon D10 digital SLR base was used. Digital pictures were taken in full colour at a resolution of 3072 x 2048 pixels and were saved in JPEG format.

#### *Focal-Calf Follows*

Focal-animal follows (Altmann 1974; Mann 1999) conducted on calves were completed within the larger group-follow of the entire sperm whale group (Whitehead 2004). Behavioural data were collected using continuous and instantaneous sampling (Altmann 1974; Mann 1999) while the calves were at the surface. Instantaneous sampling was used to determine spatial relationships between the calf and other individuals at the surface and nearest neighbour's identity (the animal closest to the focal calf) after each change in cluster composition. Continuous sampling was used for all calf behaviours, including suckling attempts. At this juncture, it is important to make clear two points of terminology:

(1) Gordon et al. (1998) defined suckling attempts as repeated short dives beneath the peduncle of adult whales but point out that it was not always possible to determine if in fact calves were receiving milk. Here, we refer to this observable surface behaviour performed by the calf as "peduncle dives" and do not assume that suckling is occurring.

(2) The distinction between the terms “suckling” and “nursing”. Here, I use “suckling” to refer to the behaviours performed by a calf in order to ingest milk from an adult female. The term “nursing” is used to describe the behaviours performed by the adult female who is presumably providing the milk during this adult-calf interaction. It is also important to note that these terms are used to define the observed behaviours of adults and calves regardless of whether or not the calf actually received milk from the adult.

A “bout” of peduncle dives was defined as a series of peduncle dives which began at the first observed peduncle dive when the dorsal fin vanished beneath the surface and ended when the nursing escort started a fluke-up foraging dive or if the calf stopped making peduncle dives or swam away from the escort. Peduncle dive bouts were timed using a digital stopwatch. The number of peduncle dives within a bout, the duration of each dive, the number of breaths during a surface interval, as well as the duration of the surface interval between dives were recorded. The side of the escort on which the calf was located while at the surface between peduncle dives (referred to as “dive side”) was also recorded, as well as any switches in the dive side during a bout. When possible, peduncle dives were observed underwater by a snorkeller alongside the mother-calf pair.

Three hierarchical levels were defined for associations with the calf: (1) *Associates*, any individual identified as part of the same social group as the calf but who was not observed in the same cluster with the calf; (2) *Escorts*, any individual identified within the cluster which contains the calf (Gordon 1987; Mann and Smuts 1998); and (3) *Mother*, when genetic data were not available, the mother is assumed to be the mature female escort from which the calf suckled and with which the calf spent the majority of

their time and thus has the highest “Half-Weight Index” (HWI) value (Gordon 1987; Whitehead 1996). To identify escort associates, individuals were deemed to be associating with the calf if they were within the same cluster at the surface. Individuals were considered to be within the same cluster if they were within approximately three adult-body lengths (~40m) from any other cluster member and were coordinating their behaviour (Whitehead 2003). Cluster membership was recorded on a continuous basis, noting the times of splits and joins at the surface. Each surfacing after a full foraging dive, identified by fluke-up dives, was considered a new cluster. Surfacing by the same individuals after a “shallow dive”, identified by their short duration (less than approximately 10 minutes) and lack of fluke-up, were not considered to end their membership of a cluster.

## ANALYSES

### *Identifications*

A quality rating (Q) between 1 and 5 was given to each photograph, where 1 indicated a very poor photograph and a non-identifiable individual, and 5 indicated a very high quality photograph of an individual highly likely to be identified (Arnbom 1987; Dufault and Whitehead 1993). The Q-value was a function of the attributes of the photograph (focus, exposure, angle of fluke relative to the negative plane, angle between the axis of the fluke and the surface of the water, and the proportion of the frame filled by the fluke) but not the quality of the markings on the fluke (Arnbom 1987; Dufault and Whitehead 1993). Only pictures with a  $Q \geq 3$  were used for the analyses. The best picture for each individual within each encounter was assigned an identification number then

matched between encounters using a computer-based matching program (Whitehead 1990).

Young calves rarely lift their flukes. These animals were individually identified using the shape of their dorsal fin and distinct markings on their dorsal fin and body. Similar criteria were used (focus, exposure, angle of dorsal fin relative to the negative plane, percent of the dorsal fin not submerged, and the proportion of the frame filled by the dorsal fin) to assign a quality rating to the calf dorsal fin photographs as those used to assign quality ratings to fluke pictures used to identify adult sperm whales in other studies (Arnbom 1987; Dufault and Whitehead 1993). Computer matching was not available for dorsal fin photographs.

#### *Peduncle Dive Duration*

A multi-factorial nested general linear model (GLM) was fitted to the peduncle dive duration data set using the backwards stepwise procedure with  $\alpha$ -to-remove = 0.15 and  $\alpha$ -to-enter = 0.15:

**Duration = Constant + Study Area + Individual (Area) + Bout (Individual) + Error**

Individuals were nested within a study area and bouts were nested within individuals.

Dive duration data were log transformed to make the data residuals more normal. The independence of consecutive dive durations within a bout was investigated by examining the autocorrelation of residuals after fitting the model, and all residuals were tested for normality using a Lilliefors Normality test.

#### *Dive Side*

The records for a bout were classified into one of two categories based on whether or not all observed peduncle dives within a bout were completed on one side of the

nursing-escort (“consistent”) or whether the calf switched sides during the bout (“switch”). Dive side was compared within and between bouts for a given individual, as was the frequency of switches. Only calves in which dive side for three or more bouts was recorded were included in these analyses ( $n = 6$  for both study areas). Finally, a t-test was used to compare the mean duration of suckling-dives on left and right sides. Dives from all individuals for which dive times and side were recorded were included in the t-test.

## RESULTS

I collected data from 177 bouts from 22 different calves (11 calves from the Caribbean Sea, 11 from the Sargasso Sea). Of those, only 23 were considered complete bouts, such that we observed them from when the calf surfaced, began peduncle diving, and either the calf stopped the repeated peduncle dives, swam away from the escort, or, as in most cases, the adult began a fluke-up dive. On average, complete bouts were 24.4 peduncle dives long (SD = 3.44, range: 19 – 31) and had a mean duration of 5.7 min. (SD = 1.14; range: 3.5 – 8.2).

### UNDERWATER OBSERVATIONS

Encounters in the Caribbean Sea were dominated by the continuous presence of one particular social unit, “The Group of Seven” (GOS), which consisted of five adult females, one juvenile male (8.8 m, 8-10 years old; T. Schulz, unpublished data), and one male calf (4.5 m, ~3 months old; length estimated using photographs with a fixed focal length from the crow’s nest on the mast of the sailing vessel and the age based on growth curve from Figure 10 of Best et al. 1984). Sexes of these individuals were determined by an ongoing genetic analysis (D. Engelhaupt, unpublished data). The GOS was



encountered on 40 different days over a 54 day period. Whenever possible, a snorkeller would enter the water with the GOS mother and calf in order to observe peduncle dive behaviour underwater. Only one observation of a bout of peduncle dives was made for another calf.

Underwater observations of the GOS calf were made for a total of 12 bouts (totalling 173 dives). The same behaviour was observed during all peduncle dives observed underwater. The calf arched down without rolling onto its side, and remaining somewhat parallel to the escort and in an upright position, the calf moved its head under the belly of the escort and pressed its blowhole to the escort's genital area (Figure 2-2, following page). The calf remained in this position for a few seconds and then turned away and surfaced. This behaviour would be repeated every dive until the escort began to fluke-up at which point the calf attempted to dive with the escort. The calf generally dove in parallel with the escort and no attempts to suckle were made while descending. The entire peduncle dive bout was accomplished while slowly moving forward. In no cases was the calf observed attempting to place its mouth near the underbelly of the escort. The same behaviour was recorded during the one bout of peduncle dives performed by the only other calf observed underwater. Above-water behaviours did not appear to differ whether snorkellers were in the water or not.



**Figure 2-2: Underwater photograph of the general position taken by the calf while making “suckling” attempts while peduncle diving. Inset shows GOS calf pressing its blowhole to the mother’s underbelly.**

## DIVE DURATION

I recorded dive durations for 981 peduncle dives, the vast majority of which were recorded while in the Caribbean Sea (95%). Of the 940 dives timed in the Caribbean, 712 or 76% were from the GOS calf, '5703'. Calves with smaller samples (>7 dives) from both the Caribbean (n = 7) and Sargasso Seas (n = 4) were used to compare and contrast results obtained from the GOS calf.

**Table 2-1: Results of the general linear model, examining factors affecting peduncle dive duration. Table entries give the number of individuals in each study area used in this analysis, the autocorrelation of residuals in the final model, the results of a Lilliefors test for normality among residuals, the proportion of the variance accounted for by the model terms, and the P-values for each of the factors in predicting the duration of peduncle dives.**

	<b>Dive Duration Model</b>	<b>P-value</b>
<b>Number of individuals per study area</b>	Caribbean: 8 Sargasso: 4	
<b>Autocorrelation</b>	0.008	
<b>Normality of Residuals (Lilliefors)</b>	See Figure 2-4	<0.001
<b>Variance accounted for</b>	0.600	
<b>Study Area</b>	Caribbean: 13.9s (5.52)* Sargasso: 20.1s (15.54)*	0.007
<b>Mean (SD)</b>		
<b>Individual</b>	See Table 2-2	< 0.001
<b>Bout</b>	See Figure 2-3	< 0.001

Pooling across all individuals in both study areas, the average duration of a sperm whale peduncle dive was 14.2 seconds (SD = 6.50). Excluding the large sample obtained from the GOS calf resulted in a similar mean of 13.8 s. (SD = 8.74). The duration of peduncle dives varied significantly between study areas (Figure 2-3, page 22; Table 2-1, previous page). Peduncle dives were approximately 6 s. longer in the Sargasso Sea when compared to the Caribbean Sea. Within any single study area, individual differences in peduncle dive duration are significant (Figure 2-3; Table 2-2, following page). Additionally, there were significant differences between the mean peduncle dive duration of an individual's bouts (Figure 2-3, Table 2-1), and within a bout for any given individual (Table 2-1; for the sake of clarity the mean within-bout standard deviation for each study area is shown only as an error bar in Figure 2-3). None of these factors were removed by the reverse stepwise procedure of the GLM which was fitted to the data. Low autocorrelation coefficients between dive-durations within bouts (Table 2-1) suggested that in no case was serial dependence substantial between dives within a bout. A Lilliefors normality test indicated that the data were not normal due to a few large outliers (Figure 2-4, page 23). We should therefore treat the p-values of this analysis with caution, although with large sample sizes and highly significant p-values it is unlikely that the result of any test is compromised by non-normality of the residuals.

Intervals between dives had a mean duration of 5.18 seconds (SD = 2.95) and varied between 1.3 and 33.6 seconds. Calves generally took one or two breaths between peduncle dives. The bimodal distribution of dive intervals reflects this time difference (Figure 2-5, page 24).

**Table 2-2: Peduncle dive durations for all sperm whale calves from both the Caribbean and Sargasso Seas. ‘N’ is the number of dives recorded.**

<b>Study Area</b>	<b>Calf ID</b>	<b>N</b>	<b>Mean (SD)</b>	<b>Range</b>
<b>Caribbean</b>	<b>5703</b>	<b>712</b>	<b>14.4 (5.41)</b>	<b>1.9 – 97.5</b>
Caribbean	5725	74	10.0 (1.89)	7.1 – 15.1
Caribbean	5701	53	10.3 (1.72)	5.9 – 14.4
Caribbean	4001	41	12.5 (3.05)	8.0 – 20.6
Caribbean	5719	19	14.4 (2.75)	10.7 – 21.4
Caribbean	4002	13	23.3 (15.5)	10.0 – 62.2
Caribbean	4003	12	18.5 (6.12)	11.9 – 30.3
Caribbean	5718	9	11.8 (1.85)	8.8 – 14.7
Caribbean	All Individuals	933	13.9 (5.52)	1.9 – 97.5
Caribbean	All except ‘5703’	221	12.3 (5.58)	5.9 – 62.2
Sargasso	5862	20	17.1 (16.83)	10.3 – 87.6
Sargasso	3016	12	30.4 (17.87)	14.2 – 65.1
Sargasso	3012	9	20.8 (1.39)	18.5 – 23.0
Sargasso	5800	7	15.8 (3.53)	11.1 – 21.2
Sargasso	All Individuals	48	20.1 (15.54)	3.3 – 87.6
Both	All Individuals	981	14.2 (6.50)	1.9 – 97.5
Both	All except ‘5703’	269	13.8 (8.74)	5.9 – 87.6

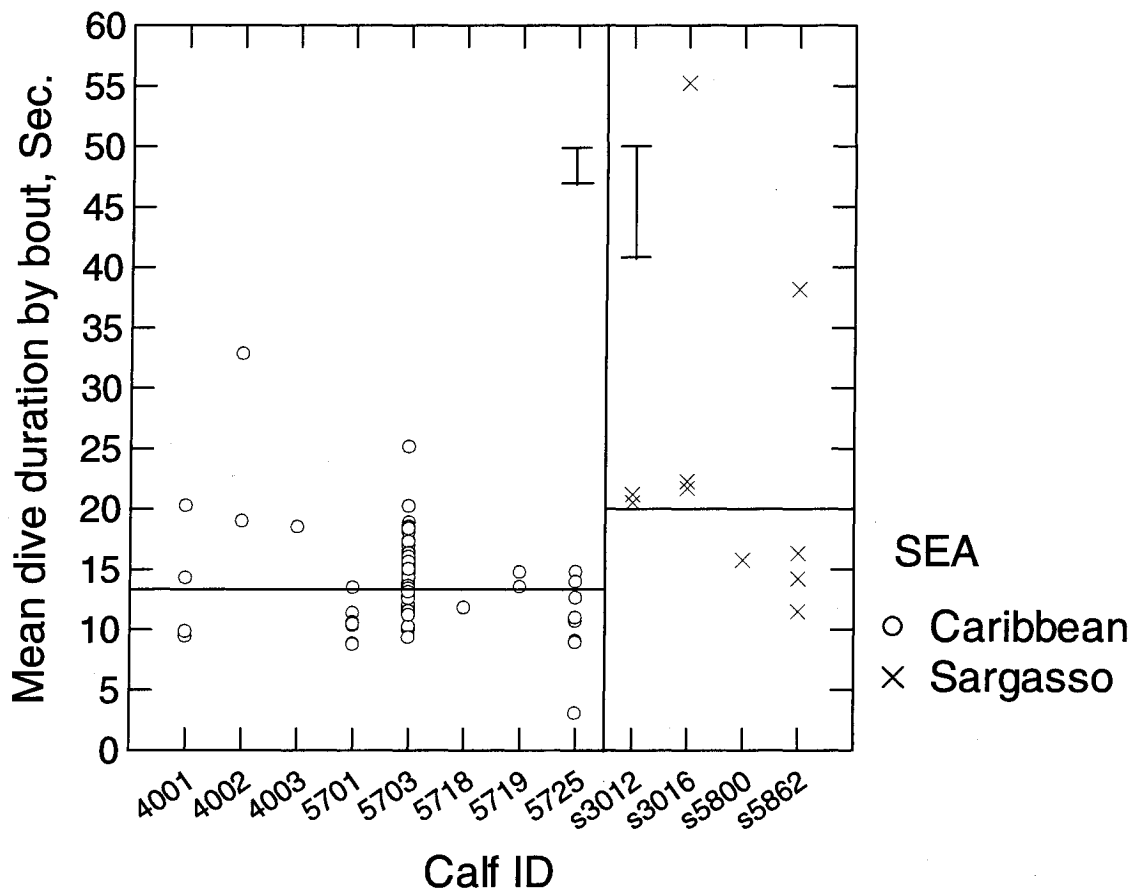


Figure 2-2: Plot of mean peduncle dive duration per bout for all sperm whale calves from both seas. Mean peduncle dive duration for each study area is shown as a horizontal line. The mean standard deviations within all bout means from each study area are shown as error bars near the top of the plot.

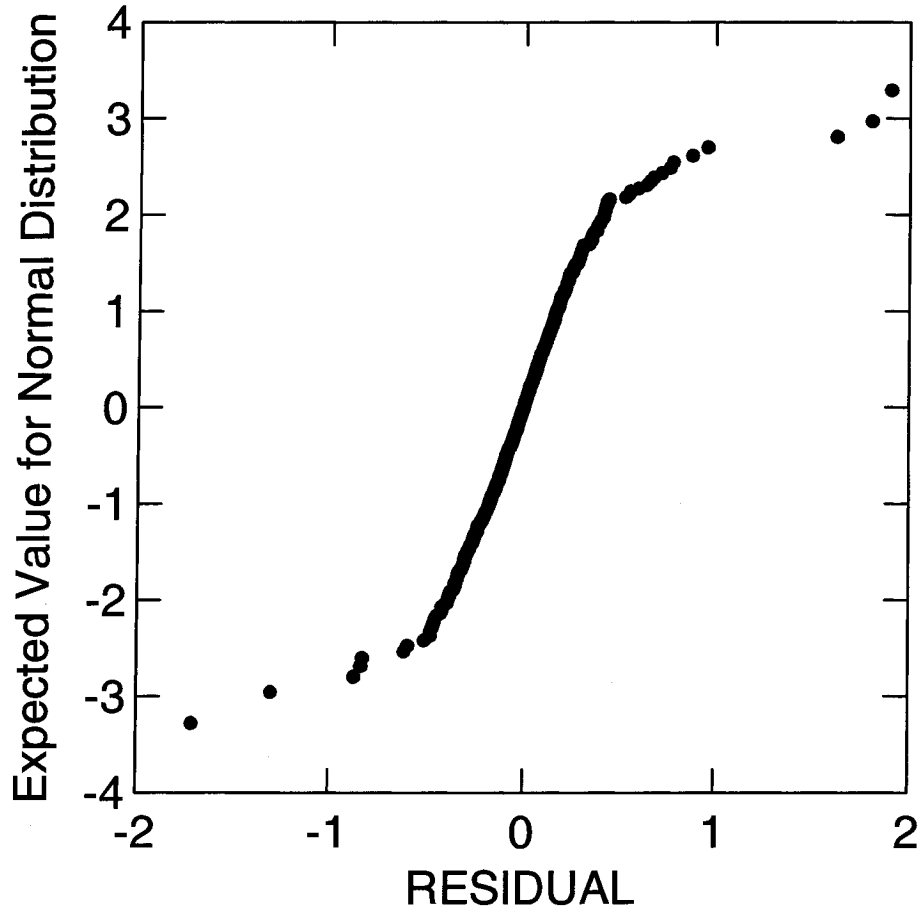
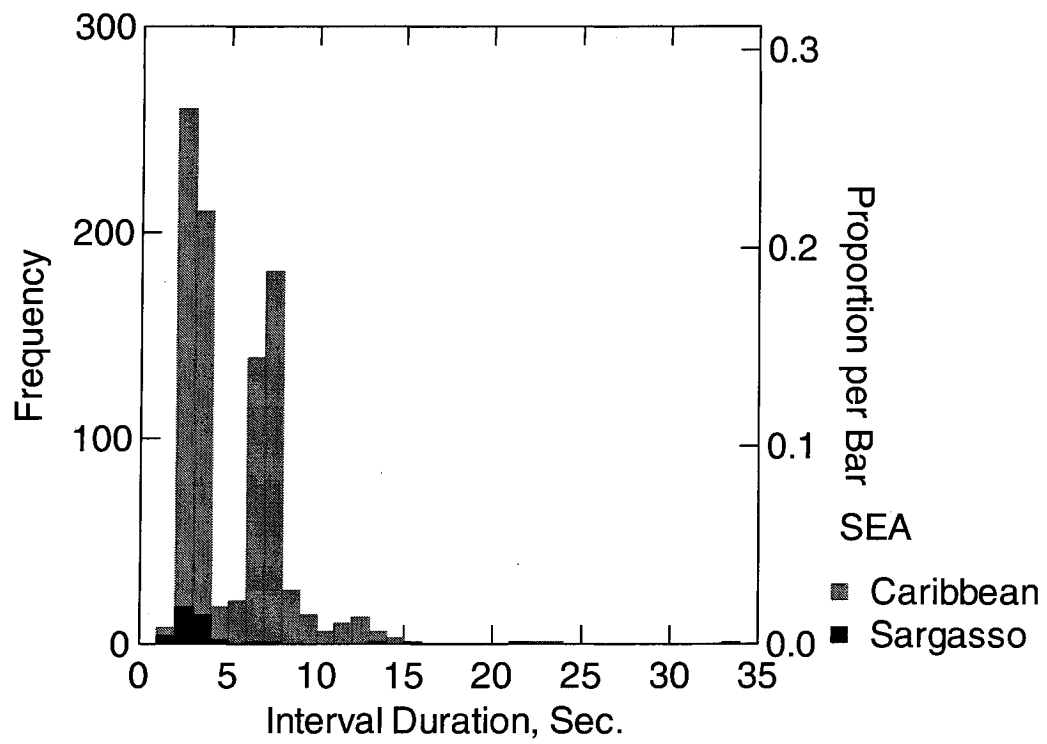


Figure 2-3: Normal probability plot of the residuals of the logged peduncle dive duration data.



**Figure 2-4: Histogram of surface interval between peduncle dives in seconds. The bimodal distribution is explained by intervals in which sperm whale calves took one or two breaths.**



## DIVE SIDE

During the great majority of bouts (89.2%), dive side was consistent throughout the bout. One would expect that if the side on which calves dove was random that the percentages of bouts on each side would be equal (50% : 50%). Most of the consistent peduncle dive bouts took place entirely on the left side of the nursing escort (69.8%), with relatively fewer occurring entirely on the right side (19.4%). When the large amount of data from calf '5703' was excluded percentages were closer to what one would expect as random, but still biased towards the left side (52.7% left; 33.3% right). Calf '5703' shows a clear preference for left-sided peduncle diving, as do calves '5725', '4001', '3002', '3016' and '3005'. Two calves show a preference to the right side ('5701' and '5862'; Table 2-3).

**Table 2-3: Proportion of peduncle dive bouts that were consistent or switch and their corresponding side. 'N' is the number of bouts observed per individual.**

Study Area	Calf ID	N	% Consistent	% Left	% Right	% Switched	% Left → Right	% Right → Left	% ≥1 switch
Caribbean	5703	82	91.5	81.7	9.8	8.5	6.1	2.4	0
	5725	13	100	92.3	7.7	0	0	0	0
	5701	7	100	0	100	0	0	0	0
	4002	6	33.3	0	33.3	66.6	16.6	50.0	0
	4001	5	80	80	0	20	20	0	0
	5718	3	33.3	0	33.3	66.6	33.3	33.3	0
	All	116	88.0	71.6	16.4	12.0	6.9	5.1	0
	Excluding '5703'	34	79.4	47.0	32.4	20.6	8.8	11.8	0
Sargasso	3012	5	100	60	40	0	0	0	0
	3002	4	100	100	0	0	0	0	0
	5862	4	100	0	100	0	0	0	0
	3009	4	100	50	50	0	0	0	0
	3016	3	100	100	0	0	0	0	0
	3005	3	66.6	100	0	33.3	33.3	0	0
	All	23	95.7	60.9	34.8	4.3	4.3	0	0
Both	All	139	89.2	69.8	19.4	10.8	6.5	4.3	0
	Excluding '5703'	57	86.0	52.7	33.3	14.0	7.0	7.0	0

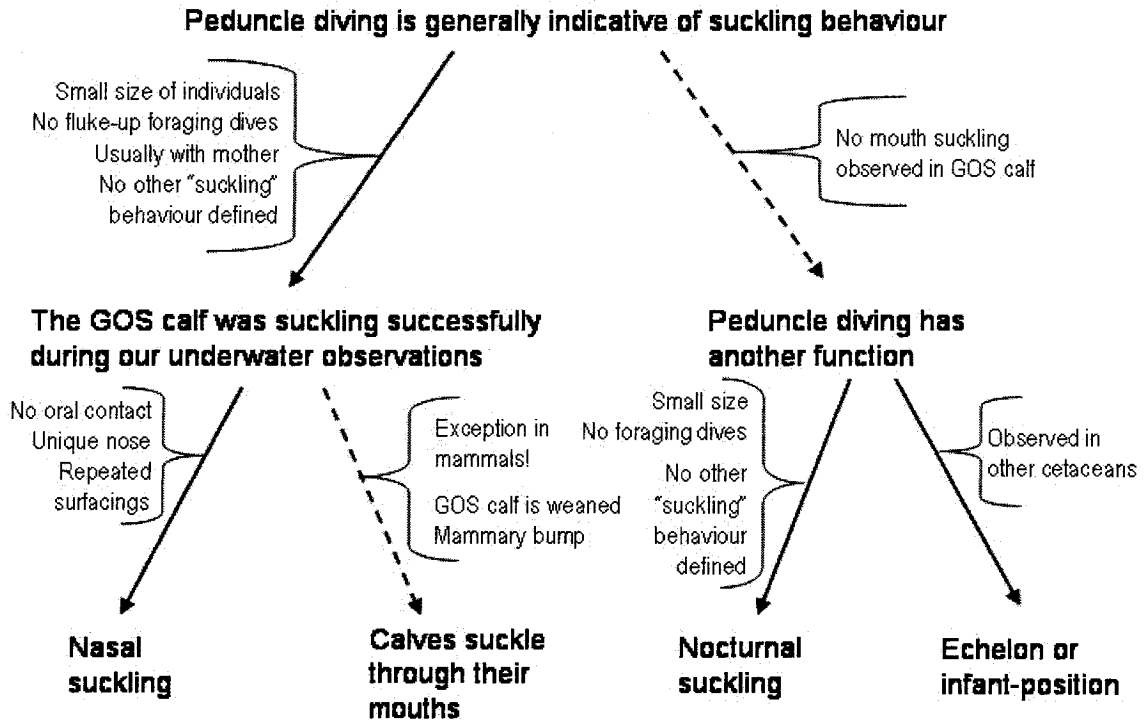
Switching sides during a bout of peduncle dives appears to be a relatively rare behaviour, accounting for 10.8% of all suckling bouts (14% when excluding '5703'). None of the animals included in this analysis switched sides more than once per bout (Table 2-3, previous page). I did observe one calf in the Caribbean who switched from the left side to the right and then back within a single bout, but this animal was excluded from this analysis because it was only identified once.

The mean dive-duration of all left side peduncle dives was 14.2 (SD = 6.34) and the mean dive on the right side was 14.0 seconds (SD = 7.77) in length. There was no difference in mean dive-duration between sides ( $t = 0.441$ ,  $df = 290.1$ ,  $p = 0.682$ ).

## **DISCUSSION**

This is the first attempt at describing quantitatively what has been assumed to be suckling behaviour of sperm whales calves. I have examined peduncle diving behaviour in both the Caribbean and Sargasso Seas, showing that peduncle dives vary in duration between study areas and certain animals prefer to make peduncle dives on a particular side. It is clear that more work is required in order to achieve a full and detailed ethogram of calf behaviour.

No observations were made while in either study area that would support the observations of surface suckling described by Best et al. (1984). As in previous work (Gordon 1987), it was assumed that suckling was occurring based on above-water observations of repeated peduncle dives beside an escort. Gordon (1987) makes a point of stating that such behavioural observations must be treated with caution. I agree, as I was unable to determine whether the calves were successfully acquiring milk from the escort or attempting to do so and failing when performing this supposed suckling behaviour.



**Figure 2-5: How the different hypotheses on the method in which sperm whale calves suckle are derived from current evidence. Solid arrows indicate the above statement is true; dashed arrows that the above statement is false. Evidence supporting each path is presented in a bracket connected to the arrow.**

During the underwater observations, I did not observe a single peduncle dive in which the calf attempted to make contact with the mother's nipple with its mouth. As such, no supporting evidence was found during this study for Gordon's (1987) description of holding the mother's nipple in the gape of the jaw in order to suckle. This begs the question, does the surface behaviour (many short dives beneath the peduncle of the escorting adult) described in Gordon (1987) generally indicate suckling? To begin our analysis of this question (Figure 2-6) let us first assume that the peduncle diving behaviour is not suckling behaviour. If this is the case, what was observed was a different behaviour having a different function. It is possible that the calf may have been

attempting to maintain some form of echelon or infant-position as described in bottlenose dolphins, *Tursiops* sp. (Reid et al. 1995; Gubbins et al. 1999; Mann and Smuts 1999) through the peduncle diving and the calf may have been suckling overnight when this behaviour was impossible to observe. However, additional evidence would suggest that peduncle dives are in fact suckling behaviour. As mammals, suckling must invariably occur for calves to survive and the peduncle diving behaviour is the only act described that is performed solely by animals within the size range one would expect suckling to occur (see Best et al. 1984). Additionally, the social evidence that peduncle diving occur mostly with one particular adult and occasionally with other females would suggest that calves are suckling primarily from their mothers and occasionally from allomothers. In the case of the GOS calf, peduncle diving was only observed with one adult member of its group, presumably the mother, although it was observed grouped with other adult females on many occasions.

These points all support Gordon's (1987) assumption that repeated peduncle dives are generally indicative of suckling behaviour. Nonetheless there is a lack of underwater observations of the GOS calf attempting to make oral contact with the escort's nipples. There are a number of reasons why the GOS calf was suckling unsuccessfully. Two potential explanations are: (1) The calf might have been attempting to initiate suckling by stimulating the female using a behaviour similar to the mammary bump in Atlantic spotted dolphins (*Stenella frontalis*) but not succeeding (Miles and Herzing 2003); and (2) The calf may have been near weaning age and no longer receiving much if any milk from the mother, but was still making attempts to instigate milk production using its nose.

However, it is extremely unlikely that a sperm whale calf estimated to be 3 months old based on its size has already been weaned

Alternatively, successful “suckling” may have occurred during my underwater observations, but through the nasal passage rather than the mouth. As our observations suggest, sperm whale calves may suckle by placing their blowhole to their escort’s nipple. If this were to be true this would be a method novel to mammals. Although seemingly unlikely, it may be anatomically possible as sperm whales may have a unique ability to take in fluids through their blowhole (Clarke 1970; Clarke 1978). The need to force the milk down to the oesophagus from the sinuses when nasal suckling could explain why sperm whale calves repeatedly surface for air between short “suckling” dives, unlike in bottlenose dolphins (*Tursiops* sp.) which do not surface between bouts of suckling (Mann and Smuts 1999). We must treat this hypothesis with caution because the data was collected over a sixth (4 months) of the period over which sperm whale calves suckle (~2 years, Rice 1989) and primarily from one calf. It is also important to note that other than the evidence which supports the assumption that both Gordon (1987) and I make that peduncle diving likely indicates suckling, the unique anatomy of the sperm whale nose, and the behavioural evidence presented here suggesting blowhole contact with the escort’s genitals, we provide no conclusive evidence that milk was being transferred from the escort to the calf via the nasal passage.

Whether milk was being received or not, individual sperm whale calves showed a preference to making peduncle dives from a particular side of the escort. Lateral asymmetries of behaviour are common in both humans and non-human primates (reviewed in Springer and Deutsch 1989; Bradshaw and Rogers 1993; Hopkins and

Morris 1993). Behavioural asymmetries have also been identified in other cetaceans (Kasuya and Rice 1970; Hoese 1971; Caldwell and Project 1993; Clapham et al. 1995; Marino and Stowe 1997). In relation to food acquisition, Clapham and colleagues (1995) and Kasuya and Rice (1970) suggest a strong population-level right-side bias in bottom-feeding in humpback whales (*Megaptera novaeangliae*) and gray whales (*Eschrichtius robustus*), respectively. This study finds a left-side bias in suckling attempts in sperm whales in both study areas. Rizhova and Kokorina (Rizhova and Kokorina 2005) suggest that the presentation of food to cows from the left-side improves lactation. It is possible that the lateral asymmetry observed here may be a result of a similar response in female sperm whales to calves peduncle diving on the left-side; however, the duration of a given peduncle dive did not differ between sides as one might expect if there was increased lactation on the left side.

Although there was no difference between sides, a significant difference in duration of peduncle dives between study areas was discovered. There appears to be a significant amount of variation in dive duration, between an individual's bouts and between individuals. Therefore, differences in peduncle dive duration between areas are likely affected by small sample sizes in the Sargasso Sea. Nonetheless, several biological factors may also determine dive duration. The most likely is that the calves differed in age, and as such suckled for different amounts of time. Alternatively, as shall be discussed in chapter three of this text, calves in the Sargasso Sea show peduncle diving behaviours with multiple escorts, unlike in the Caribbean. It is possible that it takes longer to initiate suckling from allomothers than from a calf's mother, and as a result peduncle dive durations are a few seconds longer in the Sargasso population. Finally, if

calves are in fact attempting to maintain some form of echelon or baby position in order to facilitate swimming (Norris and Prescott 1961; Mann and Smuts 1999), this may be more important in the open pelagic habitat of the Sargasso as compared to the semi-protected coastal habitat surrounding the island of Dominica in the Caribbean.

## **CONCLUSIONS**

This study has laid the groundwork for the development of a complete ethogram of sperm whale calf behaviours. It was the first to focus on the details of calf behaviour in sperm whales and has discovered a behavioural asymmetry and population differences in calf peduncle diving behaviour which is thought to be indicative of suckling. Although this study set out to resolve the confusion surrounding the method in which sperm whales suckle, it would appear that it has only added to the debate. Our findings suggest that either sperm whales are suckling significantly less than originally estimated using above-water observations of peduncle dives, or they are suckling using methods which seem physiologically unlikely. Further underwater observations of calf behaviours are required in order to answer these questions.

## **CHAPTER THREE :**

Who cares? Between-group variation in alloparental care-giving in sperm whales



## INTRODUCTION

Parental care of offspring is so common among mammals that it is the exceptions and variations that attract our attention (Klopfer 1981; Riedman 1982). Since many mammals only bear one offspring at a time, its survival is critical to the fitness of its parents. In the vast majority of mammals, mothers provide virtually all of the care for the young (Kleiman and Malcolm 1981; Clutton-Brock 1991; Reeve and Shellman-Reeve 1997). In a few species, paternal care is present (Kleiman and Malcolm 1981; Whitten 1987; Woodroffe and Vincent 1994), and in very few, alloparental care is provided by animals other than the parents (Riedman 1982; Jennions and MacDonald 1994).

Allocare can be defined as any behaviour by a non-parent which benefits the young and which would not be performed outside the presence of the young (Woodroffe and Vincent 1994). Alloparental behaviours within mammalian groups vary along a spectrum of investment by the alloparent. At the lower end are behaviours categorized as indirect, in which the alloparent does not interact directly with the young (e.g. territorial defence, herding movements, and protection via increased vigilance over young). Direct allocare behaviours, in which the alloparent actively interacts with the young (e.g. carrying, grooming, babysitting, provisioning, and adoption) are at the opposite end of the spectrum (Lewis and Pusey 1997). Alloparental care of both types is widely known and has been described in primates (reviewed in Nicolson 1987), rodents (reviewed in Mayer 1983), and carnivores (reviewed in MacDonald and Moehlman 1982); however, little is known about the existence of alloparental care in cetaceans (Anderson 1969; Haenel 1986; Johnson and Norris 1994; Whitehead 1996; Mann and Smuts 1998).

Sperm whales have an interesting form of alloparental behaviour. Unlike other dependent cetacean calves, young sperm whales do not consistently remain with only one adult female. Each calf shows a particularly strong association with one adult, presumably its mother, but also associates with other adults or subadults of both sexes while the mother is submerged during lengthy foraging dives (Best et al. 1984; Gordon 1987; Arnborn and Whitehead 1989; Whitehead 1996). The best data on sperm whale babysitting originates from the first study on living sperm whales which took place off Sri Lanka (Gordon 1987). Gordon (1987) followed a total of six calves over several days and found that they were escorted by 7 – 12 different adults. In one case, the calf appeared to make suckling attempts from two different adults. Similar patterns of escorting were observed off the Galapagos Islands, where calves were seen being escorted by different adults over the course of a day (Arnborn and Whitehead 1989); and off Dominica in the West Indies, where three different adults escorted one calf for extended periods of time over one afternoon (Gordon et al. 1998). Since calves do not dive deep and forage with their mothers and group members, babysitting in sperm whales has been hypothesized to provide greater foraging freedom to the mother while providing protection at the surface for the calf (Gordon 1987; Whitehead 1996).

Under Woodroffe and Vincent's (1994) definition of alloparental behaviour not only does the alloparental behaviour need to benefit the young, but it must only be performed in the presence of calves. To test this definition in sperm whales, Whitehead (1996) looked for differences in observable behaviour between groups with and without calves. He found differences in dive synchronicity between the groups suggesting that the dive behaviour of not only the mother, but all individuals in the group, changes with the presence of a

calf, such that there is more frequently an adult at the surface to accompany the calf (Whitehead 1996). Whitehead (1996) points out that this form of alloparental care is not necessarily altruistic since subtle changes in the scheduling of foraging dives are unlikely to have much effect on foraging success.

Kin selection (Hamilton 1964), or reciprocal altruism (Trivers 1971), have been suggested as evolutionary mechanisms behind the existence of the babysitting behaviours in mammals (Emlen 1991). Although a system of babysitting has been identified in sperm whales (Whitehead 1996), my study is the first to elucidate the identity of sperm whale caregivers and their relationship to the calves. Photo-identification, behavioural calf-follows, and common social analytical techniques were used to draw up matrices of association and interaction for adults and calves. I compared patterns of adult-infant interaction of 22 sperm whale calves in both the Sargasso and Caribbean Seas in order to determine whether these more basic explanations of kin or reciprocal based babysitting are sufficient to explain the evolution and maintenance of babysitting in sperm whales or whether there exists a more complex communal, multimodal system of babysitting, as is indicated by studies of association among adult females (Christal and Whitehead 2001).

## **METHODS**

### **FIELD METHODS**

See chapter two for a complete description of field methods. As in chapter two, suckling attempts were defined as repeated dives beneath the peduncle of adult whales (as in Gordon et al. 1998), but see chapter two for some possible reservations about this. In this chapter an additional clarification is needed. I defined allosuckling as a situation in which the calf was attempting to suckle from a female who was not its presumed mother,

and allonursing as the acts performed by an adult female who appeared to be providing milk to a calf other than her own.

## ANALYSES

### *Identifications*

Animals were identified as in Chapter II. The only additional photoidentification analysis was that the best identification photograph for each individual was also matched to the North American Sperm Whale Catalogue (NAMSC, curated by the International Fund for Animal Welfare). Of particular interest were the photo-identifications collected during trips made by *R/V Song of the Whale* (IFAW) in 1995 and 1996 as this work took place in the same Caribbean study area, off Dominica (Gordon et al. 1998). Long-term comparisons of this type would allow us easily to attribute individuals to social units, as resightings over a decade are direct evidence of a long-term bond between individuals.

### *Defining Groups*

All individuals identified during one day were assumed to be from the same group (Whitehead et al. 1991; Christal et al. 1998; Whitehead 1999; Coakes and Whitehead 2004; Whitehead and Rendell 2004). In order to determine whether groups were the same on different days, I used the same methods as in previous work (Weilgart and Whitehead 1997; Whitehead et al. 1998; Whitehead 1999; Coakes and Whitehead 2004); the cut-off similarity was set such that days were classified as the same group if at least 50% of animals identified on the day with the fewest identifications were identified on the other day.

Group size for a particular day was estimated using the identification data. Observed group size was determined as in Coakes and Whitehead (2004) and Whitehead

(2003); by dividing a given day's identifications into two sets, and then using a Petersen mark-recapture estimator to determine the number of individuals present. Typical group size was then derived from those estimates as in Coakes and Whitehead (2004).

"Typical" group size is an approximation of group size as experienced by a randomly chosen member of the population as opposed to the outside observer (Jarman 1974).

### *Defining Associations*

To identify intra-group associations, individuals were deemed to be associating if they were within the same cluster at the surface. Individuals were considered to be in the same cluster if they were within approximately 3 adult-body lengths (~40m) from any other cluster member and were coordinating their behaviour (Whitehead 2003). I used the "Half-Weight Index" (HWI) as a measure of association as it accounts best for observer biases inherent in photo-identification techniques (Cairns and Schwager 1987) and a 2hr sampling period. Further distinction was needed when defining associations with calves. I defined three hierarchical levels of association: (1) *Associates*, any individual identified within the same day as the calf but who was not necessarily observed in association with the calf; (2) *Escorts*, any individual identified within a cluster which contained the calf (Gordon 1987; Mann and Smuts 1998); and (3) *Mother*, when genetic data were not available, the mother was assumed to be the mature female escort with which the calf spent the majority of its time and thus had the highest HWI value (Gordon 1987; Whitehead 1996).

I identified an escort as having a preferred association with the calf when its association index was twice the mean index of all dyads in the group being considered for the analysis (Durrell et al. 2004) and a preferred avoidance when it was below half that

mean. These threshold values were chosen because they were approximately twice (in the case of preferred associations), or half (in the case of preferred avoidances), the value that one would expect if associations were completely random. One must be cautious in using the terms preference and avoidance as these analyses do not necessarily show that two individuals are actively drawn together or repelled from one another, there may in fact be other behaviours which make a dyad more or less likely to associate. In this case, these terms may be justified as babysitting and allomothering behaviours may draw two particular individuals together. However, it is important to note that these preferred associations or avoidances may be of three types: (1) mutualistic, in which both parties show similar tendencies, (2) unidirectional, in which only one party shows a preference or avoidance and the other shows indifference or the opposing tendency. This may be the case in which certain animals show an attraction to a class of animals, in this case calves, or to the role of babysitter, but not to the particular calf with which it is associated, and (3) obligate, in which neither party prefers the other, but the association is necessary. For example, the individual who performs the role of babysitter associates with calves regardless of their identity.

When data were sufficient, a permutation test as in Bejder *et al.* (1998) with modifications as in Whitehead *et al.* (2005) was used to test whether calves had preferred/avoided associations with adults against the null hypotheses that calves associate randomly with all adults except the mother. A rectangular portion of the association matrix (calves on one axis and adults on the other) was randomized 40 000 times with 100 flips per permutation for each analysis.

### *Long-term comparisons*

Mantel tests (Mantel 1967; Schnell et al. 1985) and matrix correlation coefficients between the elements of the association matrices of the most studied social unit for the 1995-1996 seasons and the 2005 season were calculated in order to determine whether the association indices were correlated between seasons or if patterns of association have changed over a decade. The statistical significance of each Mantel test was tested against a null hypothesis in which the dyadic HWI in one time period was unrelated to the HWI of the same dyad in the other, using 1000 random permutations (as suggested by Schnell et al. 1985). The Hemelrijk Rr-test (Hemelrijk 1990), a Mantel test variant which ranks values within rows, was used to test similarity in the dyadic associations in the two periods, controlling for changes in individual sociability. The calculation of the HWI, the permutation tests described above, and Mantel tests were carried out using *SOCPROG* (2.2, H. Whitehead, Dalhousie University, NS, Canada) in *MATLAB* 6.5 (The Mathworks, Inc. Natick, MA, USA).

### *Feeding Success*

Since feeding success may be a factor which could determine the identity of babysitters, feeding success was compared between study areas using defecation rate (proportion of defecations observed divided by the number of fluke-ups recorded) as a measure of feeding success (Whitehead 1996; Smith and Whitehead 2000; Whitehead and Rendell 2004). As identification photographs were taken when whales began a fluke-up dive, it was noted whether a defecation (a brown patch in the water) was or was not observed or whether it was unknown. Justification for, and possible limitations of, this methodology are discussed by Whitehead (1996).

## RESULTS

Encounters off Dominica were dominated by the nearly continuous presence of one particular social unit, “The Group of Seven” (GOS, encountered on 40 different days over a 54 day period), consisting of five adult females, one juvenile male (8.8 m, 8-10 years old; T. Schulz, unpublished data) and one male calf (4.5 m, ~3 months old; length measurement for the calf was determined using photographs with a fixed focal length from the crow’s nest on the mast of the sailing vessel and the age based on growth curve from Figure 10 of Best et al. 1984). Sexes of these individuals were determined by an ongoing genetic analysis (D. Engelhaupt, unpublished data). There were fewer data (ranging between 1 and 9 days) for the remaining 22 calves (10 Caribbean, 12 Sargasso), in 11 groups (6 Caribbean, 5 Sargasso) to compare and contrast with patterns observed in the detailed results of the GOS unit.

### PATTERNS OF ALLOCARE

#### *Group of Seven*

Significantly high and low intra-group associations were identified among the adults in the GOS unit, since the coefficients of variation of the observed HWIs were significantly larger than values obtained from randomly permuted data (observed CV = 0.76; random CV = 0.42;  $p < 0.0001$ ).

Suckling attempts by the GOS calf were observed only with one particular adult, presumably the mother (5722). The GOS calf was escorted by all six other unit-members, but preferentially escorted by only one non-parent, ‘5561’ (Table 3-1, following page). The mother showed a similar pattern of avoidance and association, avoiding all other unit members other than ‘5561’. The preferred escort, or “babysitter” (‘5561’), had the



highest mean HWI with other members of the group whether the calf was included or excluded (Table 3-1). If not with the mother or the preferred escort, the calf was most likely to be escorted by the only juvenile in the group, followed by the rest of the adult females in the social group.

**Table 3-1: Association matrix of HWI for the ‘Group of Seven’ in 2005. Individuals are listed in order of descending strength of dyadic HWI with the calf and labelled with letters denoting their relationship with the calf or age class (C – calf, M - presumed mother, B – “babysitter”, A – adult female, and J – juvenile male). The final column is the mean HWI for each individual when the calf is excluded.**

	5703 (C)	5722 (M)	5561 (B)	5727 (J)	5560 (A)	5130 (A)	5563 (A)	Mean HWI	Mean No Calf
5703 (C)	1	0.97 <sup>+</sup>	0.48 <sup>+</sup>	0.35	0.29	0.13 <sup>-</sup>	0.13 <sup>-</sup>	0.39	n/a
5722 (M)	0.97 <sup>+</sup>	1	0.17	0.06 <sup>-</sup>	0.12 <sup>-</sup>	0.04 <sup>-</sup>	0.07 <sup>-</sup>	0.23	0.09
5561 (B)	0.48 <sup>+</sup>	0.17	1	0.32	0.29	0.27	0.33	0.31	0.28
5727 (J)	0.35	0.06 <sup>-</sup>	0.32	1	0.53 <sup>+</sup>	0.11 <sup>-</sup>	0.07 <sup>-</sup>	0.24	0.22
5560 (A)	0.29	0.12 <sup>-</sup>	0.29	0.53 <sup>+</sup>	1	0.18	0.07 <sup>-</sup>	0.25	0.24
5130 (A)	0.13 <sup>-</sup>	0.04 <sup>-</sup>	0.27	0.11 <sup>-</sup>	0.18	1	0.09 <sup>-</sup>	0.14	0.14
5563 (A)	0.13 <sup>-</sup>	0.07 <sup>-</sup>	0.33	0.07 <sup>-</sup>	0.07 <sup>-</sup>	0.09 <sup>-</sup>	1	0.13	0.13

<sup>+</sup> preferential association (COA > twice the mean HWI)

<sup>-</sup> preferential avoidance (COA < half the mean HWI)

Other than a statistically significant preferred association between the juvenile (‘5727’) and one of the adult females (‘5560’), most associations among adult females in the GOS were preferred avoidances (Table 3-1). The babysitter (‘5561’) was the exception to this trend. None of the dyadic bonds between ‘5561’ and other adults were preferred associations or avoidances. Female ‘5561’, the babysitter and most sociable adult in the group, associated approximately evenly with the other adults. Her weakest association was with the calf’s mother (‘5722’), but interestingly, she was the strongest associate of the mother, the least sociable member of the group, when her calf is excluded (Table 3-1).

Comparison to NAMSC revealed that all five adult females of the GOS were seen together by *R/V Song of the Whale* on 14 different days in 1995 and again on 5 days in 1996 in waters off Dominica (Gordon et al. 1998). This long-term match links these individuals over 10 years, allowing us to define them as constant companions and members of the same social unit (Whitehead et al. 1991; Christal et al. 1998), and indicates long-term use of the study area by these whales.

Patterns of escorting were similar between time periods. In 1995 and 1996, the babysitter ('5561') was observed in 22 clusters, 16 of which were with calves. This is almost three times as often as the other four females who on average were only seen with calves in 25% of their clusters (observed in 9-20 clusters, with a calf in 1-6 clusters). The babysitter ('5561') was the only individual to be observed in a cluster with a calf in 1996. It is unknown whether the calf in this unit was the juvenile ('5727') with whom they were associated during our 2005 fieldwork. Length and age estimates from a concurrent study obtained using the interpulse-interval of the juvenile's usual clicks (Gordon 1991; Goold 1996) suggest that it is possible if the calf was very young during the 1995 and 1996 seasons, although it is likely that the juvenile male in 2005 was less than 10 years old (using the age-length key of Goold 1996). Suckling attempts were not consistently recorded during the 1995-1996 study and as such it was not possible to compare between time periods.

Patterns of association between adult unit members in the 1995-1996 seasons (Table 3-2, following page) and the 2005 fieldwork (Table 3-1) differed in some respects. Three individuals ('20001', '20002', and '20007') which were not seen in 2005 were observed with the five GOS adults both in 1995 and 1996. These three animals were the

least sociable of the eight (Table 3-2). For the five adults seen in 1995-6 and 2005, matrix correlations, Mantel and Rr tests gave no indication that there were similarities in the patterns of association between periods (Mantel test matrix correlation = -0.10,  $p = 0.61$ ; Rr test matrix correlation = 0.02,  $p = 0.49$ ).

**Table 3-2: Association matrix of HWI for the ‘Group of Seven’ adults and their associates sighted in 1995 and 1996. Individuals are labelled with letters denoting their relationship with the calf during the 2005 season (M - presumed mother, B – babysitter, I – identified with calf in 2005, NI – not identified with calf in 2005). The final column is the mean HWI for each individual when only animals identified in 2005 are included.**

	5722	5561	5560	5130	5563	20001	20002	20007	Mean	Mean 2005
	(M)	(B)	(I)	(I)	(I)	(NI)	(NI)	(NI)	HWI	Adults Only
5722 (M)	1	0.43	0.50 <sup>+</sup>	0.11 <sup>-</sup>	0.24	0.19	0 <sup>-</sup>	0.22	0.24	0.32
5561 (B)	0.43	1	0.26	0.10 <sup>-</sup>	0.20	0.08 <sup>-</sup>	0.10 <sup>-</sup>	0.29	0.21	0.25
5560 (I)	0.50 <sup>+</sup>	0.26	1	0.33	0.24	0.19	0.24	0.33	0.30	0.33
5130 (I)	0.11 <sup>-</sup>	0.10 <sup>-</sup>	0.33	1	0.27	0.21	0.40	0.25	0.24	0.20
5563 (I)	0.24	0.20	0.24	0.27	1	0.11 <sup>-</sup>	0.29	0.27	0.23	0.24
20001 (NI)	0.19	0.08 <sup>-</sup>	0.19	0.21	0.11 <sup>-</sup>	1	0.33	0.11 <sup>-</sup>	0.17	n/a
20002 (NI)	0 <sup>-</sup>	0.10 <sup>-</sup>	0.24	0.40	0.29	0.33	1	0.13	0.21	n/a
20007 (NI)	0.22	0.29	0.33	0.25	0.27	0.11 <sup>-</sup>	0.13	1	0.23	n/a

<sup>+</sup> preferential association (COA > twice the mean HWI)

<sup>-</sup> preferential avoidance (COA < half the mean HWI)

Overall, unit members were more sociable in 1995-1996. Four females (‘5722’, ‘5563’, ‘5560’, and ‘5130’) had a higher mean HWI in 1995-1996 than in 2005. Female ‘5722’ (the mother in 2005) was more sociable in 1995 and 1996, before her calf was born (2005 mean HWI excluding the calf = 0.09, Table 3-1; 1995-1996 mean HWI = 0.24, 1995-1996 mean HWI GOS only = 0.32, Table 3-2). The exception to this trend was the babysitter, ‘5561’, who was more sociable in 2005 (Table 3-1 and 3-2). In contrast to 2005, ‘5561’ has the lowest mean HWI of all five adults in 1995-1996. The

babysitter and the mother formed a relatively strong association in both time periods; however, the babysitter was not the mother's strongest associate in 1995-1996. The mother formed a preferred association with female '5560', which contrasts with the 2005 data in which the mother did not show any preferred associations.

#### *Caribbean Calves*

As in the detailed follow of the GOS, allosuckling was not observed during any follows of the other ten calves observed off Dominica. Patterns of association are also consistent with the GOS. Calves were observed suckling from a single adult by whom they were most often escorted (Table 3-1). They were otherwise generally escorted by a preferred escort. Other mothers in the group and their calves (if more than one calf was present), and other adult females were secondary and tertiary escorts, respectively. Table 3-3, on page 44, summarizes escorting patterns for all Caribbean calves.

#### *Sargasso Calves*

In contrast to the Caribbean Sea, in the Sargasso allosuckling was observed in follows of 7 different calves ('3002', '3005', '3006', '3012', '5862', '3016', '3009'; Table 3-4, page 46-47). In the case of Group 5, two adults were each observed nursing two different calves ('5807', '5808' with calves '3002', '3005'; Table 3-4). All other nursing escorts were observed nursing only one calf, even if more than one was present in the group (Table 3-4). Calves did not show a preference for a particular nursing escort within days, such that calves were not suckling from just one escort on one day and just another the next.

**Table 3-3: Summary of escorts by sperm whale calves from the Caribbean Sea, listed in order of descending strength of dyadic HWI with the calf. In all cases, the presumed mother had the highest dyadic HWI with the calf and was the only individual from whom the calf suckled. Nursing females are marked with an ‘N’ and the number of times the calf was observed suckling. The number of different days each group was observed and the number of identified individuals in the group are shown. Sexes determined by an ongoing genetic analysis (D. Engelhaupt, unpublished data) are noted in subscript after the ID number.**

<b>Unit</b>	<b>Calf</b>	<b>Mother</b>	<b>Escorts</b>	<b>Associates</b>	
<b>GOS</b> Days: 40 Individuals: 7	5703 <sub>M</sub>	5722 <sub>F</sub> <sup>++</sup> (N:95)	5561 <sub>F</sub> <sup>++*</sup>	None	
			5727 <sub>M</sub> <sup>*</sup>		
			5560 <sub>F</sub> <sup>*</sup>		
			5130 <sub>F</sub> <sup>-*</sup>		
<b>SSQ</b> Days: 9 Individuals: 6	5725	5724 <sup>++</sup> (N:13)	5726 <sup>+</sup>	5742	
			4001		
			5759		
			4001	5759 <sup>++</sup> (N:5)	5725
<b>ATW</b> Days: 3 Individuals: 11	4002	5723 <sup>+</sup> (N:7)	5586 <sup>++</sup>	5710 <sup>*</sup>	5713
			5720 <sup>+</sup>	5711	5714
			5719 <sup>+</sup>	5712	5721
			5719	5720 <sup>+</sup> (N:3)	5586 <sup>+</sup>
<b>WIN</b> Days: 3 Individuals: 4	5701	5163 <sup>+</sup> (N:9)	5723 <sup>+</sup>	5711	5714
			4002 <sup>+</sup>	5712	5721
			5698	5699 <sup>*</sup>	
<b>OOP</b> Days: 1 Individuals: 6	5718	5138 <sup>+</sup> (N:3)	5716 <sup>+</sup>	5137	
				5715	
				5717	
<b>OF4</b> Days: 1 Individuals: 9	4003	5745 <sup>+</sup> (N:3)	5744 <sup>+</sup>	5743	5748
			4004 <sup>+</sup>	5746	5749
				5747	
	4004	5746 <sup>+</sup> (N:1)	5748 <sup>+</sup>	5743	5747
			4003 <sup>+</sup>	5744	5749
				5745	
5747	5748 <sup>+</sup> (N:2)	None		4003	5745
				4004	5746
				5743	5749
				5744	
<b>MAR</b> Days: 1 Individuals: 8	4005	5733 <sup>+</sup> (N:2)	None	5728	5731
				5729	5732
				5730	5734

<sup>+</sup> preferential association (COA > twice the mean HWI)

<sup>-</sup> preferential avoidance (COA < half the mean HWI)

<sup>\*</sup> statistically significant based on permutation tests

General patterns in strength of association with escorts were similar between sites. Due to a lack of genetic data and multiple nursing escorts, it is difficult for us to even presume which female is the calf's mother. However, in all cases, nursing escorts were the individuals with the strongest preferred association with the calves, followed by nursing escorts of other calves, their calves, and finally other adult females in the group (Table 3-4).

Clusters including the calf were significantly larger in the Sargasso (Sargasso mean = 2.96; Caribbean mean = 1.96;  $t = -5.25$ ;  $df = 165.2$ ;  $p < 0.0001$ ). On average a calf in the Sargasso was escorted by two escorts while only one was present in the Caribbean. Typical group size estimates were twice as large in the Sargasso as compared to the Caribbean (Table 3-5, page 48). Values were similar using two different levels of precision of cut-off for group sizes to be included ( $CV < 0.25$  or  $< 0.40$ ) and when the data were divided using two different methods (at midday or  $\frac{1}{2}$  of the identifications on a given day, as in Coakes and Whitehead 2004). Finally, defecation rate, used here as a proxy for feeding success, was almost twice as high in the Caribbean as in the Sargasso (Caribbean = 29.8%, Sargasso = 16.2%).

**Table 3-4: Summary of escorts by sperm whale calves from the Sargasso Sea, listed in order of descending strength of dyadic HWI with the calf. Nursing females are marked with an ‘N’ and the number of times the calf was observed suckling. All nursing escorts had the highest dyadic HWI with the calf, with the exception of Calf #3016 where a non-nursing escort was highest, followed by the two nursing escorts and the rest of the non-nursing escorts. The number of different days each group was observed and the number of identified individuals in the group are shown. Sexes determined by an ongoing genetic analysis (D. Engelhaupt, unpublished data) are noted in subscript after the ID number.**

Group	Calf	Nursers	Escorts	Escorts & Nursers	Associates	
5 Days: 4 Individuals: 32	3002	5808 <sup>+</sup> * (N:2)	5809 <sub>M</sub> <sup>+</sup>	5808 <sup>+</sup> * (N:2)	3006 5818 5827 <sub>F</sub>	
		5810 <sup>+</sup> (N:2)	5823 <sup>+</sup>	5810 <sup>+</sup> (N:2)	5811 5819 5828	
		5807 <sup>+</sup> (N:1)	5806 <sup>+</sup>	5807 <sup>+</sup> (N:1)	5812 5820 5829 <sub>F</sub>	
			3005 <sup>+</sup>	5809 <sub>M</sub> <sup>+</sup>	5813 5821 5830	
				5823 <sup>+</sup>	5814 5822 5831	
				5806 <sup>+</sup>	5815 5824 5832	
			3005 <sup>+</sup>	5816 5825 5833		
				5817 5826 5869		
		3005	5817 <sup>+</sup> * (N:1)	5819 <sup>+</sup>	5817 <sup>+</sup> * (N:1)	3006 5816 5827 <sub>F</sub>
			5808 <sup>+</sup> (N:1)	3002 <sup>+</sup>	5808 <sup>+</sup> (N:1)	5806 5818 5828
			5807 <sup>+</sup> (N:1)		5819 <sup>+</sup>	5809 <sub>M</sub> 5820 5829 <sub>F</sub>
					5807 <sup>+</sup> (N:1)	5810 5821 5830
				3002 <sup>+</sup>	5811 5822 5831	
					5812 5823 5832	
				5813 5824 5833		
				5814 5825 5869		
				5815 5826		
	3006	5827 <sub>F</sub> <sup>+</sup> (N:2)	5828 <sup>+</sup>	5828 <sup>+</sup>	3002 5813 5822	
		5830 <sup>+</sup> (N:1)	5824 <sup>+</sup>	5827 <sub>F</sub> <sup>+</sup> (N:2)	3005 5814 5823	
			5832 <sup>+</sup>	5830 <sup>+</sup> (N:1)	5806 5815 5825	
				5824 <sup>+</sup>	5807 5816 5826	
				5832 <sup>+</sup>	5808 5817 5829 <sub>F</sub>	
					5809 <sub>M</sub> 5818 5831	
				5810 5819 5833		
				5811 5820 5869		
				5812 5821		
	5818	5814 <sup>+</sup> * (N:3)	None	5814 <sup>+</sup> * (N:3)	3002 5815 5826	
				3005 5816 5827 <sub>F</sub>		
				3006 5817 5828		
				5806 5818 5829 <sub>F</sub>		
				5807 5819 5830		
				5808 5820 5831		
				5809 <sub>M</sub> 5821 5832		
				5810 5822 5833		
				5811 5823 5869		
				5812 5824		
				5813 5825		

<sup>+</sup> preferential association (COA>twice the mean HWI)

<sup>-</sup> preferential avoidance (COA< half the mean HWI)

\* statistically significant based on permutation tests

**Table 3-4: Summary of escorts by sperm whale calves from the Sargasso Sea continued from the previous page.**

Group	Calf	Nursers	Escorts	Escorts & Nursers	Associates		
<b>10</b> Days: 4 Individuals: 10	3010	5857 <sub>F</sub> <sup>+</sup> (N:1)	None	5857 <sub>F</sub> <sup>+</sup> (N:1)	3012	5854	5858 <sub>F</sub>
					5852 <sup>*</sup>	5855	5859
					5853	5856	
	3012 <sub>F</sub>	5856 <sup>+</sup> (N:2) 5855 <sup>+</sup> (N:2) 5857 <sub>F</sub> <sup>+</sup> (N:1)	5854 <sup>+</sup> 5858 <sub>F</sub> <sup>+</sup> 5859 <sup>+</sup> 5852 <sup>+</sup>	5856 <sup>+</sup> (N:2) 5855 <sup>+</sup> (N:2) 5857 <sub>F</sub> <sup>+</sup> (N:1) 5854 <sup>+</sup> 5858 <sub>F</sub> <sup>+</sup> 5859 <sup>+</sup> 5852 <sup>+</sup>	3010	5853	
<b>11</b> Days: 3 Individuals: 11	3015	5791 <sup>+</sup> (N:2)	5862 <sup>+</sup> 5864 <sup>+</sup> 5789 <sup>+</sup>	5791 <sup>+</sup> (N:2) 5864 <sup>+</sup> 5862 <sup>+</sup> 5789 <sup>+</sup>	3014	5860	5861 <sup>*</sup>
					5792	5863	
	5862	5864 <sup>+</sup> (N:4) 5792 <sup>+</sup> (N:1)	5791 <sup>+</sup> 3015 <sup>+</sup>	5864 <sup>+</sup> (N:4) 5792 <sup>+</sup> (N:1) 3015 <sup>+</sup> 5791 <sup>+</sup>	3014	5861 <sup>*</sup>	5862 5863
<b>12</b> Days: 3 Individuals: 14	3016	5865 <sub>F</sub> <sup>+</sup> (N:2) 5801 <sup>+</sup> (N:1)	5800 <sup>+</sup> 5894 <sub>F</sub> <sup>+</sup> 5898 <sup>+</sup> 5867	5865 <sub>F</sub> <sup>+</sup> (N:2) 5801 <sup>+</sup> (N:1) 5800 <sup>+</sup> 5894 <sub>F</sub> <sup>+</sup> 5898 <sup>+</sup> 5867	5793	5799	5866 5868
					5795	5796	5797
	5800	5868 <sup>+</sup> (N:2)	5866 <sup>+</sup> 5798 <sup>+</sup> 5865 <sub>F</sub> <sup>+</sup> 3016 <sup>+</sup>	5868 <sup>+</sup> (N:2) 5866 <sup>+</sup> 5798 <sup>+</sup> 5865 <sub>F</sub> <sup>+</sup> 3016 <sup>+</sup>	5793	5797	5799 5801 5867
<b>8</b> Days: 1 Individuals: 6	3008	5844 (N:2)	3009 5841 5843		5482 <sub>M</sub>		
	3009	5841 (N:2) 5843 (N:1)	5844 3009		5842 <sub>M</sub>		

<sup>+</sup> preferential association (COA > twice the mean HWI)

<sup>-</sup> preferential avoidance (COA < half the mean HWI)

\* statistically significant based on permutation tests



**Table 3-5: Estimates of typical group size (tgs) in both the Caribbean and Sargasso Seas, calculated using the Petersen mark-recapture methods with a day's identifications divided in half by two different methods (as in Coakes and Whitehead 2004). Either the total number of identifications was split in half at its midpoint (bottom two rows), or the data were split at midday into morning and afternoon (top two rows).**

Splitting methodology	Location	Estimates with CV < 0.25		Estimates with CV < 0.40	
		N	tgs*	N	tgs*
Split at Midday	Caribbean	32	6.63 (1.51)	35	6.82 (1.57)
	Sargasso	12	12.05 (6.56)	16	12.95 (6.96)
Split by ½ of identifications	Caribbean	45	6.37 (1.48)	48	6.62 (2.00)
	Sargasso	17	12.01 (6.52)	20	11.37 (6.37)

\* Mean (SD)

## DISCUSSION

This study is the first to investigate the identity of sperm whale care-givers and has shown that individuals within a social unit have preferred associations and avoidances with calves as well as with other adult unit members. It has shown that not only do sperm whales have systems of babysitting which vary geographically, but that some allomothers appear to give direct care to another's calf in the form of allonursing.

### SYSTEMS OF ALLOPARENTAL CARE IN SPERM WHALES

My findings suggest that groups of sperm whales living in the two study areas have different systems of babysitting. The general pattern of escorting is similar between areas: calves were most often escorted by nursing escorts, then mothers with dependent calves, followed by some or all of the remaining adults in the unit or group. In the Caribbean system, a specific preferred babysitter, who had no dependent offspring and shared a strong bond with the mother, provided the bulk of the allocare, but all or most individuals escorted the calf. The system in the Sargasso differed in most of these respects. Multiple nursing escorts provided alloparental care of the young, but overall a smaller proportion of the group escorted the calves. These two different systems appear to be consistent within study areas.

#### *Incidences of Allosuckling*

The most obvious difference between the differing systems of allocare in the two study areas is the presence of allosuckling in the Sargasso. As described in chapter two, it is difficult to determine whether the calves were actually receiving milk from the allomothers, but the occurrence of suckling attempts with allomothers in the Sargasso and

the lack thereof in the Caribbean is still a significant behavioural difference between the areas.

Five major theories have been proposed to explain the occurrence of allosuckling: (1) reciprocal altruism, (2) kin selection, (3) learning-to-parent (4) milk evacuation, and (5) misguided parental behaviour (reviewed in Roulin 2002). The first three hypotheses are addressed in more detail later in this discussion, and this study was not designed to be able to assess the validity of the milk evacuation hypothesis in sperm whales, but the possibility of the last hypothesis is discussed below.

The “misguided parental behaviour” hypothesis is typically used to explain allosuckling in species that live in dense groups where confusion and “milk-theft” are more likely (Riedman and Le Boeuf 1982; McCracken 1984; Packer et al. 1992; Boness et al. 1998; Roulin 2002). These characteristics do not accurately describe the social structure of female sperm whales. It would seem unlikely that sperm whale mothers are unable to identify their offspring among the small number of calves in a social group or unit. Although there is little evidence which refutes this hypothesis from this study alone, it was shown that individuals within a unit formed preferred associations and avoidances with particular unit members including the calves. This would entail some degree of individual recognition. Additionally, I observed an instance where two mother-calf pairs suckled synchronously. The calves each swam at the surface directly towards their presumed mother and began suckling. There were no observable differences in suckling behaviours due to the presence of another suckling pair and the calves had to cross each others paths to reach their mothers. This observation would suggest at least some degree of recognition between mother and calf within a social unit and selectivity in regards to

potential nursing escorts. Whether the recognition is cued by a vocal or visual signal is unknown, but it is likely that sperm whale calves are able to identify their desired nursing escort.

#### FACTORS INFLUENCING THE IDENTITY OF ALLOMOTHERS AND THE SYSTEM OF ALLOPARENTAL CARE

The contrasting patterns of allocare among sites may be based upon variation in social systems, predation pressure, prey type and availability, or possibly culture.

##### *Social System*

The social structure of the population in which the mother-calf pair resides affects the system of alloparental care that is observed. The level of organization in which the mother spends most of her time, the demographics of those structures, as well as the nature and patterning of relationships within a social unit or group will undoubtedly influence the identity of the allomothers.

With the detailed follow of the GOS unit in the 2005 season, preferred associations and avoidances between specific individuals within a sperm whale social unit have been identified. These findings contrast with previous work which suggested that relationships within units were usually homogeneous except in the largest units (Christal and Whitehead 2001). In particular, I noted stronger associations between unit members and the babysitter, as well as, in the GOS unit, the mother's avoidance of all other adults in the unit. These non-random patterns of association may reflect differing tendencies among individuals towards the calf and the role of the "babysitter". Mann and Smuts (1998) found that certain bottlenose dolphin (*Tursiops* sp.) individuals were attracted to calves possibly due to the potential to enhance social and parenting skills and

reproductive success. Under the learning-to-parent hypothesis (Lancaster 1972), inexperienced females would escort calves in order to gain maternal experience. Although this may influence the identity of escorts in general, in this particular case, the preferred babysitter is an adult female. An alternative explanation may be derived from the hypothesis of reproductive senescence in female cetaceans (Williams 1957; Hamilton 1966; Marsh and Kasuya 1984; Marsh and Kasuya 1986; Olesiuk et al. 1990) and its connection with matrilineal social systems (Whitehead and Mann 2000). Post-reproductive females are expected in species in which the major burden of parental care falls on the females, the period of offspring dependence is long relative to both the lifespan of the mother and the modal birth interval, females bear one young at a time and have a low life-time productivity, and where females live in stable kinship groups (Marsh and Kasuya 1986). All of these criteria support the likelihood that menopause occurs and post-reproductive females are found in sperm whales. It is also significant that post-reproductive females have been identified in wild populations of African elephants, *Loxodonta africana* (Laws et al. 1970; Laws et al. 1975), a species which has many similarities to sperm whales in terms of life history traits and social structure (Best 1979; Weilgart et al. 1996), as well as in short-finned pilot whales, *Globicephala macrorhynchus* (Marsh and Kasuya 1984; Marsh and Kasuya 1986) and killer whales, *Orcinus orca* (Olesiuk et al. 1990), two other species of odontocetes. Whitehead (2003) suggests that the lack of clear evidence for menopause in sperm whales is primarily due to lack of data. The best available data (Best et al. 1984) suggest that of the 725 mature females examined none of the 22 oldest individuals (42 - 61 years old) possessed a fetus or were ovulating, although six were lactating. As a result, it is possible that sperm whales

continue to reproduce until their forties, at which point reproduction ceases but individuals continue to live for decades. Given that menopause occurs invariably in such species and likely in sperm whales, the costs of reproductive cessation are likely outweighed by the benefits of assisting kin (Williams 1957; Hamilton 1966; Marsh and Kasuya 1986; McAuliffe and Whitehead In Press). Although, McAuliffe and Whitehead (In press) state that it is unclear how menopausal grandmothers help; I propose that the presence of a preferred babysitter consistent over a decade may be evidence that grandmothers or socially bonded elders play a key role in the care for sperm whale calves. Furthermore, as in human grandmothers (Foster and Ratnieks 2005) and African elephant matriarchs (McComb et al. 2001), menopausal cetacean females have experience that might benefit other members of the matriline. The babysitters, or more generally the oldest or older members of the social unit, may act as cohesive members of the unit, which would explain the babysitter's egalitarian pattern of association within this unit. Unfortunately, the data which would suggest if the babysitter is in fact the calf's grandmother are lacking, but given the matrilineal structure of sperm whale units, it is not an unlikely situation. The merits and complications of this hypothesis can only be appreciated when the ongoing detailed genetic analysis is completed and this pattern has been identified in more than one calf in one social unit.

Although it is clear from the long-term resighting of the GOS unit that this Caribbean group consisted of just one unit, it is difficult to say what level of social organization were followed in the Sargasso. Most of our understanding of sperm whales and sperm whale social structure is derived from work carried out in the eastern tropical Pacific (Whitehead 2003). In the Pacific, the mean typical unit size is about 14

individuals (Christal et al. 1998). The difficulty in determining the level of social organization derives from uncertainty in determining whether there were smaller Atlantic units with a typical size of 6 or 7 individuals in the Caribbean, and accordingly groups containing about two units in the Sargasso; or if the units in the Sargasso Sea are of similar size to those found in the Pacific, and so the groups mostly contained just one unit. However the social demographics at the two study areas seem to differ. If individuals do differ in their tendencies towards calves and babysitting, with more immature and elders available in the groupings in the Sargasso, calves are more likely to be grouped with individuals who are willing to act as a babysitter. Whether care-givers are group or unit members likely has a great impact on the system of babysitting and particularly on the mechanisms which are likely to maintain that system, as I will touch upon later in this discussion.

#### *Prey Type and Availability*

The number and quality of escorts may vary based on prey availability and type. It seems that feeding success between the two studies differed substantially with the defecation rate being twice as high in the Caribbean. In a situation where foraging success is low, as it appears to be in the Sargasso, mothers may dedicate a greater part of their activity budget to foraging, and thus leave their calves at the surface more often and for longer periods of time. Since all females would experience the same impacts of low prey availability, the responsibility of caring for the calf may be spread over more individuals to accommodate for increased foraging effort. As such, relationships between the mother-calf unit and the care-givers may be weaker and allonursing may be required if the mother spends too much of her time away from the calf (Lee 1989). In a situation

like in the Caribbean where prey appears to be abundant, mothers may be able to spend more time with their calf and less time foraging. As a result, fewer alloparents are required and strong relationships can be forged between the calf and primary caregiver. Accordingly, allonursing would not be required to supplement the calf's diet.

Although this pattern of changes in activity based on feeding success has been observed in chimpanzees (*Pan troglodytes*) at Gombe National Park in Tanzania (Wrangham 1977), this appears not to always be the case in sperm whales (Whitehead 1999). Sperm whales in the Pacific appear to socialize at roughly the same overall rate whether feeding success is low or high. However, the GOS unit was never observed socializing during the 40 days of observations, a pattern which contrasts with the Pacific (Whitehead 2003), so direct comparisons of daily activity budgets may not always be valid.

Squid beaks were collected in the defecations of identified whales from both areas during our research such that future analysis may investigate preferred prey type at both sites and give insight into differences in foraging habits between units and groups which use differing systems of babysitting. Prey type may affect the depth and duration of foraging dives. This in turn would have an impact on the amount of time mothers spend away from their calves, and the system of babysitting.

#### *Predation Pressure*

It has been hypothesised that the care for calves was fundamental to the evolution of sociality in female sperm whales (Best 1979; Gordon 1987; Arnborn and Whitehead 1989; Whitehead 1996; Whitehead 2003). As such, it is likely that variation in predation



pressure among populations may have resulted in the evolution of different systems of babysitting.

Of all natural predators of sperm whales, the two major groups of predators have differing patterns of distribution. One in particular stands out: *Orcinus orca*, the killer whale (Jefferson et al. 1991; Pitman et al. 2001). Multiple killer whale attacks have been recorded on sperm whales in the Pacific at all latitudes (Jefferson et al. 1991; Pitman et al. 2001), but none have been observed in the Atlantic. Conversely, the species group which probably constitutes the sperm whales' second most important threat, large predatory sharks (Whitehead 2003), is found in greater diversity and abundance in the tropical latitudes. It is difficult to determine exactly how predation pressure affects the social organization of the two populations discussed here without further details on differences in the nature and extent of the two predatory threats in these two parts of the Atlantic.

### *Culture*

Cultural variation in a number of sperm whale behaviours has already been identified between supra-unit structures called acoustic clans, made up of tens of thousands of individuals which share similar vocal repertoires (Rendell and Whitehead 2003; Rendell and Whitehead 2005). Cultural variation in diet, reproductive success (Marcoux 2005), movement, habitat use, and feeding success (Whitehead and Rendell 2004) have already been identified among sperm whale clans. In view of this and the fact that recordings taken during our fieldwork in both study areas suggest that different clans use each of the areas (predominantly “2+4” and “5R” codas in the Sargasso, L. Rendell, unpublished data; and primarily Caribbean codas in the Caribbean, T. Schulz,

unpublished data), it is possible that the observed systems of babysitting are culturally inherited. This would imply that differing patterns of communal care for calves are transmitted through social learning.

Whitehead (2003) has previously suggested that differences in dive synchrony between the two principal clans that use Galapagos waters may have effects on their ability to protect calves. He suggests that the less synchronous “+1” clan may be more effective at protecting its calves from predation as individuals are more often at the surface to escort them.

If escorting is not limited to unit members, it may be that clan membership acts as a boundary for babysitting behaviours (Rendell and Whitehead 2001). There is a relationship between culture and altruism in humans, in so much as culture determines altruistic norms and social commitments are primarily reserved for those in the same linguistic group (Wilson 1978; Milroy 1987; Nettle 1999; Ehrlich 2000).

#### EVOLUTIONARY MECHANISMS

It is likely that a combination of the above factors have resulted in the differences observed between the two systems of babysitting. Here I discuss possible evolutionary mechanisms which maintain them.

##### *Kin Selection*

The matrilineal structure of social units would suggest that kin selection likely plays a role in the identity of escorts. Kin selection may be more evident in the smaller more closely related units as opposed to the larger groups or within clans. Unfortunately, relatedness results were not available for this analysis, but preliminary results from an ongoing genetic study suggest that all individuals of the GOS have the same mtDNA

haplotype (D. Engelhaupt, unpublished data). This initial finding is consistent with the matrilineal structure of sperm whale social units and suggests that all members of the GOS unit are matrilineally related. However, this does not prove this fact unequivocally as this particular haplotype is the most common around the globe being found in 30% of the global population (Lyrholm et al. 1996). Many facets of this issue including how relatedness affects the other hypotheses mentioned in this discussion will be clarified once the ongoing detailed genetic analysis is completed on these animals.

### *Reciprocal Altruism*

Two general models have been proposed for reciprocal altruism (Trivers 1971). In the following, I consider the two-party model, or dyadic reciprocal altruism, then address the more complex multiparty model.

I present two possible temporal scenarios for dyadic reciprocation of alloparental behaviours in sperm whales: (1) *concurrent*, in which allomothers have dependent offspring at the same time and reciprocation presumably takes place over periods of hours to days; and (2) *delayed*, in which the mother and the allomother do not both have dependent offspring at the same time, and thus reciprocation occurs across years. The importance of the two scenarios of reciprocation may differ between populations and in their impact on allomaternal behaviours as allonursing and babysitting involve differing levels of energetic investment. Concurrent reciprocation may be favoured in sperm whale populations which spend the majority of their time living in larger social groups as opposed to smaller, longer-term social units. If care-givers are group members, but not necessarily unit members, the increased size of groups makes it likely that mothers are able to find allomothers with dependent calves with which to enter into a reciprocal

relationship (Trivers 1971). Escort reliability, however, maybe low among group members as group stability is only on the order of hours to days, making delayed reciprocation unlikely. Concurrent reciprocation may also be preferable for females in those groups living in areas with higher predation pressure, as reciprocation over the long-term may be less likely to occur due to higher calf or escort mortality. Conversely, delayed reciprocation may be favoured in the setting of the smaller social unit whose membership is stable over long time periods, where the presence of multiple calves is less likely but escort reliability is higher over time.

None of my findings suggest that concurrent reciprocal allonursing is occurring in the Caribbean Sea, as all calves suckled from one adult even if more than one calf was present. Nor is there evidence of concurrent reciprocation of escorting, as most primary escorts were not concurrent mothers of small infants themselves. Females with dependent calves were secondary escorts in many units, but escorts who were mothers, never escorted another calf alone, their offspring was always present. This would suggest that the behaviour of the allomother may not be changed by the presence of the other calf, but that the adult is only present to escort their offspring.

In contrast to the Caribbean, concurrent reciprocation of babysitting may be occurring in the Sargasso study area as several presumed mothers were observed alone with several different calves. It is also likely that the larger groupings in the Sargasso allow for concurrent reciprocal allosuckling, which is less likely in smaller social units observed in the Caribbean. Roulin (2002) points out that there are only three situations in which females would be able to allonurse: concurrently with an offspring, soon after the loss of an offspring, or by spontaneous lactation.

It is important to note that the time scale over which this study was conducted is too short to identify delayed reciprocation of either allomaternal behaviours. Comparing the individual roles among adults in the GOS unit between the 1995-1996 and the 2005 seasons would suggest that delayed reciprocation is not occurring in this Caribbean social unit. The primary escort in the GOS unit in 2005, female '5561', appears to also be the babysitter for the calf in 1995-1996. Although there is little data to suggest the identity of the calf or who the mother of the calf might be, it would appear the identity of the preferred escort is consistent between time periods which would indicate against reciprocation.

Although some interactions between mothers and certain escorts may be explained by dyadic reciprocal altruism, both temporal scenarios fail to completely explain the patterns of allocare for escorts in all sperm whale groups. Taken at the level of the unit, group, or clan, it is possible that a combination of both concurrent and delayed reciprocation may be occurring between the mother and each of the escorts. In close-knit social groups, Trivers (1971) argues that selection may favour more complex interactions. In multiparty models, individuals show generalized altruistic tendencies in which altruistic acts are not confined to animals which can or will reciprocate (Trivers 1971; Connor and Norris 1982). This model functions because altruistic acts are eventually returned to the benefit of the donor assuming that many or most individuals act in a similar way, even though the act may not be reciprocated directly by the original recipient (Trivers 1971; Connor and Norris 1982). The multiparty model does perhaps provide some insight into the complexity of sperm whale allocare. Multiparty reciprocal relationships are able to accommodate for the possibilities of within-group babysitting

and babysitting between unrelated but culturally tied individuals within clans. A multiparty model would also accommodate for differences in the quality and quantity of the interchanged behaviours. Individuals would not be restricted to “absolute” reciprocity, in which individuals reciprocate the exact quantity and nature of the behaviour accomplished for them (Hemelrijk 1990). More complex interactions in which babysitting is reciprocated for allonursing or vice versa, as well as when individuals vary in the quality and type of care they are able to provide are accounted for in the multiparty models.

## **CONCLUSIONS**

This study has shown that more than one system of babysitting exists among sperm whales. Each system differs in the identity and number of escorts, as well as the nature and quality of the relationships between the mother-calf pair and the caregivers. These systems likely differ due to a complex combination of ecological, behavioural, and cultural differences between populations. This study has helped clarify the fact that dyadic reciprocal altruism is not sufficient on its own to explain the evolution and maintenance of the systems of babysitting observed in this species. Finally, this study suggests that allosuckling does occur in some sperm whales populations, but that it is not universal.

## **CHAPTER FOUR :**

### **GENERAL DISCUSSION**

## KEY RESULTS AND FUTURE DIRECTIONS

Here, I summarize the key findings of this thesis and outline priorities for future research. I conclude with a commentary on unique noses and babysitters, their significance, and their relation to my work.

My study was designed to elucidate the behaviours involved in sperm whale allocare while focusing on three objectives: (1) to ascertain who cares for whose calf and whether kin selection (*i.e.* caring for calves that are related to you) and/or dyadic reciprocal altruism (*i.e.* I care for your calf and you care for mine) are sufficient to explain babysitting in sperm whales or whether there exists a communal, multinodal system, more consistent with the pattern of relationships found among adult females and the predictions of cultural evolution; (2) To determine whether or not allosuckling occurs (*i.e.* suckling milk from a non-parent); and (3) To investigate the specifics of calf suckling behaviour, specifically suckling-dive durations and practices.

Chapter two dealt with the last of these objectives first. Due in part to the lack of calves in previous study areas (Whitehead 2003), until this thesis little directed research had been completed on calf behaviour. Addressing questions concerning the suckling behaviour of sperm whale calves in Chapter II, I have attempted to fill major gaps in our knowledge of the basic daily behaviour of sperm whales calves. Although, this study has provided needed description of dive durations and has exposed laterality in suckling dives, it is clear that more work is needed to finally settle the confusion surrounding how sperm whale calves suckle. I add a new alternative hypothesis into this debate as the previous assumption that multiple short dives under the peduncle of an adult or an escort indicates suckling is wrong. Either this behaviour often does not indicate suckling, or



sperm whale calves can suckle through their nasal passages, a pattern never previously described for any mammal. Further directed studies on calf behaviour and underwater observation are needed to clarify this debate.

In Chapter three, I tackled the remaining two objectives. The bulk of the work for this thesis, this chapter aimed to determine the identity and relationship of the care-givers in sperm whale society. I have shown that sperm whales have at least two systems of alloparental care that are found in different geographical regions. The systems differ in the number of alloparents and the types of allocare provided. Factors influencing the identity of caregivers and the evolutionary mechanisms which maintain the differing systems are discussed. As this chapter is the first study directed at the social relationships behind the care for sperm whale calves it has resulted in multiple new hypotheses and avenues for new research.

## **LIMITATIONS AND UNCERTAINTIES**

During the course of my research, I encountered some limitations that may have affected results presented here; specifically, sample size in both chapters, a lack of existing data from the Atlantic, and the inevitable presence of our vessel. In the following, I address these limitations and attempt to gauge their impact on the findings.

There was a lack of balance in the sample sizes of identifications and in the number of suckling bouts observed between individuals and the two study areas. In chapter two, the number of suckling bouts observed in the Sargasso was considerably smaller than the number observed in the Caribbean. Furthermore, the majority of the dive data collected in the Caribbean was of a single individual. This issue was in part corrected by the nature of the nested GLM model used to make the comparisons;

however, it is important to note that it is likely that the significant findings between study areas may not have been so evident with an increased sample size from the Sargasso.

In chapter three, a similar issue may have arisen, in so far as, the number of resightings for most calves was a great deal less than for the calf from the GOS unit. Until this study, the longest amount of time spent with a single unit of sperm whales was 21 days (Unit A; Christal and Whitehead 2001). In some ways, this issue only exist because our data on the GOS calf was so complete and consumed the majority of our field days. It takes many resightings of an individual or unit over time in order to make conclusions about animal social relationships. Although, I have made arguments about calf relationships in general, the relatively short period over which this study was completed and a low number of resights for the majority of subjects precludes me from making decisive conclusion about each unit or group.

Many of the uncertainties touched upon in chapter three result from a lack of existing data from the Atlantic. The timelines required for the completion of complex genetic analyses and attributing squid beaks to a given species using keys, as well as a lack of previous social structure and identification data from the Atlantic made comparisons between populations difficult. Unfortunately, completing such complex analyses in addition to the fieldwork requirements required to achieve the detailed social structure results reported here is near to impossible under the timeline of a Master's thesis.

Finally, the data reported here were collected under the assumption that the presence of our vessel had little to no impact on the observable behaviours of the calves, and the association patterns among individuals. With the presence of multiple

whalewatching operators, cruiseliners, and commercial vessels in the waters off of the Commonwealth of Dominica, it is clear that the whales have had more encounters with vessels than the individuals living far offshore in the Sargasso Sea. It has recently been reported in a population of bottlenose dolphins (*Tursiops sp.*) that more sensitive individuals depart from areas with even minimal vessel traffic and some females suffer reduced reproductive success (Bejder 2005). Following this, it is possible that the animals off of Dominica are more habituated to vessels and responded less to our presence. In the Sargasso the opposite may be true. Even though we took steps to minimize our impact on the whales we were following, it is possible that whales may have altered their behaviours due to our continued presence. However, it is also possible that over a follow of several days the whales would become less affected by our presence.

### **BIG NOSES AND BABYSITTERS**

A large portion of the sperm whale's body is in its nose. By virtue of its world record size (proportionately 16 to 22 times the size of the homologous structure in common dolphins, *Delphinus delphis*, for female and male sperm whales respectively; (Cranford 1999)) and complex inner structure, the function of this strikingly enormous evolutionary development has been the source for heated debate over the years. Its function has been attributed to buoyancy control (Clarke 1970; Clarke 1978) and as a battering ram during aggressive encounters (Carrier et al. 2002), but it would seem that the sperm whale nose functions primarily as the worlds most powerful natural sonar system (Mohl et al. 2000; Madsen et al. 2002).

But what is the significance of a unique nose? Whitehead (2003) developed a theory in which uniquely successful noses lead to foraging advantages and ecological

dominance by outcompeting members of their guild. This in turn leads to intraspecific competition and towards a slow life history process (Whitehead 2003). He cites the example of elephants who much like sperm whales, have uniquely useful noses (Sukumar 1991) and have become ecologically dominant in a terrestrial environment drastically different from that of the oceanic sperm whales. Yet, these two species share many life history traits and are both ecologically dominant (Weilgart et al. 1996). Given a species in which its unique nose has had such an impact on its evolution, it seems less surprising that it may be the only mammal which uses its nose to suckle.

If we continue with the theory developed by Whitehead (2003), unique noses lead to foraging advantages, ecological dominance, and slow life history traits; which in turn leads to highly sociable groups. Long lives and low reproductive rates allow for strong social bonds to develop as individuals are able to interact repeatedly with a small number of conspecifics (Whitehead 2003). Social relationships allow for cooperation to exploit resources and for the communal defence against predators. Here too, we find similarities between sperm whales and elephants, who share very similar social structures in which long-term social units provide communal care for offspring. This project has added to these similarities supporting the hypothesis that allosuckling is occurring in some groups of sperm whales, as it does in elephants (Moss and Poole 1983; Lee 1987), and that related or socially bonded elders provide the majority of the care at least in one Caribbean social unit.

This work has focused on behavioural developments which are fundamental to the evolution of sperm whale societies under Whitehead's (2003) theory. These findings, although without equal in the marine environment, do not compare to the depth of our

knowledge about elephant societies and allocare. The parallels between sperm whales and elephants do provide cetologists with hypotheses to test in the marine environment. Of particular interest is whether or not sperm whales have matriarchs. Currently, it is unclear, but some of the findings of this study suggest that individuals do have an intricate set of relationships within a social unit and individuals may show differing tendencies to fill different roles. Future work on both species will lead to the development of hypotheses to be tested on the other.

Having said this, it is important to note that work will not be able to continue if all the whales are gone. Both of these species, although ecological dominant, are not able to compete with the enormous impact which the human species has on their habitats. These species, like humans, live in closely bonded family groups with grandmothers and babysitters (Moss and Poole 1983; Whitehead and Weilgart 2000), which have dialects (Rendell and Whitehead 2003), traditions (McComb et al. 2001), as well as cultures (Rendell and Whitehead 2001). It is time that the most ecologically dominant species at the global scale recognize the effects of its realized dominance. Be it from poaching or hunting, noise pollution or land pollution, oil production or urban sprawl, these animals are being threatened by our actions...and there is nothing a unique nose or any number of babysitters can do about that. A better understanding of the biology of these species can lead to better mitigation of those impacts. As ecological dominants of their respective environments, an understanding of how these impacts affect their survival will allow us to achieve an understanding of how to minimize our impacts on the entire ecosystem. However, scientists should not be as arrogant to assume they can fix the problems alone; politicians, policy makers, and economists, as well as the private sector will need to work

together to make a concerted effort to protect these animals and the ecosystem in which they reside.

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**APPENDIX 1:** Terminology describing the spatial and temporal structure of associations of female and immature sperm whales, adapted from Whitehead (2003).

<b>Term</b>	<b>Definition</b>
Concentration	In large-scale surveys, sperm whales are often seen in patches over an area of a hundred km across
Aggregation	Within concentrations, groupings of sperm whales that span 10-20 km
Group	2-3 units associating over short time periods, whales moving in a coordinated fashion, although often spread out over hundreds of kilometers
Unit	Long term structure of ~11 animals (often kin)
Cluster	At the smallest scale, a few whales that are swimming in the same direction at the surface within 1-3 body lengths of each other
Associate	Any individual identified on the same day of a given encounter
Escort	Any individual identified within the cluster which contains the calf