ON THE DYNAMICS OF SOCIAL RELATIONSHIPS AND VOCAL COMMUNICATION BETWEEN INDIVIDUALS AND SOCIAL UNITS OF SPERM WHALES

by

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To the whale mothers who have so patiently allowed me to share in their lives;

Erica, whose perennial optimism in people and belief in our ability to change the world should give us all hope;

And to Grayson, may the ocean be as blue when you first see it.

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ABSTRACT

Within-population behavioural variation can greatly affect the ecology of a species and the outcome of evolutionary processes. This study aimed to determine how variable sperm whale social and vocal behaviour is between both individuals and their social units.

The population of whales off Dominica is small and isolated from communities in neighbouring waters. Female and immature whales live together in social units containing about 7 animals. I analysed their social relationships and their 'coda' communication signals using an unparalleled dataset of social and vocal interactions at the level of the individual.

Within units, calves were significant nodes in their social unit's network, and thus I provide quantitative support for the hypothesis that communal calf care acts as the primary evolutionary driver for group formation in this species.

Social relationships within and between units were diverse, while the spatial spread of individuals within units and their travel speeds were similar among all of the units. I identified long-term patterns of association between units consistent over decadal time scales.

Social units had characteristic vocal repertoires, but all were dominated by the '1+1+3' and '5R' coda types. Differences between units resulted from some units using specific 4-click coda types. Units and individuals used different accents on their '5R' codas, but the '1+1+3' coda was stereotyped across all individuals and units studied. The repertoires of different units were as similar as units within vocal clans in the Pacific. My results support the hypothesis that the '5R' coda may function in individual identification. The stability of the '1+1+3' coda may be the result of selection for a marker of clan membership. Individual repertoires differed consistently across years; and contrary to an existing hypothesis, new mothers did not vary their repertoire to be more distinct after giving birth. However, calves did use a class-specific '3+1' coda.

In summary, sperm whale social and vocal behaviour vary between individuals and among units. Variation in the social and vocal behaviour of female sperm whales results from a trade-off between individuality and conformity within units and clans.

LIST OF ABBREVIATIONS AND SYMBOLS USED

AET	Association Evasion Tropicale
AWW	Anchorage Whale Watch
CCC	Cophenetic correlation coefficient
CV	Coefficient of variation
df	Degrees of freedom
DAL	Dalhousie University
ETP	Eastern tropical Pacific
GPS	Global Positioning System
GRD	German Society for Dolphin Conservation
h	Hour
HWI	Half-Weight Index
ICI	inter-click interval
IFAW	International Fund for Animal Welfare
IPI	Inter-pulse interval
k	Number of clusters using k-means clustering methods
kHz	Kilohertz, frequency in thousands of cycles per second
km	Kilometre
m	Metre
msec	Millisecond
n	Sample size
NSERC	Natural Sciences and Engineering Research Council of Canada
ORES	Oceanic Research and Education Society

p0	Initial pulse of a sperm whale click
p1	Pulse subsequent to initial pulse (p0)
p#	Pulses subsequent to p1 numbered sequentially
Q	Photograph quality for identification purposes
RHIB	Rigid-hulled inflatable boat
S	Social differentiation
SD	Standard deviation
SE	Standard error
SWF	Sea Watch Foundation
TGS	Typical group size
WHOI	Woods Hole Oceanographic Institute
VRC	Variance Ratio Criteria

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CHAPTER 1
INTRODUCTION

The hardest battle in life, is to be nobody but yourself, in a world that is working night and day to make you like everybody else.

~ E.E. Cummings

THE IMPLICATIONS OF WITHIN-POPULATION BEHAVIOURAL DIFFERENCES

Within-population behavioural variation can greatly affect the ecology of a species. Furthermore, behavioural variation, and not only genetically-caused behavioural variation, can determine evolutionary processes by affecting the direction or outcome of natural selection (Dingemanse and Réale 2005; Duckworth 2009). Populations which exhibit high levels of behavioural variation may be more stable in the face of competition or predation (Lomnicki 1978; Lomnicki 1980; Lomnicki 1984), exert different forms of selection on prey species (Sherrat and MacDougall 1995), survive extreme changes in environment (Whitehead and Rendell 2004), and diversify more readily (Abrams *et al.* 1993; Doebeli and Dieckmann 2000).

Behavioural traits expressed by an individual may vary due to the influence of their genetic make-up, epigenetic, including maternal, effects, their environment, and, in some species, a complex combination of individual and social learning. This behavioural variation among individuals has traditionally been ignored as noise; but in the last decade, there has been a shift in the perspective of many evolutionary behavioural ecologists to take these differences into account (Réale *et al.* 2010). Individuals are no longer perceived as homogenous agents, but unique individuals which respond to stimuli differently.

INDIVIDUAL DIFFERENCES: ANIMAL PERSONALITY

The majority of ecological and evolutionary theory assumes that individuals will use the most adaptive behaviour in a given context in order to maximize their fitness. In contrast, an increasing body of work suggests that animals often show only limited behavioural plasticity (Sih *et al.* 2004) and often vary consistently in their responses to external stimuli in their physical or social environments (Wilson 1998; Gosling 2001). 'Animal personality' refers to this phenomenon in which individuals differ consistently in their behaviour across time and situations or contexts (Wolf and Weissing 2012). Personalities have been identified in a wide variety of species from mammals to insects (Hayes 1997; Gosling and John 1999; Sih *et al.* 2004; Groothuis and Carere 2005; Réale *et al.* 2007), and individuals may differ both in the behaviours themselves (*e.g.* individual foraging specializations are common in a diversity of taxa, see Bolnick *et al.* 2003), but also in their behavioural flexibility (Dingemanse and Wolf 2010). For example, individual differences in behaviour flexibility in great tits (*Parus major*) result in some individuals being able to readily alter their foraging behaviour to changes in the experimental feeding regime while others continue to use the techniques which were previously effective despite decreased success (Verbeek *et al.* 1994). Individual behavioural variation can affect various aspects of life ranging from dispersal, movement, and social interactions on a smaller scale; to speciation, community structure, and adaptive potential at the population level (Dingemanse and Réale 2005; Réale *et al.* 2010; Wolf and Weissing 2010).

DIFFERENCES BETWEEN GROUPS: CULTURAL GROUP SELECTION

For species which live in groups, within-population variation may occur between social groups. Groups can vary in their common behaviours due to consistent genetic differences or their differing local environments, but for some species much cultural variation occurs at the level of the group. When differences between groups are consistent over time and across contexts and these differences are marked by overt cues, in-group favouritism can lead to increases in within-group homogeneity of behaviour, but also increases in between-group heterogeneity (Henrich 2004; Efferson *et al.* 2008). Furthermore, these differences can affect the fitness of the different groups, and when one group is more successful than the others, their traits spread in the population over time though the process of cultural group selection (Boyd and Richerson 1990; Boyd and Richerson 2010).

When cultural groups are overtly marked by symbolic cues it can facilitate cooperation with strangers and large scale cooperative societies (Boyd and Richerson 1987; McElreath *et al.* 2003). Ethnic groups emerged among humans as symbols became used to identify membership of different cultural groups. Cultural identity has been both a unifying and a divisive force among human populations. On the one hand, people are more likely to help or share rewards with members of their own group than with members of a perceived out-group (Turner 1978). Moreover, in humans, culture determines altruistic norms, and social commitments are primarily reserved for those who share a similar language, or other ethnic marker, such that there is a relationship between culture and cooperation (Nettle and Dunbar 1997; Nettle 1999). On the other hand, strong adherence to certain behaviours has acted as a catalyst for between-group competition (Perry 2009). Wars are often fought over differences in apparently arbitrary cultural traditions, but which, for whatever reason, have assumed a perceived significance. Over the course of history, the behavioural variation between ethnic groups has greatly affected the structure of human society, and thus our evolution.

Recent work has suggested that humans are not the only cultural species and that animal cultural traditions can pervade most areas of life (see Laland and Galef 2009). Differing behavioural traditions among groups have been shown in many species including: apes (Whiten *et al.* 1999; van Schaik 2003), monkeys (Kawai 1965; Perry and Manson 2003), fish (Laland and Hoppitt 2003; Freeberg and White 2006), birds (MacDougall-Shackleton and MacDougall-Shackleton 2001; Freeberg and White 2006; Bluff *et al.* 2010; Byers *et al.* 2010) and cetaceans (Noad *et al.* 2000; Rendell and Whitehead 2001; Mann and Sargeant 2003; Wells 2003).

INDIVIDUALS AND CULTURES IN THE OPEN OCEAN:

The cetaceans are a particularly interesting taxon as they exhibit both individual behavioural variation and group-specific behavioural traditions. Compared to terrestrial species, marine species experience substantially greater environmental variation over periods of months or longer (Steele 1985). Once predictable variation over diurnal or seasonal scales is removed, environmental noise in terrestrial environments tends to have a white spectrum, while oceanic environments tend to be red or brown (Vasseur and Yodzis 2004). For example, Cyr and Cyr (2003) show that temperature varies differently in the ocean as compared to terrestrial environment. As a result of living in a variable ocean, cetaceans operate on relatively larger spatial (Stevick *et al.* 2011) and temporal scales (George *et al.* 1999) compared to those of terrestrial mammals, and show little evidence of territoriality (Connor *et al.* 1998; Connor 2000)

Moreover, the variability of the marine environment creates a situation in which social learning is favoured over individual learning or genetic determination of behaviour (Whitehead 2007). Together with the fact that many cetaceans live in stable social groups with prolonged parental care, including some species with natal philopatry in which both sexes remain in the family unit (Connor 2000), the opportunities for cultural transmission of behaviours are high with traits being passed consistently within groups, but less often between them (Whitehead 1998). As a result, several species exhibit high levels of behavioural variation between social groups, much of which is thought to be due to cultural lineage (Connor 2000; Connor *et al.* 2000; Connor 2001; Rendell and Whitehead 2001; Yurk *et al.* 2002; Sargeant and Mann 2009; Riesch *et al.* 2012; Whitehead *et al.* 2012).

Among the cetaceans, the sperm whale (*Physeter macrocephalus*, Linnaeus 1758) provides a good example of cultural behavioural variation between groups. Female and immature sperm whales, including immature males, stay in tropical and sub-tropical waters and live their entire lives in stable social groupings, called units, characterised by long-term social relationships between individuals (Christal *et al.* 1998; Whitehead 1999; Whitehead and Weilgart 2000). Unit members are often but not always matrilineally related (Richard *et al.* 1996a; Lyrholm and Gyllensten 1998; Whitehead and Weilgart 2000; Mesnick 2001; Mesnick *et al.* 2003). Given that dependent calves do not make deep dives with their mothers, unit members provide alloparental care in the form of babysitting (which acts as anti-predator vigilance) and, in some units, allonursing (Whitehead 1996a; Gero *et al.* 2009). In the Pacific, individual social units associate for periods of a few days with other units to form temporary groups (Christal *et al.* 1998), while group formation is less common in the Atlantic (Whitehead *et al.* 2012). Each social unit has a distinctive repertoire, or dialect, as they show different usage patterns of a type of social vocalization called, 'codas' (Watkins and Schevill 1977; Weilgart and Whitehead 1997; Rendell and Whitehead 2003b). Units are also highly mobile, covering ranges spanning 1000 to 1500 kilometers (Dufault and Whitehead 1995; Whitehead *et al.* 2008) and as a result encounter and interact with other, presumably sometimes unknown, units regularly. In the Pacific, units only interact with other units possessing similar coda repertoires which suggests in-group favouritism based on dialect (Rendell and Whitehead 2003b). When cultural groups are symbolically marked and in-group favouritism in social learning occurs, this can reinforce conformist transmission of other culturally inherited behavioural variants and increase differences between groups (Henrich and Boyd 1998; Richerson and Boyd 2005). This is the case in this species as vocal clans, hundreds of units which share a common repertoire, also differ in movement patterns, habitat use, and foraging success (Whitehead and Rendell 2004); as well as diet (Marcoux *et al.* 2007b) and reproductive success (Marcoux *et al.* 2007a). Vocal clans may represent the numerically largest example of culturally-defined cooperative groups outside of humans (Rendell and Whitehead 2003b). Most significantly ecologically and evolutionarily, these vocal markers appear to segregate behaviour within sperm whale society to an extent that it affects the differential feeding and reproductive success of the cultural groups. During some periods, certain clans succeeded while others failed (Whitehead and Rendell 2004). These fitness consequences allow for the process of cultural group selection to function and for behavioural variation to direct the evolution of this species.

While behavioural variation among sperm whale units and clans has been well studied, relatively less is known about variation between individuals within units. Relatedness may structure individual-level social relationships within social units such that more closely related individuals interact more often (Gero *et al.* 2008) and that a mother's closest relative is more likely to act as babysitter than other females (Gero *et al.* 2009). Nonetheless, sociality is clearly vital to the way sperm whales live. Sociality is thought to have evolved among females in order to provide alloparents for their defenceless calves (Best 1979; Arnbom and Whitehead 1989; Whitehead 1996a). In a variable ocean, a sperm whale's social companions are their only constant. The primary difference between individuals is in their social environment, not the physical one. Therefore, a better understanding of how whales interact with their conspecifics socially is critical to understanding individual or group level variation in sperm whale behavior. The ocean limits visual and olfactory communication but is highly favourable to acoustic signals; therefore sperm whales' social communication is likely dominated by vocal signals. If vocal communication mediates much of their social interaction, then further study of variation in social and vocal behaviour in this species is warranted.

SOCIAL AND VOCAL COMPLEXITY

The social intelligence hypothesis proposes that individuals which live in complex social environments must not only deal with the challenges of the physical environment but must also solve problems related to their social interactions (Byrne and Whiten 1988; Whiten and Byrne 1997). Increased cognitive function is needed to deal with these issues in highly social species (Barton and Dunbar 1998). In particular, individuals need to be able to recognize and remember their interaction histories with other individuals in order to manage and express their behavioural intentions with each other. As a result, individuals which live in socially complex societies have a need for a more varied and functionally diverse communication system (Freeberg *et al.* 2012). That is to say that species which live in large social groups that have multiple social roles and flexible patterns of interaction would face selective pressures for more complex communicative signals in order to mediate this diversity of social interactions (Freeberg *et al.* 2012). There is a wealth of studies to support the idea that social complexity drives communicative complexity, in particular vocal communication, among a wide variety of species including: birds (Kroodsma 1977; Freeberg 2006), rodents (Blumstein and Armitage 1997), bats (Wilkinson 2003), and primates (McComb and Semple 2005).

The social and vocal complexity of cetacean societies covers a wide continuum. Humpback whales (*Megaptera novaeangliae*) form primarily unstable associations and their offspring have a comparatively short period of dependence with their mothers (<1 year; Clapham 2000). Although they produce hierarchically complex songs (Payne and McVay 1971; Suzuki *et al.* 2006) which change over time (Noad *et al.* 2000), all individuals in the population use the same song such that there is only population-level variation in song (Payne and Guinee 1983). By contrast bottlenose dolphins (*Tursiops* spp.) live in a dynamic fission-fusion system of ever changing social partners, some of which are longer term associates and others rare encounters within the social network of their communities (Wells 1991; Connor *et al.* 2000). Social learning likely contributes to behavioural development in bottlenose dolphins as they have long periods of dependence on their mothers (3-8 years; Mann *et al.* 2000a). Bottlenose dolphins have individually-specific signature whistles which identify individuals and are thought to facilitate these more complex individualized interactions (Caldwell and Caldwell 1965). Furthermore, the similarity between the signature whistles of pairs of individuals relates to their type of association. Males who generally disperse farther from their mothers than females, have signature whistles which are similar to their mother's, while female offspring develop novel whistles quite distinct from their mother and other close associates in their community (Sayigh *et al.* 1990; Fripp *et al.* 2005). Females will retain their distinct whistles (Sayigh *et al.* 1990), while males alter their whistles to be more similar with their partners' when forming stable alliances at sexual maturity (Smolker and Pepper 1999; Watwood *et al.* 2004). But the coevolution of diverse communication systems and complex social structure among cetaceans is best exemplified among killer whales (*Orcinus orca*). Fish-eating 'resident' killer whales live in matrilines, within which both sexes remain their whole lives. Matrilines associate into 'pods' with other matrilines which share a similar socially learned traditional vocal dialect. Several genetically related ‘pods’ which share some similar vocalizations are grouped into ‘clans’ and several clans make up vocally distinct communities which use distinct, although sometimes overlapping, geographic areas but never mix socially (Ford 1991; Ford 2002b; Ford 2002a; Ford and Ellis 2006; Deecke *et al.* 2010; Ivkovich *et al.* 2010). Across species of cetacean, the variation in vocal communication is closely related to the complexity of social structures (Tyack 1986; Tyack and Sayigh 1997).

As for sperm whales, their vocalizations are almost entirely clicks (Backus and Schevill 1966). There are two main categories of click use, which are thought to function in social communication and echolocation respectively. Although the clicks used in each case are structurally different (Madsen *et al.* 2002), the key difference between the two is in the temporal patterning of the clicks themselves. The most common vocalization sperm whales produce is the ‘usual’ click, which is made almost continuously, at fairly regular 0.5-1s intervals, as echolocation while foraging (Madsen *et al.* 2002). The second common type of vocalization produced by sperm whales is most often recorded when socializing. Whales produce short stereotyped sequences of clicks, termed ‘codas’ (Watkins and Schevill 1977), which have also been recorded during the descent and ascent phases of foraging dives (Watwood *et al.* 2006; Schulz *et al.* 2008; Schulz *et al.* 2011).

The unique anatomy of the sperm whale nose creates a fortuitous feature of sperm whale clicks, their multi-pulsed structure (Norris and Harvey 1972). The click is made up of a set of uniformly spaced pulses with decaying amplitude, labelled p_0 and upwards (Figure 1-1).

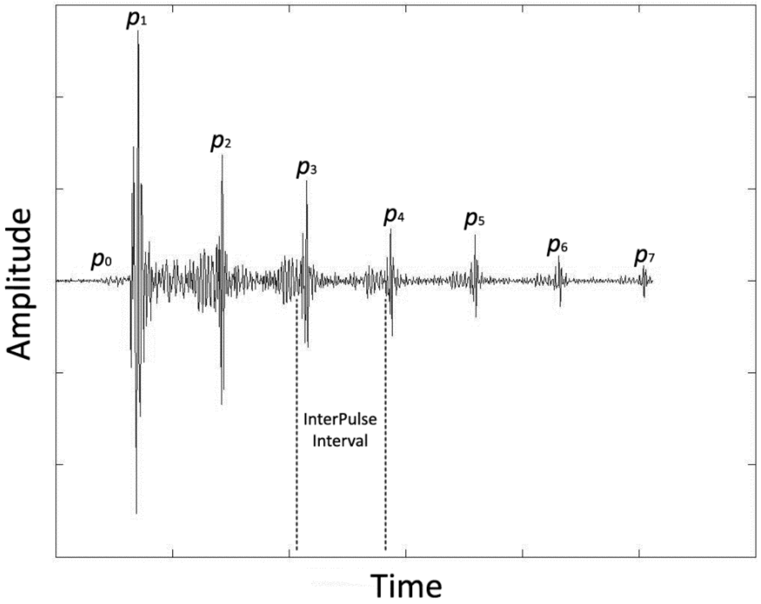


Figure 1-1: Illustration of a waveform and the interpulse interval (IPI) in a single coda click with a clear multi-pulse structure, adapted from Schulz (2007). Waveforms of echolocation clicks differ in that they are dominated by the energy content of the p1 pulse such that the subsequent pulses are far smaller in comparison.

The p_0 is the initial onset of the sound created at the phonic lips whose energy is transmitted directly into the water and does not travel through the spermaceti and junk bodies like the successive clicks (Figure 1-2, following page). The p_1 pulse makes up the bulk of the sound's energy and travels the length of the spermaceti and is reflected off the frontal air sac into the junk before entering the water (Møhl *et al.* 2003). The remaining clicks (p_2-p_7) are the result of a fraction of the p_1 pulse that does not enter the junk but is returned to the spermaceti organ by the frontal air sac which is then reflected back by the distal air sac before again reflecting off the frontal air sac and into the junk. This series of reverberations occurs once in the case of the p_2 pulse or an increasing number of times for successive pulses (Møhl *et al.* 2003). The assumed sound path of a usual click from generation site, the phonic lips, through the spermaceti organ and the junk bodies is indicated by arrows in Figure 1-2. The coda click differs in that it is not redirected into the junk and the sound energy is retained within the spermaceti organ and reverberates between the air sacs (Madsen *et al.* 2002). The interpulse interval (IPI) can be measured with the aid of a computer by simply measuring the time lag between pulses. By the nature of the sound's path, the time lag has a direct relationship with the size of the spermaceti organ (Gordon 1991; Rhinelander and Dawson 2004; Teloni *et al.* 2007). This in turn can, and has been, used to accurately measure individual animals using an equation which relates the IPI, and thus the length of the spermaceti, to actual body length (Adler-Frenchel 1980; Gordon 1991; Leaper *et al.* 1992; Pavan *et al.* 2000; Drouot *et al.* 2004; Rhinelander and Dawson 2004; Teloni *et al.* 2007; Growcott *et al.* 2011; Schulz *et al.* 2011).

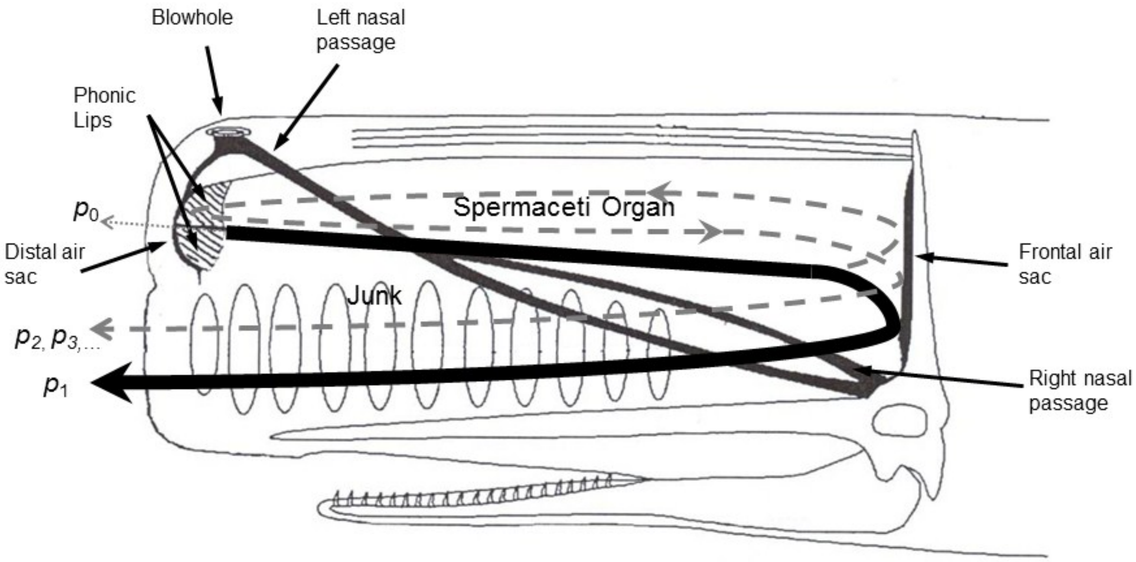


Figure 1-2: Assumed path of sound for successive pulses of an echolocation click adapted from Madsen *et al.* (2002). The thin dotted arrow shows the direct path taken by the p0 pulse. The dark black arrow marks the path taken by the p1 pulse which makes up the bulk of the sound's energy. The dashed grey arrow indicates the path taken by the remaining pulses.

These methods were further developed by Schulz *et al.* (2011), who used individually distinct IPI measurements to assign the identity of the vocalizing whale in small groups. They linked photoidentifications of diving whales to the IPI of their echolocation clicks made just after the onset of the dive, and further allowed codas produced by unidentified whales to be attributed to known whales based on their IPIs. Antunes *et al.* (2011) used these methods to study variation in the way individuals produce specific coda types. They concluded that individuals within one well-studied unit differed in the way they produced the '5R' coda type and suggested that this coda may function as an individual identifier. Both of these studies were major steps forward in our understanding of the vocal complexity of this species.

Extending from individual-level work by Schulz *et al.* (2011) and Antunes *et al.* (2011) in the Atlantic, and group-level studies in the Pacific by Whitehead, Weilgart, Rendell, and their collaborators (Weilgart and Whitehead 1997; Rendell and Whitehead 2003b; Rendell and Whitehead 2004; Rendell and Whitehead 2005), this research asks: how homogeneous is sperm whale social and vocal behaviour? What, if anything, causes heterogeneity of social or vocal behaviours; and at what level does it occur? Recent advances in methodology (Schulz *et al.* 2011) and fortuitous characteristics of the Caribbean population (Gero *et al.* 2007) will allow me for the first time to dissect these questions at the level of the individual. This detailed level of social data among individuals is rare in mammals and has provided me with the opportunity to study this species at an unparalleled scale.

The first three chapters of this thesis focus on levels of social association, while the other two data chapters examine their corresponding vocal complexity. To begin the social analysis, in chapter 2, I broadly describe the social structure of the population of whales upon which this work focuses. While not explicitly testing hypotheses, descriptive studies like this one, which establish residency times, resighting rates, group sizes, and other general features of the study population are needed in order to provide the framework for comparative studies, particularly in species like the sperm whale, in which there is great geographic variation in behaviour and social structure (Whitehead *et al.* 2012). Chapter 3 extends previous work from my Master's thesis (Gero *et al.* 2008) that showed that there is variation in social patterns between individual unit members. In this chapter, I examine the dynamics of these individual-level interactions within social units across time and changes in social role within 7 different social units. Using multi-year social networks, I focus on the hypothesis that communal care for calves drives sociality in this species and test whether calves are in fact significant nodes in the network of sperm whale social units. Chapter 4 looks at heterogeneity of social associations both within and between the units which regularly use the waters off the island of Dominica. Given our definition of social units, one would expect that relationships within units are stronger than between them, but the stability of relationships between social units of sperm whales is poorly understood. Family units among African elephants (*Loxodonta africana*), a terrestrial mammal which is socio-ecologically similar to the sperm whale (Weilgart *et al.* 1996), exhibit long term preferences for other units which share part of their home range. Adding data collected over a decade prior to my own study, in Chapter 4, I am able to examine the stability of relationships between units over decadal timescales for the first time. As the final part of Chapter 4, I also test for variation in individual spatial positioning within units while foraging, given that structuring of social interactions often affects individual spatial relationships within groups (Hall and Fedigan 1997; Peterson *et al.* 2002; Hirsch 2007).

Chapters 5 and 6 focus on vocal complexity. If coda repertoires function in social identification at multiple levels, we would expect that the coda repertoires of different individuals and units might be distinguishable in two obvious ways: 1) by their repertoire of codas (*i.e.* variation in the presence, absence, and pattern of usage of various coda types), or 2) by an accent on given coda types (*i.e.* variation among individuals or members of different units in the acoustic characteristics of specific coda types which might be shared among some units). Chapters 5 and 6 test for significant levels of variation in repertoire and accent on coda types within and between individuals and units, respectively.

In the final chapter, I summarize vocal and social variation across the levels of sperm whale social structure and between ocean basins. I discuss the broad lessons learnt from thousands of hours of observation of sperm whale units and how these have improved our knowledge of sperm whale society. I conclude with a discussion of the implications of what I have learnt on our obligation to protect this species and conserve their ocean habitat.

CHAPTER 2

THE BEHAVIOUR AND SOCIAL STRUCTURE OF THE SPERM WHALES OF DOMINICA

We all grow up with the weight of history on us. Our ancestors dwell in the attics of our brains as they do in the spiraling chains of knowledge hidden in every cell of our bodies.

~Shirley Abbott

INTRODUCTION

At least 30 cetacean species have been listed as members of the fauna of the Caribbean Sea (Debrot and Barros 1994; Debrot *et al.* 1998; Mignucci-Giannoni 1998; Ward and Moscrop 1999; Ward *et al.* 2001). Much of our knowledge of the presence, distribution, and abundance of these animals stems from strandings, opportunistic sightings during research with other goals, commercial/military vessels with observers on board, catches from directed fisheries, or from a few directed research studies (Caldwell and Erdman 1963; Erdman 1970; Caldwell *et al.* 1971; Erdman *et al.* 1973; Caldwell and Caldwell 1975; van Bree 1975; Caldwell *et al.* 1976; Taruski and Winn 1976; Watkins and Moore 1982; Whitehead and Moore 1982; Reeves 1988; Matilla and Clapham 1989; Watkins *et al.* 1997; Gordon *et al.* 1998; Cardona-Maldonado and Mignucci-Giannoni 1999; Rosario-delestre *et al.* 1999). Most of these studies focused on a single species or family, or within the waters adjacent to a particular island or country, although, in more recent years, some inter-island data has become available (Jefferson and Lynn 1994; Roden and Mullin 2000; Mignucci-Giannoni *et al.* 2003; Swartz *et al.* 2003; Gero *et al.* 2007). Compared to the neighbouring Gulf of Mexico, relatively less work has been completed in the Caribbean Sea. As such, the cetacean inhabitants of the Caribbean Sea remain understudied and poorly known.

The sperm whale (*Physeter macrocephalus*, Linnaeus 1758) is considered to be 'cosmopolitan' in the Caribbean Region (Ward *et al.* 2001; Reeves 2005). They are an ecologically dominant species which feeds primarily on mesopelagic squid (Clarke 1980; Kanwisher and Ridgway 1983). Much of what is known about sperm whale behaviour has been garnered from a longitudinal study in the Eastern Tropical Pacific, but more recent work in the Atlantic has highlighted consistent social, vocal, and behavioural differences between populations in the two oceans (Whitehead *et al.* 2012).

In the Lesser Antilles, research opportunities are provided by the taller islands, Guadeloupe and Dominica in particular, within the calm lees of which researchers can find deep water close to shore in which to study sperm whales. Since the 1970's only a handful of studies have focused on sperm whales, and relatively little is known about their abundance, distribution or behaviour in the Caribbean compared to the wealth of information from the Eastern Tropical Pacific (summarized in Whitehead 2003) upon which the model for sperm whale behaviour and social structure is based. In the early 1980s and 1990s a research group from Wood Hole Oceanographic Institution led by Dr. William Watkins began studies on diving behaviour and vocalizations of sperm whales from Guadeloupe to the Grenadines (Watkins and Moore 1982; Watkins *et al.* 1985; Moore *et al.* 1993; Watkins *et al.* 1993; Watkins *et al.* 1999). More recently, a multiyear (1995, 1996, and 2000) study was undertaken by the International Fund for Animal Welfare to examine the distribution and residency of sperm whales off Dominica in an effort to assess the implications of a developing whalewatch industry (Gordon *et al.* 1998).

The population of sperm whales in the Eastern Caribbean is small and isolated from other animals in neighbouring parts of the North Atlantic Ocean (Gero *et al.* 2007). The high resighting rates, relatively long residency times (Gordon *et al.* 1998; Gero *et al.* 2007) and small unit sizes (Gero *et al.* 2009; Jaquet and Gendron 2009) have allowed us, for the first time, to conduct a detailed study of sperm whale individuals by tracking social units across an 8 year study. This level of understanding of the social interactions among individuals is rare in studies of large mammals in the wild, and never before achieved in a large pelagic cetacean. Here, I summarize the behaviour and social structure of the sperm whales of Dominica. The implications of these findings are discussed from a conservation perspective within the complex multinational management area that is the eastern Caribbean.

METHODS

FIELD METHODS

Groups of female and immature sperm whales were located and followed both acoustically, using hydrophones; and visually, by observers on one of four platforms (a dedicated 12m auxiliary sailing vessel, a dedicated 5m outboard skiff, a dedicated 11m outboard RHIB, or an 18m whale watch vessel) in an area that covered approximately 2000 km^2 along the entire west (leeward) coast of the island of Dominica (N15.30 W61.40), in waters sheltered from the trade winds. Research was conducted in the winters and/or spring of 2005 through 2012 for a total of just over 3056 hours with whales across 388 days of effort (Table 2-1). During outboard skiff seasons, the skiff was unable to operate on heavier weather days and so the research team boarded the larger whale-watch vessel to continue work. Whale watch tours focused their search effort on sperm whales. As a result, methods remained the same across all three platforms, with the work on those days being restricted only by the length of time spent at sea by the whale watch vessel.

Table 2-1: Effort across years

Year	Start Date	End Date	Days Effort	Platform
2005	January 14	April 13	62	Sailing only
2006	January 17	February 11	21	Whalewatch only
2007	January 28	February 28	30	Skiff and Whalewatch
2008	February 8	May 8	75	All
2009	January 11	March 29	64	Skiff and Whalewatch
2010	January 20	April 18	72	Sailing only
2011	March 5	April 14	35	RHIB only
2012	May 5	June 6	29	Sailing only

During daylight hours, clusters of individuals (an individual was considered part of a cluster if it was within approximately 3 adult-body lengths of any other cluster member, a ~40m "chain rule", and their behavior was coordinated, as in Whitehead 2003) visible at the surface were approached, and photographs were taken to identify individuals. If a calf was present in a given cluster, priority was given to taking dorsal fin pictures of the calf from alongside the larger animals, before moving the vessel behind the adults in the cluster to photograph distinct markings on the trailing edge of their flukes for individual identification purposes (Arnbom 1987).

Additional photoidentification data were collected off several islands by seven different organizations across 31 years. Field methods were of two types distinguished based on platform (Table 2-2): research vessels dedicated to comprehensive sperm whale research, including photoidentification, and opportunistic photoidentifications collected from whale watch vessels. Data collected by Woods Hole Oceanographic Institution (WHOI) in 1981, 1983, 1984, 1987, 1990, and 1991 were collected as a part of dedicated research on sperm whales which primarily focused on diving behaviour and acoustics (Watkins and Moore 1982; Watkins *et al.* 1985; Moore *et al.* 1993; Watkins *et al.* 1993; Watkins *et al.* 1999). The International Fund for Animal Welfare (IFAW) data from 1995 and 1996 (Gordon *et al.*, 1998), as well as 2000, were collected while groups of female and immature sperm whales were being actively located and followed using similar methods outlined above. The Ocean Research and Education Societies' (ORES) vessel *R/V Rambler* collected photoidentifications opportunistically in 1984. Between 2006 and 2009, opportunistic photoidentifications were also collected by observers onboard Anchorage Whale Watch's (AWW) motorized catamaran whale watch vessel which also actively searches for whales during 3 hour tours using both omnidirectional and directional hydrophones. A small number of photographs were collected opportunistically aboard another motorized catamaran whale watch vessel while Peter Evans from the Sea Watch Foundation (SWF) was in Dominica running a Multiple Land Use Project. Photoidentifications collected by the German Society for Dolphin Conservation (GRD) were collected from AWW's catamaran during either chartered day trips or their standard tours. Identifications collected by Association Evasion Tropicale (AET) between 2000 and 2009 and by Dalhousie University while in Guadeloupe in 2004 were taken from the Association's auxiliary sailing vessel which actively searched for sperm whales using a directional hydrophone.

In summary, while some of the data were collected opportunistically, approximately 92% of the photographs were collected by Dalhousie University during dedicated research between 2004 and 2012. Supplementary data, such as the age/sex class (as age/sex classification was completed in the field based on size, adult females and immatures are lumped as it is difficult to sex animals in the field, as such only three age/sex classes are used: mature male, adult female/immature, and dependent calf) of the animal identified, the exact date and time of the identification, time and date of encounters, and information about associations, was only readily available for fieldwork completed by the Dalhousie University and IFAW groups.

ANALYSES

Identifications:

A quality rating (Q) between 1 and 5 was assigned to each photograph, where 1 indicated a very poor photograph, and 5 indicated a very high quality photograph (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 a temporary identification code and then matched between encounters and to the Atlantic catalog using a computer-based matching program (Whitehead 1990). When two or more individuals fluked synchronously and could not all be photoidentified, in a few cases (<5% of identifications), well-known individuals whose flukes were observed by SG were recorded as having been identified and given a Q-rating of 6. Calves, which do not regularly fluke, were individually identified using the shape of its dorsal fin and distinct markings on its dorsal fin and body (Gero 2009). The best picture for each individual calf within each encounter was then matched between encounters by eye. An encounter was defined as the period of time from the first positive acoustic detection of sperm whales until 2 hours since last detection or when it was decided to leave the animals.

Assigning Groups:

During work off Dominica (Dalhousie only, 2005-2012), I defined a 'group' as all animals which are coordinating their movement and behaviour which are encountered on the same day (adapted from Whitehead 2003). Group size was estimated using the identification data. Observed group size was calculated by dividing the day's identifications into 2 sets (either by splitting at midday or by using half of the day's identifications) and then using a Petersen mark-recapture estimator to estimate the number of individuals present (Coakes and Whitehead 2004). Mean typical group size, an approximation of group size as experienced by a randomly chosen individual of the population as opposed to from an outside observer's perspective (Jarman 1974), was then calculated from those estimates as in Coakes and Whitehead (2004) using two levels of precision since the precision of these estimates decreases within increases in group size (Whitehead 2003).

Defining Units:

Units were delineated using methods following Christal *et al.* (1998) with more stringent minimum durations of association: a unit is a set of individuals for which each pair was observed associated during two different years (Christal *et al.* used a 30 day minimum rather than different years). That unit members were associated across years suggests stable, long-term companionship as defined by Whitehead *et al.* (1991). Here, I use a more relaxed definition of association in that individuals were deemed to be associating if they were identified within 2 hours of each other. This more permissive level of association allows for the inclusion of more individuals into defined units, but given the more stringent

Table 2-2: Details of the field projects, photographs, and individuals identified. Research Groups: WHOI-Woods Hole Oceanographic Institution, ORES-Oceanic Research and Education Society, IFAW-International Fund for Animal Welfare, SWF-Sea Watch Foundation, AET-Association Evasion Tropicale, AWW-Anchorage Whale Watch, GRD-German Society for Dolphin Conservation, and Dalhousie-Dalhousie University. Type defines the research platform as either D – dedicated research vessel or W – whale watch.

Dates	Nearest Island	Project Leader	Research Group	Type	# of Photos	Individuals Identified*
1981-1991	Dominica	William Watkins	WHOI	D	44	2
1984	Dominica	George Nichols	ORES	D	18	13
1995	Dominica	Jonathan Gordon	IFAW	D	218	59
1995	Grenada	Jonathan Gordon	IFAW	D	7	7
1996	Dominica	Jonathan Gordon	IFAW	D	81	36
2000	Guadeloupe	Carole Carlson	IFAW	D	7	6
1999	Dominica	Peter Evans	SWF	W	7	6
2000	Guadeloupe	Caroline Rinaldi	AET	W	9	8
2001	Guadeloupe	Caroline Rinaldi	AET	W	17	15
2002	Guadeloupe	Caroline Rinaldi	AET	W	11	9
2003	Guadeloupe	Caroline Rinaldi	AET	W	23	22
2005	Guadeloupe	Caroline Rinaldi	AET	W	275	75
2006	Guadeloupe	Caroline Rinaldi	AET	W	217	61
2007	Guadeloupe	Caroline Rinaldi	AET	W	170	46
2008	Guadeloupe	Caroline Rinaldi	AET	W	165	43
2009	Guadeloupe	Caroline Rinaldi	AET	W	6	4
2006	Dominica	Petra Charles	AWW	W	20	11
2007	Dominica	Pernell Francis	AWW	W	141	49
2008	Dominica	Pernell Francis	AWW	W	154	48
2009	Dominica	Pernell Francis	AWW	W	15	12
1999	Dominica	Andrea Steffen	GRD	W	7	3
2000	Dominica	Andrea Steffen	GRD	W	9	5
2001	Dominica	Andrea Steffen	GRD	W	48	14
2003	Dominica	Andrea Steffen	GRD	W	25	9
2004	Dominica	Andrea Steffen	GRD	W	11	6
2005	Dominica	Andrea Steffen	GRD	W	19	6
2006	Dominica	Andrea Steffen	GRD	W	18	6
Feb - Mar 2004	Guadeloupe	Shane Gero	Dalhousie	W	23	22
Jan – Apr 2005	Dominica	Hal Whitehead	Dalhousie	D	812	53
Mar 10 2005	Martinique	Hal Whitehead	Dalhousie	D	16	7
Mar 20 2005	St. Lucia	Hal Whitehead	Dalhousie	D	3	3
Jan – Feb 2006	Dominica	Shane Gero	Dalhousie	W	143	25
Feb 2007	Dominica	Shane Gero	Dalhousie	D/W	465	27
Feb–May 2008	Dominica	Shane Gero	Dalhousie	D	4137	112
May 11 2008	St. Vincent	Hal Whitehead	Dalhousie	D	45	7
Jan – Mar 2009	Dominica	Shane Gero	Dalhousie	D	1345	84
Jan – Mar 2010	Dominica	Shane Gero	Dalhousie	D	7322	83
Mar –Apr 2011	Dominica	Shane Gero	Dalhousie	D	2996	69
May –Jun 2012	Dominica	Shane Gero	Dalhousie	D	2868	52
Totals					**21872**	**419**

*Individuals identified are unique within each field season (row). Total number of individuals identified is unique across all seasons.

minimum durations between identifications (years apart) it still likely reflects stable, long-term companionship. Specifically, it includes individuals which might often be identified alone, as opposed to in clusters with other unit members, but still within close spatio-temporal association with its unit members across years. In addition, unit membership is transitive in that if A and B are unit members and so are B and C, then A and C are members of the same unit as well.

Distance to Shore and Depth of Encounters:

I calculated the distance to shore and depth of our position at the start of each encounter with whales. In order to standardize the temporal resolution of GPS tracks across years (2005-2012), only the first GPS location occurring during each encounter was used. Associated distance and depth values were extracted using Spatial Analyst Tools in ArcGIS 10 and averaged across years. Depths were obtained from a 100 by 100 meter resolution bathymetric model with a 1 meter accuracy provided by the Institute de Physique du Globe de Paris (IPGP)/ Institut Francais de Recherche pour l'Exploitation de la Mer (IFREMER), based on data collected by the IPGP/IFREMER in 1998 during the Aguadomar campaign. Distance from the shoreline was extracted from a 5 by 5 meter resolution raster layer created in ArcGIS 10, with the Euclidean Distance Tool, from shoreline information obtained from the Government of the Commonwealth of Dominica, Land and Surveys Division. Calculated averages do not include data from 2006, since no GPS positions were available for that year.

RESULTS

IDENTIFICATIONS ACROSS YEARS:

To date, 419 individual sperm whales (mature males, adult female/immatures, and calves) have been photographically identified in the Eastern Caribbean, primarily off the islands off Dominica and Guadeloupe. The number of individuals identified roughly correlated with effort, such that when more pictures were taken, more individuals were identified. Table 2-2 (on page 17) summarizes the number of individuals sighted during each field season by each organization and Figure 2-1 (on the following page) plots the discovery curves by date and by cumulative number of identifications. The plots suggest that every year fewer new individuals are being identified, but the curves are still rising. A summary of confirmed reidentifications across years is given in Table 2-3 (on the following page). Of the 419 individuals, 175 (42%) where identified in different years between 2 and 14 times from

1984 to 2012. Only two individuals were resighted from the oldest data from 1984, one of which was resighted in 2011 with a total period spanning 27 years between the first and most recent identifications.

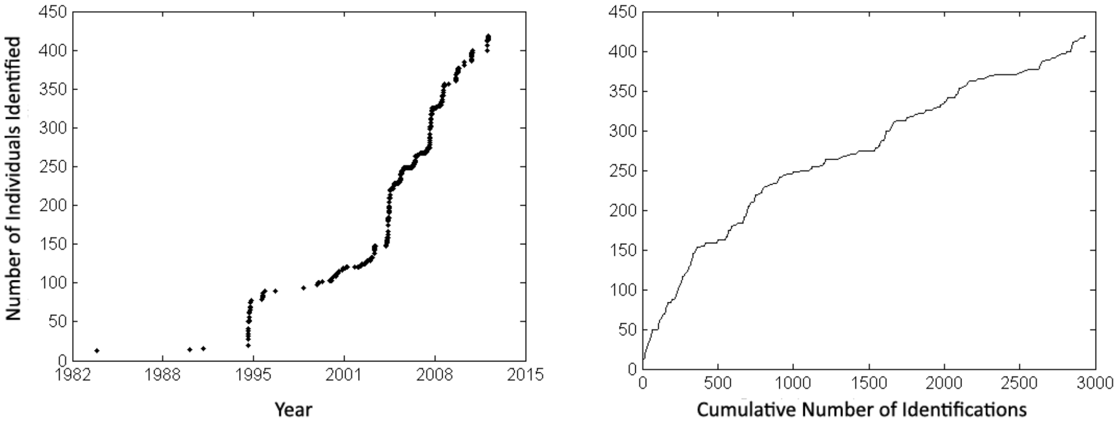


Figure 2-1: Discovery curves for individuals by date and by cumulative number of identifications.

Table 2-3: Reidentifications of sperm whales in the Eastern Caribbean including waters off Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent and Grenada between 1984 and 2012. Numbers of individuals identified in each year are given in bold along the diagonal. Only years in which individuals (mature males, adults, and dependent calves) were identified with Q≥3 photographs are shown.

1984	**13**																		
1990	0	**1**																	
1991	0	0	**1**																
1995	0	1	1	**65**															
1996	0	1	1	25	**36**														
1999	0	1	0	4	4	**9**													
2000	0	0	1	8	2	1	**19**												
2001	0	1	1	12	6	3	2	**27**											
2002	0	0	0	4	3	0	0	3	**8**										
2003	0	0	1	13	10	1	4	9	2	**30**									
2004	0	1	1	6	7	2	3	8	2	8	**27**								
2005	1	1	1	20	13	6	11	15	7	15	14	**134**							
2006	1	1	1	19	13	2	10	11	8	15	16	61	**90**						
2007	2	1	1	22	13	4	11	10	7	10	9	52	53	**85**					
2008	2	1	1	22	13	5	11	10	7	10	7	60	52	66	**146**				
2009	1	1	1	14	8	3	6	7	2	7	7	29	25	31	54	**88**			
2010	1	1	1	13	8	5	11	6	3	7	8	36	30	36	50	34	**82**		
2011	1	1	1	13	6	4	8	5	0	5	5	28	25	37	46	31	31	**70**	
2012	0	1	0	7	4	1	2	4	3	2	5	17	15	20	28	20	13	19	**52**
	1984	**1990**	**1991**	**1995**	**1996**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**	**2007**	**2008**	**2009**	**2010**	**2011**	**2012**

Encounter rates were high from January through May during the longitudinal work off Dominica (2005-2012). Whales were followed on a mean across years of 80.4% of days at sea (or portion thereof; range = 54-94%). The longest gap of time with effort without any encounters with whales was 18 straight days during the 2009 season. When whales were encountered off Dominica, we were able to track the animals for just over 10 hours on average but encounters ranged between 12 minutes and 5.5 days (133 hours). Short encounters were often ended due to weather and sea state conditions, which are often worse in the channels between islands. On average encounters occurred at 9.3 km from shore 95% CI = 0.5 - 18.8 km) in waters which averaged 3025 meters deep (95% CI = 1475 – 4575 m).

Mean typical groups sizes encountered off Dominica during longitudinal work are between 7 and 9 individuals depending on the method used (Table 2-4). Mean unit size off Dominica was 6.76 (SD = 2.80; range = 3 - 12) indicating that most groups encountered at sea include only one social unit. Cluster sizes are usually small off Dominica with an average of only 1.75 individuals (SD = 1.24; range = 1-11) observed together at the surface. Within a day, the lag between subsequent identifications of the same individual in different clusters has a mean of 94.1 minutes (maximum = 10.9 hours). Figure 2-2 plots time lag between sequential identifications. The multimodal distribution of Figure 2-2 would suggest that most individuals were identified every dive (~1 h), if not every other dive (~2 h); however, the longer lags suggest that some individuals are not identified multiple times on any given day. While it is difficult to get an accurate measure of dive time (fluke-up to surfacing) based on our methods, the mean time lag between identifications (fluke-up to fluke-up, and therefore, including the surface interval, sometimes called “cycle time”) is 57.1 minutes, when limited to lags between 40 and 70 minutes (the largest peak in Figure 2-2).

Table 2-4: Estimates of typical group size (TGS, mean and SD) observed off Dominica including only adults (excluding mature males and calves), calculated using Petersen mark–recapture methods with a day’s identifications divided in half by 2 different methods and 2 levels of the coefficient of variation (CV; as in Coakes and Whitehead 2004).

	CV < 0.25		CV < 0.40	
Splitting Method	*n*	TGS	*n*	TGS
Split at Midday	125	8.65 (4.40)	145	9.20 (4.10)
Split by half of Identifications	216	7.93 (4.55)	258	8.52 (4.25)

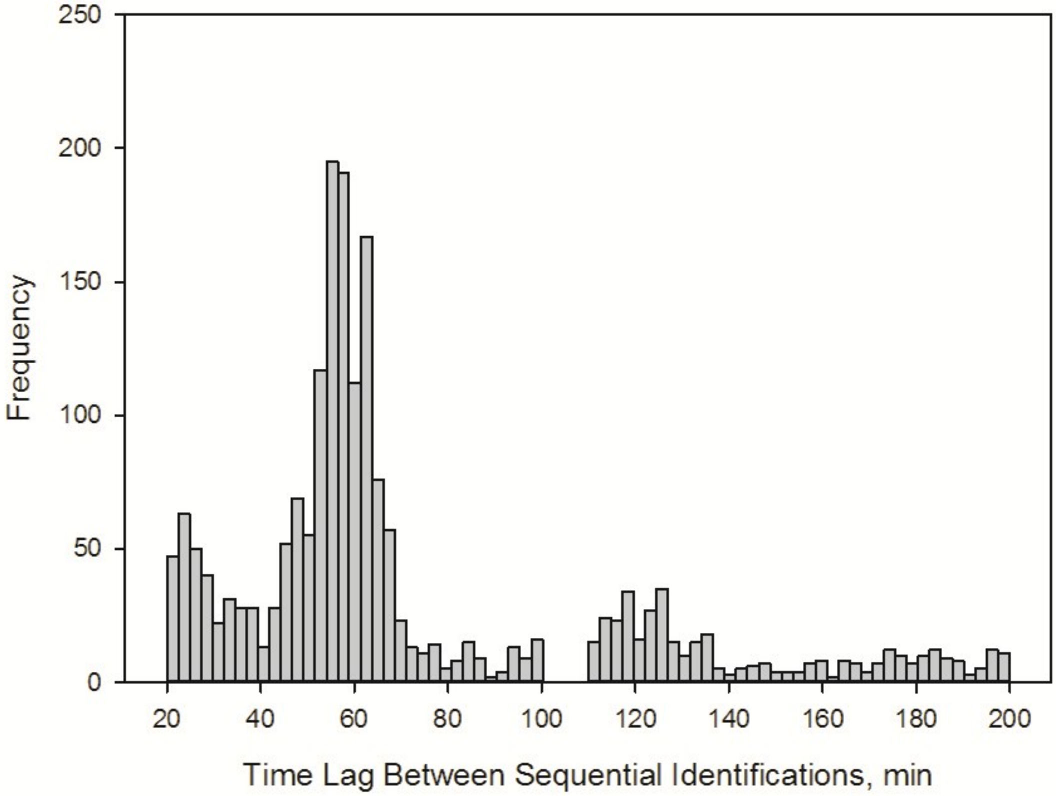


Figure 2-2: Time lags between sequential identifications of individuals on the same day for all lags less than 200 minutes.

SOCIAL UNITS:

Table 2-5 summarizes the observation records and composition of 17 social units identified off Dominica. Figure 2-3 visualizes the residency off Dominica for each unit based on identifications by year. Below, I briefly describe each unit's social dynamics. The composition and membership described are as of the year of last sighting. Potential members, which are individuals which were identified associated with unit members only within one season, but not at any other time, are also quantified. These potential members are likely members of the focal unit for which not enough data are available to assign them membership, or possibly also members of a totally unidentified unit which was seen grouped with the focal unit. As a result, many of the units for which fewer data are available have several individuals which are designated only as potential members.

Table 2-5: The 17 social units identified off Dominica. First and last year sighted, number of years and days in which at least one member was identified, total number of identifications (1984-2012), number of individuals, and composition as of the most recent year are given (A=Adult, C=Calf). Potential members are individuals which were identified as associated with unit members within only one year but never identified otherwise.

Unit	First	Last	Years	Days	Identifications	Composition	Potential
A	1996	2010	8	39	1943	7A 4C	1A
C	2004	2006	3	14	56	9A	2A
D	1984	2011	6	36	1223	5A 2C	None
F	1995	2012	15	173	3583	5A 2C	None
G	2007	2010	3	3	76	3A 1C	3A 1C
I	2008	2009	2	2	60	3A 1C	None
J	1995	2011	8	57	1496	4A 1C	None
K	2008	2012	3	6	128	4A 2C	3A
L	2005	2008	2	2	89	2A 1C	5A
N	1995	2012	12	119	1304	7A 2C	1A
P	1995	2012	10	21	426	9A	4A 3C
Q	2006	2011	5	9	105	5A	2A 2C
R	2001	2011	8	55	873	6A 2C	None
S	2004	2012	7	37	557	3A	None
T	1995	2011	11	68	1872	7A 2C	None
U	1990	2012	17	105	913	3A 1C	None
V	1995	2011	11	64	619	9A 3C	None

Unit A: 'The Atwood Collective'

Only one member of Unit A was identified prior to the initiation of continuous work off Dominica in 2005. Female #5586 was identified in 1996 and 1999 off Dominica, but no association data were available. Unit A was seen every year between 2005 and 2010. Unit A has at its base 4 adult females: 'Atwood' (#5586), 'Lady Oracle' (#5712), 'Oryx' (#5723), and 'Fruit Salad' (#5720). Two of which, Lady Oracle and Oryx, have had a second calf since our first encounter with them in 2005. Oryx had 'Crake' (#57232) between the 2009 and 2010 seasons. Her previous calf, 'Snowman' (#57231), which was born prior to 2005 but in 2012 still only very rarely makes fluke-up dives when alone, and so may not be fully weaned. Lady Oracle had her second calf, 'Anna' (#6088), between the 2007 and 2008 seasons. Her previous calf, 'Rounder' (#5714), is now weaned and often babysits its new sibling. Atwood recently had a calf between the 2009 and 2010 seasons and female Fruit Salad has an older (born prior to 2005), but still dependent, calf, 'Soursop' (#5710) which was only starting to be seen alone in 2011-2012. In this unit, calves have only been seen making suckling attempts off of their mothers. Another adult, #5710, is of unknown sex and may be a juvenile male. Finally, whale #5713 was seen with members of this unit in 2005 and 2008 but not since, so while the individual meets the definition of unit member it is uncertain if this animal is always with the unit, whether it has died or if it has simply not been identified in subsequent years.

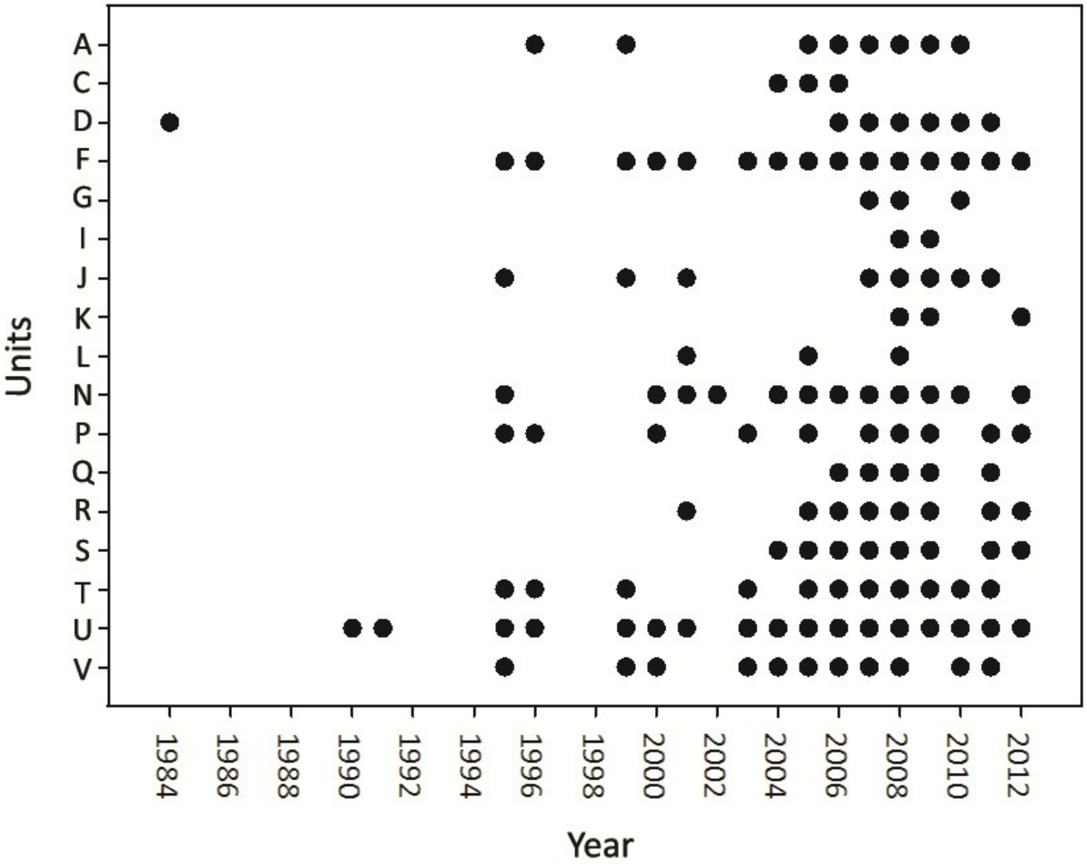


Figure 2-3: Years in which at least one member of a given unit was identified. No data available for 1985-1990, 1992-1994, and 1997-1999.

Unit C:

Unit C is a lesser known unit which was observed in three sequential years (2004-2006), but has not been reidentified since. Three members were first identified off Guadeloupe in 2004, then all nine were subsequently identified off Dominica in 2005 and six were reidentified in 2006. There are an additional two adults, who have only been identified with members of Unit C, but only within a single year: one which was sighted with them only in 2004 and one only in 2006.

Unit D:

As of 2011, this unit is made up of three mother-calf pairs and one smaller juvenile of unknown sex. The juvenile was only identified with the unit in two of the six years sighted (2008 and 2009). 'Duplex' (#5742) and 'DoubleBend' (#6087) make up the first mother calf pair. DoubleBend was first identified in 2008. The second is 'Divergent' and 'Distinct' (#6959), but Distinct was already almost weaned when first encountered in 2007 and only rarely suckled. In this unit, calves have only been observed making suckling attempts on their mothers. The last mother calf pair is 'Drifter' (#5973) and 'Drop' (#6069). Drifter was one of only two animals to be identified in 1984. If we assume that when one unit member is identified that the probability of the other unit members being present is high (Whitehead *et al.* 1991), then this would suggest that this unit has been using the waters off Dominica for at least 27 years. Other than Drifter's identification in 1984, this unit has been identified every year between 2007 and 2011.

Unit F - The Group of Seven

Unit F, or 'The Group of Seven', has at its base five adult females, who have been consistent associates since at least 1995. This unit has been observed every year for which I had photoidentification data from 1995 to 2012 with the exception of 2002. They have been identified off Guadeloupe and Dominica. Its members are the most sighted individuals during our work in Dominica (table 4). There have been several changes in the composition of the unit over the eight seasons of study. One female ('Fingers' #5722) lost her calf ('Thumb' #5703) after the 2005 season. The adult female 'Puzzle Piece' (#5130) disappeared between the 2005 and 2006 seasons and has not been sighted since, and three new calves have been born: 'Enigma' (male, #6068) to 'Mysterio' (#5561) in 2005, 'Tweak' (male, #6070) to 'Pinchy' (#5560) in 2007, and 'Digit' (unknown sex, #57221) to Fingers in April 2011. The three young calves were born after the field season in their birth year and so do not appear in data until the following year's research (*e.g.* Tweak was born late 2007 after the 2007 fieldwork, so the first year he is included is 2008). In this unit, calves have only been observed making suckling attempts on their mothers. Lastly, there is an immature male, 'Scar' (#5727), who is starting to become socially ostracised from his natal unit since the birth of his half-brother, Tweak, in 2007 (CHAPTER 3). Based on his length, Scar was estimated to be between 8 and 10 years old in 2005 (Schulz 2007), making him between 15 and 17 in 2012. Mysterio and Enigma have not been identified since 2010.

Unit G:

Only identified on a single day of each of three years, Unit G is still mostly unknown. Three adults fit our definition of unit members. Two had calves in 2008, but were not seen escorting them in 2010. The third adult had a calf in 2010, but not when initially encountered in 2008. Three other adults and one calf were identified in clusters with the three members of Unit G in 2010 but only in that one year. Given that 61% of the identifications were taken in 2010 alone and the scarcity of the data collected on this unit in 2007 and 2008, it is likely that these potential members were simply not identified. Additional sightings will confirm membership.

Unit I:

Unit I is made up of three adult females which barely meet the definition of unit members in that they were seen on a single day in each of two sequential years (2008 and 2009). One female has a large calf which still suckles.

Unit J: 'Jocasta's Unit'

Members of Unit J were identified in three different years (1995, 1999, and 2001) prior to the onset of continuous work off Dominica in 2005. A small unit of only four adults and one calf, Unit J is regularly seen off Dominica. When first encountered in 2007, 'Oedipus' (#5978) was still suckling from 'Jocasta' (#5987) and 'Sophocles' (#5979) and 'Laius' (#5981) often escorted Oedipus. Between the 2009 and 2010 seasons, 'Antigone' (#59871) was born. While this calf appears to make suckling attempts on both Oedipus and Laius, it is most often escorted and nursed by Jocasta. While maternity is uncertain, this is one of several units which provide potential evidence of allonursing within units in the Caribbean.

Unit K:

This unit had not been identified until 2008 and even then only rarely for a total of 6 days in 3 different years (2008, 2009, and 2012). Four adults meet my definition of unit members and there are an additional three which have been identified with them in single years. Members of this unit have only been identified off Dominica.

Unit L:

Only two females meet the definition of unit members to form Unit L. They were identified together in 2005 off Guadeloupe and reidentified with several other animals in 2008 off Dominica. One of these females had a dependent calf in 2008. There are an additional five adult females which were identified with the two members of unit L in 2008 and one of those was first identified in 2001 off Dominica.

Unit N:

As of 2012, there were seven adult females and two dependent calves in Unit N. One hard-to-identify, clean fluked, juvenile identified with them in 2010, but with no marks on its flukes it is unlikely that it would be identified between years. This unit has been identified off Guadeloupe and Dominica.

Unit P:

Another large unit, Unit P has nine adult females as of 2012. There are three calves with uncertain maternity. Members of Unit P have been identified in 10 different years for which data are available. Several members were first identified in 1995 and 1996 and most recently they were followed in 2012. This unit has been identified both off Dominica and Guadeloupe.

Unit Q:

Unit Q is a large and fairly unknown unit. Membership is still unclear, but as of 2011 at least five adult females fit our definition of unit members. First identified in 2006 and 2007 of Dominica, more individuals were identified off St. Vincent in 2008, before being identified again off Dominica in 2009 and 2011. There are an additional two adults and two calves with uncertain maternity that are possible members of this unit, but have only been identified in one year.

Unit R: 'RIP's Rascals'

Members of Unit R have been identified in 8 of the years for which data are available (2001, 2005-2009 and 2011). This unit has been identified off Martinique, Dominica and Guadeloupe. There are six adult females in this unit of which two have calves. 'Rita' (#5733) has a calf 'Rosalita' (#57331) which was first identified in 2005, likely as a young of the year. 'Raucous' (#5732) has a more independent calf 'Routine' (#6033). This unit has close interactions with Unit S.

Unit S: 'Sam's Squad'

Due to fairly sparse identifications in the early years, the membership of this unit was difficult to determine in part due to individuals transferring between units. At its base Unit S has a single female, Sam (#5726) whose associates have changed over the years. Sam was first identified in 2004 when no association data was available. In 2005, Sam was identified with two other adults each with a dependent calf. One of these adults was never reidentified, while the other ('TBB' #5759) was identified in 2006, as was Sam, but three days apart. Sam was identified in 2008 with a new female (#6052) with which she was identified in 2009, 2011, and 2012. TBB was reidentified in 2008, but was exclusively in clusters with members of Unit R until December 2008 when Sam was identified with TBB and the rest of Unit R. In 2009, Sam, TBB and #6052 were seen on two different days together. Unit S was not seen in 2010, nor was Unit R. In 2011 and 2012, TBB was only seen in clusters with Sam and/or #6052 even if members of Unit R were identified on the same day.

Unit T: 'Tooth's Team'

Tooth's Team, or Unit T, is a larger unit with seven adults and two calves. There are three mother-calf pairs. 'Tooth' (#5163) had 'Tusk' (#5701) prior to the onset of continuous work in Dominica and Tusk is now independent. There are two dependent calves which still suckle. 'Tina' (#5698) had 'Turner' (#56981) between the 2009 and 2010 seasons, and 'Tip' (#5585) had 'Top' (#6093) between the 2006 and 2007 seasons. Each of these calves has a primary babysitter. 'Tabitha' (#5946) and 'Terka' (#5699) babysit and appear to nurse Top and Turner, respectively. However, this unit is unique in that when both of the mothers are at depth feeding and Tabitha is not around, both of the calves will make suckling attempts from Terka at the same time while one is on each side of her. 'Teagan' (#5559) was identified with Unit T in 1995, 1996, 2007 and in 2008 escorting a calf, but has not been identified since. Members of Unit T were identified in 4 different years (1995, 1996, 1999, and 2003) prior to the longitudinal work off Dominica. They have been identified every year between 2005 and 2011 and off both Guadeloupe and Dominica.

Unit U: 'The Utensils'

Unit U, or The Utensils, is a small unit of 2 adult females, a juvenile female, and one male calf. 'Fork' (#5151) is 'Spoon's' (#6035) mother. Spoon is still dependent on Fork and still occasionally suckles. The unit also contains 'Canopener' (#6058), an independent juvenile female, and 'Knife' (#5562), the other adult female. Maternity for Canopener is still uncertain, but her size would suggest that Knife would likely be the mother given that Fork still has a dependent calf. Knife and Fork were first identified in 1990 and 1991, respectively; and members of this unit have been identified in 17 of the 19 years for which data were available (1990-2012 except 2002). They have been identified off Dominica and Guadeloupe. This unit is often associated with members of Unit F, The Group of Seven.

Unit V: 'Vive la France'

Unit V is a large unit of nine adult females and three dependent calves which is most often seen off Guadeloupe. While members of Unit V were first identified in 1995, 1999, and 2000 off Dominica, they have been seen yearly off Guadeloupe from 2003 to 2008 but not off Dominica even with the large amount of research effort between 2005 and 2008. They were identified in 2010 and 2011 off Dominica.

SINGLETONS:

Two individuals have been reidentified across sequential years, but spent each year with members of a different well-known unit. 'Carr' (#5988) was first identified with Unit F twice in 2006 and then spent all of 2007 with Unit F, in particular in clusters with a juvenile male from Unit F ('Scar', #5727). In 2008, however, Carr was consistently identified in clusters with Unit J. 'Sphinx' (#5989) showed a similar pattern spending the whole 2007 season with Unit J, but was only identified with members of Unit P in 2008. Neither singleton has been seen since even though all of the units have been encountered in subsequent years.

MATURE MALES:

A total of 25 mature males have been identified between 2005 and 2012 off Dominica. Mature males were observed in 6 of the 8 years with between 2 and 6 different males in a given year (none seen in 2009 and 2012). Clusters are twice as large when mature males are present (with males: mean= 3.75, SD = 3.16, n = 78; without males: mean = 1.70, SD = 1.10, n = 2967, Mann-Whitney: $p < 0.001$). Most males were only sighted on a single day, but a total of six males were identified on different days within the same year. The longest span between sightings of males within a year was 34 days, suggesting that residency of mature males in the waters off Dominica is on the order of a few days to a few weeks at a time (observed mean = 3.76 days, range = 1 – 34 days). While males were observed in clusters with females with dependent calves, mature males were never seen escorting a calf alone. When associating with units of females, males were not always initiating social or breeding behaviour. Males often behave in qualitatively similar way to the females, making foraging dives with them or resting when the units rest. In one extreme case, a mature male charged in from offshore swimming purposefully and quickly at the surface, while making the sex-specific 'clang' vocalization (Weilgart and Whitehead 1988), towards members of Unit J. However, Unit J had just gone into a resting/sleep state (vertical suspension underwater; Miller *et al.* 2008). Rather than the females waking in response to his arrival, the male began to rest/sleep within a few minutes of joining them. Several hours later, upon waking up, there was an exchange of codas with little interaction and the male departed in the opposite direction of the unit which resumed normal foraging behaviour.

On only one occasion (two days with a 4 day span between) were two mature males sighted together. In this case, both produced clangs when with the females. The two were seen with the same unit of different days (Unit R) and only one of the two males was identified with Unit R two days later. Their interactions were not antagonistic and were seen in clusters together at the surface without females in close proximity.

Only two males were identified in different years and only one of them was identified in three different years, but in each case they were identified on only one day each year. The first was sighted in 2001 and then again in 2004. While association data was not available for 2001; in 2004, this male was seen on the same day as Unit C. The other was first identified in 2000 and then again in 2008 and 2010. In 2008, this second male was identified on three different days each with members of a different unit: Unit A, Unit R, and Unit U. Then he was identified again in 2010 with members of Unit J and Unit D on one day. Association data were not available for this male in 2000.

DISCUSSION

During this work in Dominica, we were able to track social units of sperm whales across days, months and between years. In many ways, their behaviour differs from the model from the Pacific. Caribbean units appear to range over smaller areas than in other regions (Whitehead *et al.* 2012), which has allowed us to collect an unparalleled dataset at the level of the individual and to observe differences between social units. I have spent much more time with Unit F, 'The Group of Seven', than with most of the other units by a large margin. As a result, they have served as the exemplar for sperm whale behaviour in the eastern Caribbean. However, other units do differ from the way Unit F behaves. Based primarily on observations of Unit F, it was concluded that allonursing was not occurring in the Caribbean (Gero *et al.* 2009). The females of Unit F babysit each other's calves but appear not to nurse them; however, at least two other units provide evidence of allonursing or attempted allonursing in the Caribbean. Interestingly, both units appear to do so differently. In Unit J, the calf attempted to suckle from every adult in the unit, while in Unit T, each of the two calves had a different primary babysitter, but when both calves ended up with one particular female, she nursed them both at the same time. Calves are present in the vast majority of units which is in strong contrast to those studied in the Pacific in which calves were rare. Calves appear to create much of the social dynamics within units (CHAPTER 3) and babysitting may be one factor leading to group formation (Best 1979; Best *et al.* 1984; Whitehead 1996a).

While Unit F is about average in size, the largest of the units are almost double in size and the smallest units are only two mature females and their offspring. Overall, units in the Caribbean are smaller when compared to the Pacific and other parts of the Atlantic (Jaquet and Gendron 2009; Whitehead *et al.* 2012). Units also appear to differ vocally, in that different units have distinguishable coda repertoires, while all share the predominant coda types of the Eastern Caribbean Clan (CHAPTER 6).

In most cases, units have only been identified off the coasts of Dominica and Guadeloupe, but these islands have by far the most effort in their waters. Identifications off islands further south are primarily based on opportunistic photographs. The longest distance between reidentifications is between the islands of Dominica and Grenada (~450km). However, all of the Lesser Antilles are separated by less than 1000km in a straight line which would suggest that these units may range across the entire eastern Caribbean given that sperm whales are known to travel distances over 1000 kilometers regularly (Whitehead *et al.* 2008).

The two roving singleton animals provide interesting new insight into the immature years of male sperm whales. A plausible interpretation of their association patterns is that these are subadult males who have recently separated from their natal family units. Separating from the natal unit occurs slowly, and can take several years, as immature males spend less and less time with their mothers and their unit members (CHAPTER 3). Young males who have recently left their natal unit may fill this lack of social interactions by seeking companionship with other young males, as may have been the case with Carr and Scar in 2007. I can speculate that these encounters with roving subadult males may encourage immature males to leave their units to join them in a bachelor group.

While mature males have been sighted alone without any females in close proximity, generally mature males appear to aggregate otherwise dispersed units of females. Cluster sizes are significantly larger when males are present. Residency of mature males in the water off Dominica appears to be on the scale of a few days to a few weeks which compares with previous results off Dominica (Watkins *et al.* 1999) and the Galapagos Islands (Whitehead 1993). In one case, members from six different units were identified off the coast of Dominica on the same day within proximity of a single male. If we assume all unit members were present that would result in an aggregation of 44 females and immature, a substantial part of the whole eastern Caribbean population, in addition to the mature male. This would provide some support for the suggestion that female choice plays an important role in their mating system (Whitehead 2003). Another mature male was reidentified off Dominica on single days in three different years spanning a total of ten years. Unfortunately, I can only speculate as to the ranging behaviour between resightings of males like this one. Males may be 1) leaving the Caribbean on a regular or irregular basis for colder more productive waters but returning annually or repeatedly over several years, 2) leaving the Caribbean but roaming widely through the tropics in search of mates across long periods of time, including revisiting the Caribbean, followed by long periods in colder waters feeding, 3) remaining in the Caribbean to breed for several years, or some combination of these. Currently, I have little evidence to choose among these possibilities. Mature males are difficult to study as they cover large spatial and temporal scales. It is now known that immature males use a similar coda repertoire to that of their natal unit (Schulz *et al.* 2011). What still remains to be seen is if males ever return to their natal waters to breed or if the coda repertoire is used to prevent inbreeding (Whitehead 2003). The nuclear genetic homogeneity across oceans and clear female philopatry (Lyrholm *et al.* 1999; Engelhaupt *et al.* 2009) would suggest that males may show a preference for females from vocal clans other than their own (Rendell *et al.* 2005). Alternatively, this pattern may be the result of females showing a preference for males from different vocal clans than their own such that males avoid areas which are predominantly populated by units from their natal clan. In either case, the males seen in the Eastern Caribbean likely originate from elsewhere in the Atlantic as vocal clans are geographically structured in the Atlantic (Antunes 2009).

Several units have been identified off the islands every year for the last decade and there is some evidence that members of one unit have been using the waters off Dominica for the last 27 years. Almost half (42%) of the individuals have been reidentified across years in the study area. These residency times and high resighting rates within their small ranges would suggest that this is preferred habitat for these social units, thereby, leaving these animals vulnerable to the degradation of this relatively small area. Furthermore, this residency, and close proximity to populated coasts, exposes these small units to repeated interactions with whale watch vessels and makes them vulnerable should the current whale watching activities in the Caribbean grow substantially. Groups encountered off Dominica are small, often containing only one unit, and usually there seems to be just one group off the island. This would indicate that at any one time there are only about 7 animals off the western coast of the island. With so few animals offshore on any given day, tour boat effort is not easily diffused, although current whale watching in Dominica appears not be preventing these units from using preferred habitat over many years. However, based on research into the impacts of whale watching and boat traffic in other regions (Nowacek *et al.* 2001; Williams *et al.* 2002a; Williams *et al.* 2002b; Constantine *et al.* 2004; Lusseau 2004; Lusseau and Higham 2004; Scheidat *et al.* 2004; Lusseau 2005; Bejder *et al.* 2006a; Bejder *et al.* 2006b; Lusseau 2006; Williams *et al.* 2006; Williams and Ashe 2007;), this could easily change with the addition of only one or two more commercial vessels, with an increase in non-commercial approaches from private yachts, or increased commercial shipping into Dominica. Specifically, sperm whales appear to alter their surface intervals, breathing rates, and echolocation patterns in response to boat presence (Richter *et al.* 2006). Alternatively, we might already be dealing with a shifted baseline so that the animals we observe, or most of them, are already habituated to anthropogenic disturbance, already tolerate high levels of boat traffic, and that the more sensitive animals have already emigrated from the area (Bejder *et al.* 2006b; Richter *et al.* 2006).

Perhaps of greater concern are the bourgeoning commercial swim-with-the-whale operations in Dominica. Operators have begun offering tourists the opportunity to swim-with cetaceans. The focus of these operations is primarily the sperm whales, but in-water observations have been attempted with several other species including short-finned pilot whales (*Globicephala macrorhynchus*), rough-toothed dolphins (*Steno bredanensis*), as well as, pygmy (*Feresa attenuata*) and false killer whales (*Pseudorca crassidens*). Current knowledge indicates that in many cases swim-with activities are disturbing to targeted animals (Constantine 2001; Samuels *et al.* 2003; Lundquist *et al.* 2012). Nevertheless, intense popular demand for swim-with programs is pushing the growth of the industry, in Dominica and elsewhere, beyond what might be considered prudent based on current data. Effective management of tourism operations will be vital in securing a long-term future for this small sperm whale population.

The animals present in Dominican waters are members of a small population which spans the waters of most of the nations in the Eastern Caribbean. As a result, individual states will not be able to effectively manage the population in isolation, as they will effectively be only managing a part of the individuals' range and any threat to these species in one jurisdiction will therefore represent a threat in others. As such, local governments should consider working towards drafting international agreements governing sperm whales as a cross-border species of concern.

CHAPTER 3
CALVES AS SOCIAL HUBS: SOCIAL DYNAMICS OF SPERM WHALE UNITS

The family. We were a strange little band of characters trudging through life sharing diseases and toothpaste, coveting one another's desserts, hiding shampoo, borrowing money, locking each other out of our rooms, inflicting pain and kissing to heal it in the same instant, loving, laughing, defending, and trying to figure out the common thread that bound us all together.

~Erma Bombeck

INTRODUCTION

Among mammals, group formation is thought to provide increased access to resources or improved protection from predators (Alexander 1974). For the cetaceans, it is believed that the latter is the primary factor promoting groups (Connor 2000). By living in groups, individuals reduce the chances of being preyed upon through increased vigilance, dilution, predator mobbing, or predator confusion (Connor 2000). In my study species, the sperm whale (*Physeter macrocephalus,* Linnaeus 1758), the sexes have different patterns of gregariousness, presumably due to differing selective pressures. Female and immature sperm whales live in stable social groupings, called units, characterised by stable long-term social relationships between individuals (Christal *et al.* 1998; Whitehead 1999; Whitehead and Weilgart 2000) which are often, but not always, matrilineally related (Richard *et al.* 1996a; Lyrholm *et al.* 1999; Mesnick 2001). However, males disperse from their natal units in their early teens and live relatively solitary lives at higher latitudes (Whitehead and Weilgart 2000). Based on these contrasting patterns, group living among females is thought to have evolved through an increase in offspring survival as a result of providing babysitters for calves at the surface while mothers make long (ca. 40 min), deep (ca. 500m) foraging dives (Best 1979; Gordon 1987; Whitehead 1996a; Whitehead 2003). In contrast adult males are solitary or form ephemeral groups, presumably because there is no benefit to permanent grouping (Whitehead 2003). Thus, it can be hypothesized that the evolution of communal care for calves was the driving force for sociality in female sperm whales (Best 1979; Arnbom and Whitehead 1989; Whitehead 1996a).

Should this evolutionary framework hold, one would expect that calves play a central role in the social relationships within a unit. Social network analysis has been used to study a variety of aspects of animal interactions including information transfer (Krutzen *et al.* 2005), cooperative behaviors (Croft *et al.* 2006), and social role (Lusseau 2007). However, many have used binary or filtered networks which are static in time; here, I construct weighted social networks based on yearly matrices of associations and correlate them across years to study changes in the animals' social network and examine why these changes have occurred. Gero and colleagues (Gero *et al.* 2008) showed that individuals within a particularly well-studied social unit of sperm whales have preferred associates and avoidances among their unit-members and that these associations are correlated with genetic relatedness. Changes in composition within this unit over the course of this study allowed us to compare changes in relationships and network statistics with changes in age and social role and to investigate reciprocity of allocare. I then compared the patterns observed in this unit with those in six other units for which I had sufficient data to conduct similar analyses. In particular, I focused on the hypothesis of communal care and sociality and test if calves are significant nodes in the network of sperm whale social units.

METHODS

FIELD METHODS

Social units of female and immature sperm whales were located and followed in an area that covered approximately 2000 km^2 along the entire west (leeward) coast of the island of Dominica (N15.30 W61.40). Research was conducted from one of three platforms (a dedicated auxiliary sailing vessel, a dedicated outboard skiff, or a whale watch vessel) during the winters of 2005 through 2010 for a total of 2549 hours with whales across 324 days of effort (Table 3-1). During outboard skiff seasons, on heavier weather days, when the small (5m, 88hp) skiff was unable to operate, the research team operated from a larger (60ft, twin 420hp) whale watch vessel. Whale watch tours focused their search effort on sperm whales. As a result, methods remained the same across all three platforms, with the work on those days being restricted only by the length of time spent at sea by the whale watch vessel.

Table 3-1: Effort across years

Year	Start Date	End Date	Days Effort	Platform
2005	January 14	April 13	62	Sailing only
2006	January 17	February 11	21	Whalewatch only
2007	January 28	February 28	30	Skiff and Whalewatch
2008	February 8	May 8	75	All
2009	January 11	March 29	64	Skiff and Whalewatch
2010	January 20	April 18	72	Sailing only

During daylight hours, clusters of individuals visible at the surface were approached and photographs were taken to identify individuals. Priority was given to taking dorsal fin pictures of the calf from alongside the animals if calves were present, before moving behind the adults in the cluster in order to photograph distinct markings on the trailing edge of their flukes for individual identification purposes (Arnbom 1987). Sloughed skin samples were collected in the slicks of individuals after identification for genetic determination of sex, haplotype, and pairwise relatedness, (Whitehead *et al.* 1990; Amos *et al.* 1992; Richard *et al.* 1996a; Richard *et al.* 1996b). Relatedness of the individuals in this study was determined previously as in Gero *et al.* (2008)

Additional data had been collected, using similar methods, by the International Fund for Animal Welfare (IFAW) during the winters of 1995 and 1996 (dedicated sailboat, 59 days effort; see Gordon *et al.* 1998). These data were used to provide a long-term comparison of association patterns over more than a decade.

ANALYSES

Identifications

A quality rating (Q) between 1 and 5 was designated to each photograph, where 1 indicated a very poor photograph, and 5 indicated a very high quality photograph (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 encounters was assigned a temporary identification code then matched between encounters using a computer-based matching program (Whitehead 1990). In a few cases (<5% of identifications), well-known individuals which could not be photographed when multiple animals fluked synchronously but whose flukes were observed by SG were recorded as identified and given a Q-rating of 6. Calves, which do not fluke, were individually identified using the shape of their dorsal fin and distinct markings on the dorsal fin and body. The best picture for each individual calf within each encounter was then matched between encounters by eye.

Defining Associations

Units were delineated using methods following Christal *et al.* (1998) with more stringent minimum durations of association: a unit is a set of individuals for which each pair was observed associated during two different years. (Christal *et al.* used a 30 day minimum rather than different years). That unit members were associated across years suggests stable, long-term companionship as defined in Whitehead *et al.* (1991).

To examine social relationships within units, individuals were deemed to be associating if they were within the same cluster at the surface. The 'gambit of the group' or the assumption that membership in the same spatio-temporal grouping indicates probability of behavioural interaction (Whitehead and Dufault 1999) is likely satisfied in this case as individuals clustered together at the surface often interact vocally by matching or echoing codas, a social vocalisation, upon initiating dives (Schulz *et al.* 2008). An individual was considered part of a cluster if it was within approximately 3 adult-body lengths of any other cluster member (~40m "chain rule") and their behaviours were coordinated (Whitehead 2003). A 2hr sampling period was used (such that individuals observed in the same cluster during a two hour sampling period are said to be associated within the sampling period) along with the "Half-Weight Index" (HWI), as this measure of association accounts best for observer biases that are usually inherent in photo-identification techniques (Cairns and Schwager 1987). The HWI estimates the proportion of time when a whale is at the surface and is clustered with the other whale.

Calculation of Network Statistics

I constructed weighted social networks based on yearly matrices of association and calculated five nodal network measures: Strength (a measure of gregariousness), eigenvector centrality (a measure of how well an individual is connected), reach (a measure of indirect connectedness), clustering coefficient (a measure of how well one's associates are connected with each other), and affinity (a measure of the average weighted strength of associates). All measures are defined and calculated as described in Lusseau *et al.* (2008) and Whitehead (2008a; 2009), so that if the association index of individuals I and J is a_{IJ}, a_{II} is always 0, and the matrix of all association indices is a, the measures for individual I are:

Strength: $s_{\mathbf{I}} = \sum_{\mathbf{J}} a_{\mathbf{IJ}}$

Eigenvector centrality: e_{I} = (first eigenvector of $\boldsymbol{a}$)$_{\mathrm{I}}$

Reach: $r_{\mathbf{I}} = \sum_{\mathbf{J}} a_{\mathbf{IJ}} \cdot s_{\mathbf{J}}$

Clustering coefficient: $$c_{\mathbf{IJ}} = \frac{\sum_{\mathbf{J}} \sum_{\mathbf{K}} a_{\mathbf{IJ}} \cdot a_{\mathbf{IK}} \cdot a_{\mathbf{JK}}}{\mathbf{max}(a_{\mathbf{JK}}) \cdot \sum_{\mathbf{J}} \sum_{\mathbf{K}} a_{\mathbf{IJ}} \cdot a_{\mathbf{JK}}}$$

Affinity: $f_{\mathrm{I}} = r_{\mathrm{I}}/s_{\mathrm{I}}$

Standard errors around measures are based on 1000 bootstrap replicates (Lusseau *et al.* 2008).

Between-Year Comparisons

Mantel Z-tests (Mantel 1967; Schnell *et al.* 1985) and matrix correlation coefficients between matrices of associations calculated between the adults within each year indicated whether the association indices were correlated between years or if patterns of association change through time. A test variant, the Rr-test, was also used as it controls for individual gregariousness by replacing the values of association with their within-row ranks (i.e. within-individual ranks; Hemelrijk 1990). Correlations between studies separated by the same number of years were averaged in order to get an average correlation coefficient for a given time lag.

The calculation of the HWI and network statistics, as well as the Rr-tests described above were carried out using *SOCPROG* 2.3 (Whitehead 2009) in *MATLAB* 2006B (The Mathworks, Inc., MA, USA).

RESULTS

UNIT F - THE GROUP OF SEVEN

Unit F, or 'The Group of Seven' (GOS), has at its base five adult females, who have been consistent associates since at least 1995 (Gero *et al.* 2007). This unit has been observed every year from 2005 to 2010 and its members are the most sighted individuals during our work in Dominica (average 182 clusters per individual whale; range 91-262). There have been several changes in the composition of the unit over the six seasons of study (Figure 3-1). One female ('Fingers' #5722) lost her calf ('Thumb' #5703) after the 2005 season, 'Puzzle Piece' (#5130) disappeared between the 2005 and 2006 seasons and has not been sighted since, and two new calves have been born: 'Enigma' (#6068) to 'Mysterio' (#5561) in 2005 and 'Tweak' (#6070) to 'Pinchy' (#5560) in 2007 (Figure 3-1). The two young calves were born late in the year and so do not appear in data until the following year's research (*e.g.* Tweak was born late 2007 after the 2007 fieldwork, so the first year he is included is 2008). Lastly, there is an immature male, 'Scar' (#5727), who, based on his length, was estimated to be between 8 and 10 years of age in 2005 (Schulz 2007), making him between 13 and 15 years old in 2010.

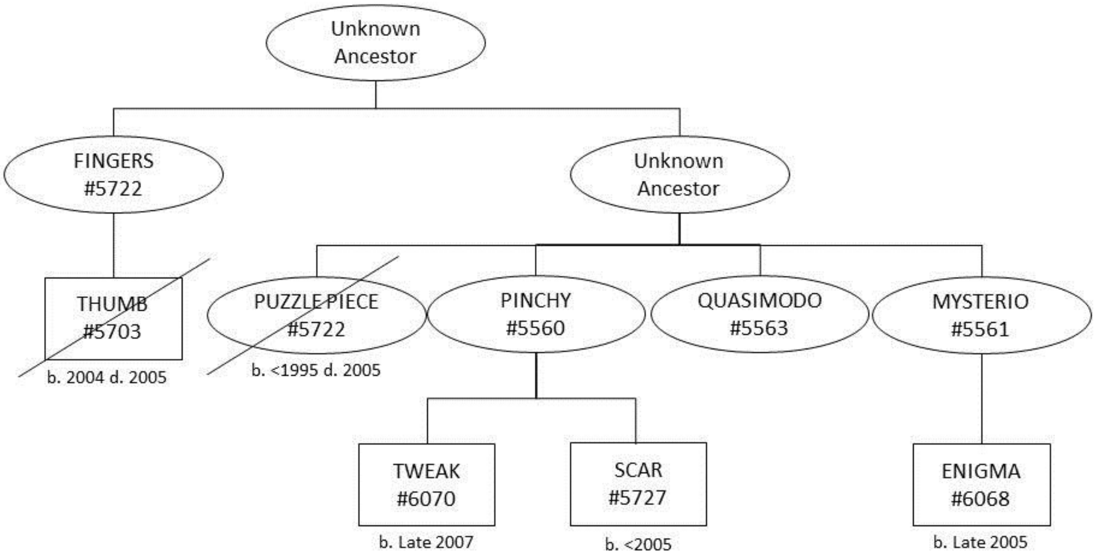


Figure 3-1: The Group of Seven from 2005-2010 laid out in a likely pedigree (S. Gero and C. Herbinger, unpublished data) based on 13 microsatellite markers (Gero *et al.* 2008). Males are squares, females are circles, and deceased animals are crossed out.

Relationships across Years

Matrix correlations between years suggest that social relationships build upon themselves and are not constant. Mantel Z-tests between some pairs of sequential years showed a greater correlation than expected by chance (2005-2006: Mantel Z-test; p = 0.028; matrix correlation of association matrices 0.68063; and 2006-2007: Mantel Z-test; p = 0.007; matrix correlation of association matrices 0.79097), but as the time lag increases, the correlation coefficients between association matrices for each year decrease (Table 3-2). For the five GOS females seen in 1995-1996, as well as, during the 2005-2010 fieldwork; Mantel and Rr-tests gave no indication that there were similarities in the patterns of association between pooled periods over a decade apart (Mantel Z-test: matrix correlation = 0.30, p = 0.23; Rr-test: matrix correlation = 0.12, p = 0.403) or between any particular year and the pooled 1995-1996 dataset (Table 3-2). Patterns of association did not differ whether Q6 identifications were included or excluded.

Table 3-2: Rr-Test correlation coefficients and lagged means of Group of Seven association matrices from 2005-2010 excluding calves.

Year	2005	2006	2007	2008	2009	2010	Time Lag	Mean
1995-1996	-0.36	0.29	0.13	0.31	-0.26	0.25	**With 95/96***	0.06
2005	1	0.21	0.25	-0.28	-0.49	-0.08	**1 Year**	0.23
2006		1	0.68	0.14	0.08	0.09	**2 Year**	0.21
2007			1	0.23	-0.02	0.09	**3 Year**	-0.04
2008				1	-0.07	0.46	**4 Year**	-0.20
2009					1	0.09	**5 Year**	-0.08**
2010						1		

Mothers and Calves

Mothers and calves appear to be the center of the unit's social network. All calves in the Group of Seven had high or the highest values for all of the network statistics calculated. The mothers, Pinchy (#5560) and Mysterio (#5561), both show sharp drops in Strength and Connectedness in the first year of their new calves' lives (Figure 3-2). Reach also appears to drop in the first year for both mothers.

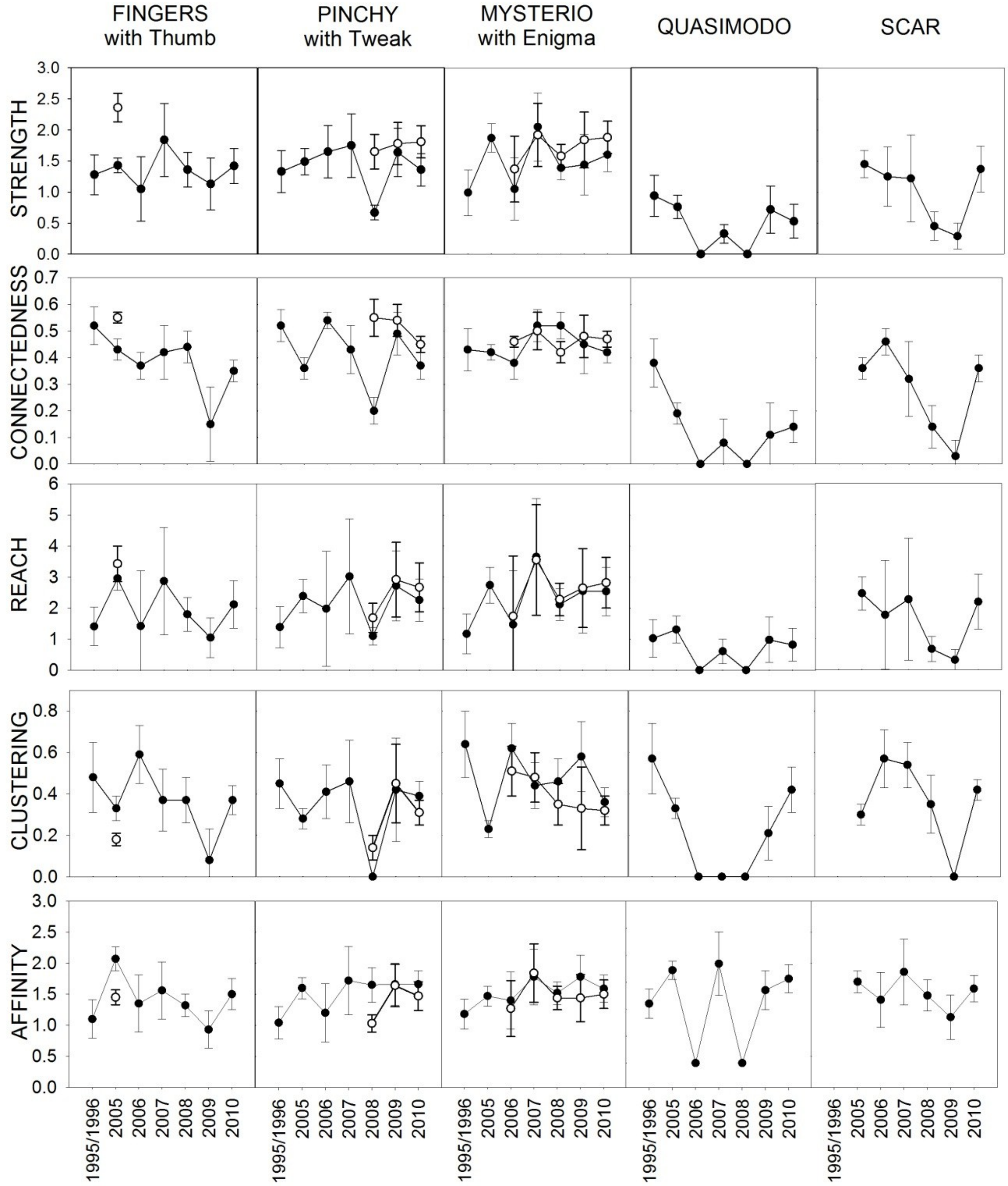


Figure 3-2: Plots of all network measures for GOS adults, excluding Puzzle Piece (#5130) who was only identified during the first year of the study. 1995 and 1996 data from IFAW data (Gordon *et al.* 1998). Calves shown on mothers' plots in white symbols. Error bars are standard errors based on 1000 bootstrap replicates.

Relationships through Changes in Social Role

Over the course of the study, Fingers (#5722) has played several roles in her unit. Figure 3 plots the decrease in the measure of connectedness for Fingers as her social role changes with the death of her calf and birth of the new ones. In 2005, Fingers was the only mother in the unit and had accordingly high values of connectedness. In 2006, her calf died and she was the primary babysitter to the newest calf, Enigma (#6068; see Gero *et al.* 2009) for a definition and justification of "primary babysitter"). Being involved with the care for the calf, Fingers' connectedness measures remain stable. Then, in 2008, with the birth of Tweak (#6070), the two mothers, Mysterio and Pinchy, babysat for each other and Fingers (#5722) only escorted the calves occasionally. Without being involved in the care of either calf, her connectedness values dropped off. In 2009, Fingers spent most of her time with Quasimodo (#5563) and Scar (#5727), both socially peripheral animals. Figure 3-3 shows a rise in connectedness in 2010, when Fingers spent more time with her fellow unit members as the entire unit was sighted multiple times in the same cluster with mature breeding males. A larger number of males were encountered in 2010 (6 in 2010, 0-3 in other years except 2005 where 5 were identified). Due to the socialization with the males, cluster sizes amongst the GOS were larger in 2010. Mean size of clusters including Fingers in 2010 was 3.46 individuals (n = 56 clusters), as compared to the population mean in 2010 which was 1.90 individuals (n=993 clusters).

Maturation of a Juvenile Male

Scar (#5727), a juvenile male, who was estimated to be between 8-10 years old based on his size at the onset of the study in 2005 (Schulz 2007), was already weaned when we encountered him for the first time (sperm whales nurse for at least 2 years, Best 1984). Figure 3-2 plots the steady decrease in almost all networks measures as he aged into maturity (11-15 years old by 2010). As is observed with Fingers, there is a similar rebound in most of his measures in 2010 due to the entire unit socializing with mature males. Mean cluster size of clusters including Scar in 2010 was 4.14 individuals (n=44 clusters). The mother-calf bond with this juvenile male appears to remain strong until the birth of the mother's next calf (Figure 3-4). Before the birth of Tweak, Scar and his mother, Pinchy, have a preferred association (HWI > twice the unit mean), but in 2008, the year Tweak was born, Pinchy and Scar were not observed clustered together (Figure 4).

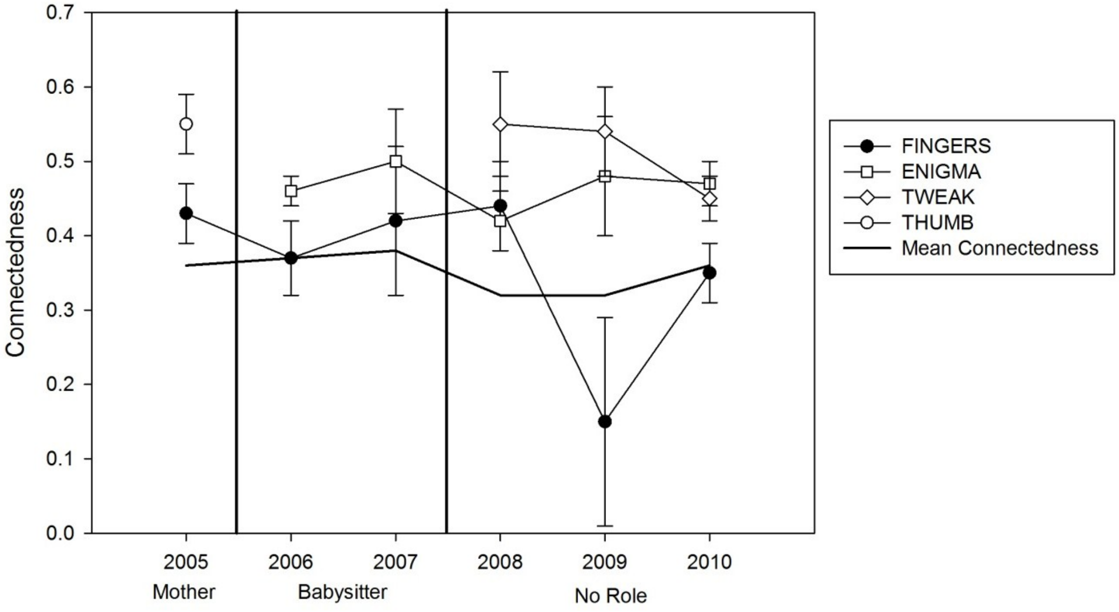


Figure 3-3: Connectedness across years for Fingers (#5722; black symbol), and the three GOS calves (white symbols). Note the decrease in connectedness with changes in social role (Mother in 2005, Babysitter in 2006 and 2007, and No Role in 2008-2010). Error bars are standard errors based on 1000 bootstrap replicates.

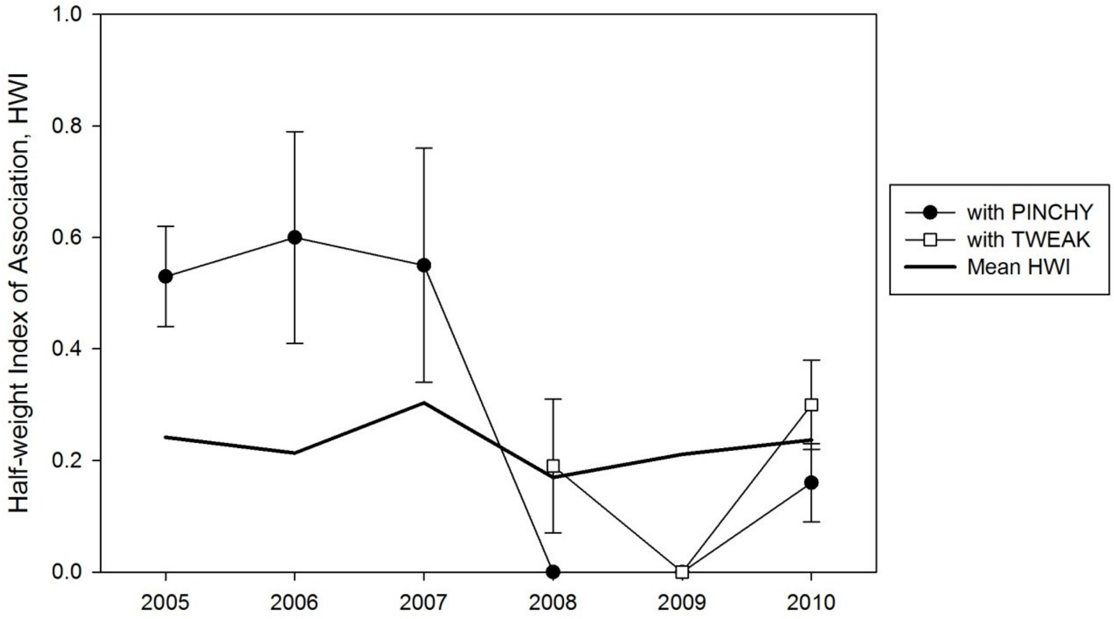


Figure 3-4: Half-weight Index of Association between Scar and his mother, Pinchy (black circles), and his half-brother, Tweak (white squares). Mean HWI for the unit shown in bolded black. Error bars are standard errors based on 1000 bootstrap replicates.

Non-Reproductive Females:

The only female in the Group of Seven to not reproduce over the 6 years of observations was Quasimodo (#5563). Quasimodo had the lowest values for all network measures in most years (Figure 2); however, this was a decrease from the 1995-1996 dataset in which she had similar association values to other adult females in her unit (Table 3-3). Since 2006, other than when the entire unit is together, Quasimodo was predominantly sighted alone or with just Fingers.

PATTERNS ACROSS UNITS

These broad patterns appear to be consistent across units. Over all seven units considered, calves had high or the highest values for all network statistics (Table 3-4). Mothers had intermediate values for most of the measures, but high values for connectedness and affinity. Unfortunately, there are no individuals in the other units studied with which to compare the changes in social patterns of either maturing juvenile males, like Scar, or non-reproductive females who had no role in allocare, such as Quasimodo.

Table 3-3: Mean HWI for Quasimodo across years (1995-1996 and 2005 through 2010) as compared to Unit Means. Note that Quasimodo had a mean very close to the unit mean in 1995-1996 but had closer to half of the mean in the years 2005-2010.

Year	Unit Mean HWI	Mean HWI of dyads including Quasimodo
1995-1996	0.27	0.24
2005	0.24	0.13
2006	0.21	0
2007	0.30	0.07
2008	0.17	0.11
2009	0.21	0.12
2010	0.24	0.09

Table 3-4: Mean network statistics for calves, mothers and adults across six social units across all years of the study (2005-2010).

Unit	Years	Class	n	Strength	Eigenvector Centrality	Reach	Clustering Coefficient	Affinity
A	3	Calves	4	1.48	0.34	2.17	0.23	1.36
		Mothers	3	1.38	0.34	2.18	0.35	1.64
		Adult	5	0.93	0.17	1.22	0.25	1.09
D	3	Calves	3	1.21	0.48	1.25	0.18	1.01
		Mothers	3	0.92	0.42	1.09	0.19	1.11
		Adults	3	0.59	0.16	0.63	0.24	0.83
F	6	Calves	3	1.80	0.49	2.63	0.34	1.45
		Mothers	3	1.40	0.42	2.37	0.4	1.67
		Adults	3	1.03	0.27	1.55	0.30	1.36
J	4	Calves	2	1.74	0.57	2.59	0.52	1.42
		Mothers	1	1.41	0.50	2.10	0.53	1.47
		Adults	3	1.03	0.38	1.57	0.49	1.21
N	2	Calves	2	1.26	0.52	1.60	0.38	1.26
		Mothers	2	1.38	0.56	1.74	0.38	1.25
		Adults	4	0.29	0.10	0.27	0.11	0.54
T	3	Calves	3	1.68	0.53	2.13	0.30	1.22
		Mothers	3	1.37	0.47	1.94	0.39	1.36
		Adults	4	0.84	0.26	1.26	0.37	1.28
U	3	Calves	1	0.79	0.67	0.57	0.26	0.70
		Mothers	1	0.72	0.64	0.57	0.35	0.77
		Adults	2	0.31	0.19	0.17	0.36	0.35

DISCUSSION

Sperm whale families, like human families, are dynamic. Relationships evolve, growing stronger or fading as individuals grow older and change, as offspring are born, and as individuals pass away. Matrix correlations and Mantel tests quantified these changing relationships by showing that patterns of dyadic association among adults in sequential years were correlated, while non-sequential years were progressively less correlated as the time lag increased. This suggests that the social dynamic within the unit builds on itself.

The primary source of the change appears to be the births of new calves. New life brings with it new roles. Females become mothers, older siblings become independent, and someone in the unit becomes the new calf's primary babysitter. New found responsibilities or freedoms come with changes in social patterns. New mothers appear to become slightly more socially isolated (Pinchy and Mysterio show drops in network statistics in the first year of their new calves' lives; Figure 3-2), but remain connected to the rest of the unit through their calves' social relationships and thus show accordingly high values of connectedness, clustering coefficient, and affinity. It is likely that this isolation is the result of spending the majority of surface time with their new dependent calves nursing when not otherwise at depth feeding in order to meet the new energetic demands of producing milk.

If involvement in the care of the calves is central to the social relationships in the network of a unit, then Quasimodo provides an interesting case of a female who did not reproduce. Quasimodo had the lowest values for all network measures calculated across all years of this study (2005-2010). This differs when I compared them to her measures from ten years prior to this study using data collected from 1995 and 1996. Her social connections with members of her own unit have decreased with age, in particular her measure of connectedness has dropped since the mid-ninety's. This social peripheralization might be the result of age as has been observed in old world primates. Among several species of monkey, older females show a trend of social withdrawal and peripheralization (Waser 1978; Hrdy 1981; Hauser and Tyrell 1984; Nakamichi 1984). However, this trend has been disputed (Pavelka 1991). I was unable to determine Quasimodo's age relative to that of the other adult females in her unit. Alternatively, as her nickname implies, she may be peripheralized due to illness. Quasimodo was nicknamed as such due to a large growth surrounding her dorsal fin, which may or may not have been malignant.

The birth of a new calf leaves older siblings to become more independent. It seems that the bond between mother and juvenile males lasts far beyond weaning, but with the birth of his new half-brother, Tweak, Scar's relationship with his mother diminished dramatically. This coincided with the first recordings of Scar producing vocalizations similar to "clangs" or "slow clicks" (S.Gero, unpublished data), a vocalization typically made by mature males (Weilgart and Whitehead 1988). Interestingly, other than a few sightings with Fingers, Scar only spent time with his new half-brother in 2008. The fact that juvenile males do provide some alloparental care to calves in their natal unit (Gero *et al.* 2009), Scar's association with his new half-brother when his mother was not present, and his abrupt social sequestration by the other adult females in the unit after the birth of the new calf, would suggest that juvenile males are socially ostracized from the unit by the adult females instead of leaving on their own volition at sexual maturity. Among African elephants (*Loxodonta africana*), males show variability in their growth towards independence. Some male elephants leave quickly while others leave gradually over several years. A few males leave when quite young, while others leave well into maturity (range 9-19 years old), typically when their mothers had another calf (Lee and Moss 1999). While the onset of Scar's separation from his natal unit appears quite quick, his final departure from the unit had been drawn out across the last few years. To the knowledge of the authors, Scar is the first juvenile male sperm whale to be observed going through the transition of splitting from his natal unit, offering a first insight into this stage of life in this species.

Alloparental care is thought to be the driving force for the evolution of groups in this species (Best 1979; Arnbom and Whitehead 1989; Whitehead 1996a). In this Caribbean population, each calf appears to have one primary babysitter, although all unit members escort the calf at some point (Gero *et al.* 2009). Those individuals who contributed substantially to the care of calves had higher values for most network measures than those who did not. As the hypothesis that alloparental care is the driver of sperm whale sociality would predict, a female is less central to the unit's social relationships if she is not contributing directly to raising the calves. In the case of Fingers, her network measures remained stable after losing her calf as a result of playing an important role in babysitting Pinchy's new calf, Enigma. However, when her role as babysitter ended in 2008, when the two mothers began to babysit for each other's calves, her network measures decreased as she became less central to the social network of the unit. At the very end of the fieldwork in the spring of 2011, a new calf was born in the Group of Seven. Behavioural observations and association patterns suggest that Fingers is likely the mother (S.Gero, unpublished data). Should these patterns remain consistent, Fingers will once again be central to the family's social patterns. This would support the conclusion that females seem to cycle in and out of the center of the family's social network with new births. The social bonds between the females that maintain the social unit are reaffirmed with every new calf.

This study also sheds some light on the mechanisms which may maintain alloparental care within units of sperm whales. Prior to Thumb's death in 2005, Mysterio was his primary babysitter. With the loss of Thumb and the birth of Enigma to Mysterio in 2006, it provided a unique opportunity to examine reciprocity of alloparental care in this species for the first time. Direct reciprocity (A helps B because B helped A before; Axelrod and Hamilton 1981) would predict that Fingers should return the act of babysitting. As predicted, in 2006, Fingers did return Mysterio's investment in her calf by becoming the primary babysitter for Enigma. When direct reciprocity is delayed across repeated interactions, over a year apart in this case, individuals have the possibility of cheating by not repaying benefits received from an earlier interaction (Trivers 1985; Enquist and Leimar 1993; Clutton-Brock 2009). As a result, delays of this length in reciprocity among mammals are rare; however, a similar example exists in a socio-ecologically similar terrestrial mammal, the African elephant (Lee 1987). In 2008, with the birth of a second calf in the unit, Pinchy and Mysterio babysat for each other rather than having an external babysitter for each calf. Sperm whale allomothers do lactate (Best *et al.* 1984) and allonursing has been shown in this species (Gero *et al.* 2009; CHAPTER 3), so Pinchy's lactation alone is an unlikely explanation for this change. Pinchy is; however, more closely related to Mysterio than is Fingers (Figure 3-1), so kin-selection may play a role in determining primary babysitters. However, concurrent mothers may simply end up as each other's babysitters if calves are attracted to each other at the surface given they cannot dive as long as their mothers. However, concurrent mothers may also choose to reciprocate allocare instead of having another female act as a babysitter as it reduces the risk of defection by eliminating the delay. However, given the long-term social reliability between related female unit members (Whitehead *et al.* 1991), limited dispersal between social units (Christal *et al.* 1998), the ability to recognize and interact preferentially among unit members (Gero *et al.* 2008), and the fact that the vast majority of females contribute to escorting the calves (Gero *et al.* 2009), it seems unlikely that any unit members would be likely to defect; especially given that escorting a calf at the surface while babysitting is likely not a very costly behavior (Whitehead 1996a).

An alternative explanation would be generalized reciprocity, in which A helps B because A had help from C before, where the identities of B and C are unimportant within the boundaries of a small group (Hamilton and Taborsky 2005; Pfeiffer *et al.* 2005). In this case, individuals would freely offer allocare among unit members given prior experience of allocare, while the specific role of primary babysitter may be determined by kin-selection (Gero *et al.* 2008). Generalized reciprocity allows for the evolution of generous strategies and the possibility of prosocial norms (Pfeiffer *et al.* 2005). Within these small, long-term, stable social units of sperm whales, reciprocity may be viewed not merely as a pattern of exchange, but as a social norm (Gouldner 1960). Morality, social norms, and the recognition of inequity among animals are being increasingly discussed (Flack and De Waal 2000; Flack *et al.* 2004; Sapolsky and Share 2004; Broom 2006; Flack *et al.* 2006; Brosnan 2011; Pierce and Bekoff 2012). Reputation of helping (indirect reciprocity; Nowak and Sigmund 1990; Nowak and Sigmund 1998), which can also lead to helping as a social norm (Wedekind and

Braithwaite 2002), may also play a role in this species but is difficult to elucidate with the current data. Stating that one mechanism alone is responsible for this system of group living and allocare likely oversimplifies the complex interactions between kin-selection, the various forms of reciprocity, commensality (calves approaching nearby adults at the surface) and social norms in explaining the evolution and maintenance of allocare and group living in sperm whales.

Overall, calves appear to be social hubs within social units of sperm whales because they were significant parts of the social relationships among unit members across the seven units studied. Change in the relationships among adult females is provided by the deaths, relatedness, increased age or perhaps illness, but primarily by the birth of new calves. These findings are consistent with the theory that allocare was the primary evolutionary force driving the formation of social units in sperm whales.

CHAPTER 4

CROSS-SCALE ANALYSIS OF LONG AND SHORT TERM SOCIAL RELATIONSHIPS BETWEEN INDIVIDUALS AND UNITS OF SPERM WHALES

Call it a clan, call it a network, call it a tribe, call it a family. Whatever you call it, whoever you are, you need one.

~Jane Howard

INTRODUCTION

Cross-scale studies are important when trying to understand the factors driving social behavior, in particular when social interactions are complex and hierarchically organized (Couzin and Krause 2003; Couzin 2006). One individual's actions can affect its group's decisions that then in turn create emergent properties in the next tier of the social structure, which, though feedback across levels of society, may then affect an individual member's behavior (Couzin 2006).

Long-lived, cognitively-complex animals across a range of taxa display substantial social complexity, sometimes including multilevel hierarchically-organized social structures. Species as ecologically different and phylogenetically remote as primates (*e.g.* Smuts *et al.* 1987; Strier 2007), elephants (*e.g.* Moss and Poole 1983; Wittemyer *et al.* 2005), and bats (*e.g.* Boughman and Wilkinson 1998; Vonhof *et al.* 2004) have societies that involve both long-term cooperative relationships and a high degree of fluidity and movement. In such societies, individuals encounter and interact with others whom they know very little or not at all, in addition to well-known long-term associates. The challenges of interacting not only within social groups but between them, leads to more complex communicative signals, hierarchical recognition, and potentially to large scale cooperative societies (Boyd and Richerson 1987; Richerson and Boyd 1998; McComb and Semple 2005; Freeberg 2010; Grueter *et al.* 2012a; Grueter *et al.* 2012b).

The cetaceans are thought to have cognitive capacities, communication systems and societies which rival their terrestrial counterparts in complexity (Mann *et al.* 2000b). Historically, knowledge of cetaceans has lagged behind that of their terrestrial mammalian counterparts primarily due to the difficulties of working at sea at the large spatial (Stevick *et al.* 2011) and temporal (George *et al.* 1999) scales over which these species operate. The sperm whale (*Physeter macrocephalus*, Linnaeus 1758) has a particularly interesting multileveled social structure including what may be the largest cooperative groups outside of humans (Rendell and Whitehead 2003b; Whitehead *et al.* 2012).

While mature males tend to live relatively solitary lives, there are several hierarchically-organized tiers of female social structure: Mother-calf pairs, social units, temporary groups of social units, vocal clans, and populations. While this model is primarily based on research conducted in the Pacific, there is considerable, and consistent, variation between ocean basins (Whitehead *et al.* 2012). Several adult females, their dependent calves and immature offspring form the fundamental tier of female social structure, the unit; however, relatedness creates structure even among the adult female unit members and mother-calf bonds last well beyond weaning (Gero *et al.* 2008). While most females will live out their life as members of their natal units, care for each other’s calves and defend themselves against predators communally (Whitehead 1996a; Pitman *et al.* 2001; Gero *et al.* 2009), transfers between units, fissions and fusions have been documented in the Pacific (Christal *et al.* 1998). Although units in the Pacific typically have multiple matrilines within them, those studied in the Caribbean all share the same haplotype (Mesnick 2001; Gero *et al.* 2008). Units can assemble into groups whose associations last from a few hours to a few days (Whitehead *et al.* 1991). Within groups, however, association generally still remains stronger among unit members than between members of different units gathered within a group (Christal and Whitehead 2001). In the Pacific, units associate only with those who share a similar vocal dialect. Such vocal clans may contain thousands of individuals in hundreds of units and span thousands of kilometers (Rendell and Whitehead 2003b). While definitions of populations in this species are vague and many argue that they may be in need of review given recent findings (Dufault *et al.* 1999; Gero *et al.* 2007; Engelhaupt *et al.* 2009; Whitehead *et al.* 2012), populations in the Pacific appear to be structured along cultural lines rather than geographically (Rendell *et al.* 2012).

Here, I examine social relationships across two levels of social structure. I focus on the diversity of social relationships within units and contrast those with relationships between units using an unparalleled dataset of nine intensely studied social units collected across a 6 year study. Specifically, I am able to address several questions about social and spatial relationships between individuals and units. Firstly, how structured are relationships within social units and does the degree of structuring differ consistently between units? Differing patterns of social interaction can affect spatial relationships between individuals; as such, I also test if individuals have consistently distinctive spatial positions within units when foraging and if the spatial spread of individuals or their speed through the water when foraging differ consistently between units. Finally, I investigate associations between units and, using supplementary data collected over a decade prior to this study, I also examine if associations between units persist over decadal time scales.

Greater insight into the fine scale social interactions within and between social units allows for a better understanding of the evolutionary pathway which gave rise to vocally marked, large-scale cooperative groups like the vocal clans in this species.

METHODS

FIELD METHODS

Social units of female and immature sperm whales were located and followed both acoustically and visually by observers on one of three platforms (a dedicated 12m auxiliary sailing vessel, a dedicated 5m outboard skiff, or an 18m whale-watch vessel) in an area that covered the entire west (leeward) coast of the island of Dominica (N15.30 W61.40), in waters sheltered from the trade winds. Research was conducted in the winters of 2005 through 2010 for a total of 2549 hours with whales across 320 days of effort (Table 4-1). During outboard skiff seasons, the skiff was unable to operate on heavier weather days and the research team worked from the larger whale-watch vessel. Whale watch tours focused their search effort on sperm whales. As a result, methods remained the same across all three platforms, with the work on those days being restricted only by the length of time spent at sea by the whale watch vessel.

During daylight hours, clusters of individuals visible at the surface were approached and photographs were taken to identify individuals. If a calf was present in a given cluster, priority was given to taking dorsal fin pictures of the calf from alongside the larger animals, before moving behind the adults in the cluster to photograph distinct markings on the trailing edge of their flukes for individual identification purposes (Arnbom 1987). Sloughed skin samples, for genetic determination of sex, haplotype, and pairwise relatedness, were collected in the slicks of individuals after identification (Whitehead *et al.* 1990; Amos *et al.* 1992; Richard *et al.* 1996a; Richard *et al.* 1996b).

Table 4-1: Effort across years

Year	Start Date	End Date	Days Effort	Platform
2005	January 14	April 13	62	Sailing only
2006	January 17	February 11	21	Whalewatch only
2007	January 28	February 28	30	Skiff and Whalewatch
2008	February 8	May 8	75	All
2009	January 11	March 29	64	Skiff and Whalewatch
2010	January 20	April 18	72	Sailing only

Additional data were collected, using similar methods, by the International Fund for Animal Welfare (IFAW) during the winters of 1995 and 1996 (13m dedicated auxiliary sailboat, 59 days effort; see Gordon *et al.* 1998). The presence of calves was noted in field notes, but they were not individually identified during this fieldwork.

ANALYSES

Identifications

A quality rating (Q) between 1 and 5 was assigned to each photograph, where 1 indicated a very poor photograph, and 5 indicated a very high quality photograph (Arnbom 1987; Dufault and Whitehead 1993). Only pictures with a Q≥3 were used for the analyses. The best picture for each individual within each encounter was assigned a temporary identification code and then matched between encounters using a computer-based matching program to the Atlantic catalog (Whitehead 1990). In a few cases (<5% of identifications), well-known individuals which could not be photographed when multiple animals fluked synchronously but whose flukes were observed by SG were recorded as having been identified and given a Q-rating of 6. Calves, which do not fluke, were individually identified using the shape of its dorsal fin and distinct markings on its dorsal fin and body. The best picture for each individual calf within each encounter was then matched between encounters by eye.

Defining Units

Units were delineated methods following Christal *et al.* (1998) with more stringent minimum durations of association: a unit is a set of individuals for which each pair was observed associated during two different years (Christal *et al.* used a 30 day minimum rather than different years). That unit members were associated across years suggests stable, long-term companionship as defined by Whitehead *et al.* (1991). Individuals were deemed to be associating if they were within the same cluster at the surface. An individual was considered part of a cluster if it was within approximately 3 adult-body lengths of any other cluster member (~40m "chain rule") and their behavior was coordinated (Whitehead 2003).

Social Differentiation within Units:

Social differentiation is the estimated coefficient of variation (standard deviation divided by mean) of the true association indices. This relates to the actual proportion of time associated, between members of a unit. If the social differentiation of a unit is 0, then relationships among members are completely homogeneous. Conversely, if the social differentiation is >1.0 there is considerable diversity among the relationships among the pairs of individuals within a unit (Whitehead 2008a). Social differentiation within units was estimated, using a half-weight index (HWI) of association (Cairns and Schwager 1987), defining association as being sighted in the same cluster, and using 2-hour sampling periods as in previous work in this species (Christal *et al.* 1998; Christal and Whitehead 2001; Gero *et al.* 2008; Gero *et al.* 2009). The likelihood method described by Whitehead (2008a) was used to calculate values of social differentiation and its standard error (SE) was estimated using the nonparametric bootstrap with sampling periods chosen randomly with replacement for each of 1000 bootstrap samples. Social differentiation within units was examined within years, thus avoiding heterogeneity that could be due to recruitment, mortality, emigration, or immigration. I then used the unit-year estimates of S in a one-way analysis of variance to test if units had consistently different social differentiation across years. Overall means across units for all years were then calculated only for those units with an estimated SE <0.2.

Spatial Spread of Individual and Units

From the research vessels, I could not collect direct measurements of the spatial spread of individuals within units, but used an indirect method to measure the spatial dispersion of foraging units similar to that used by Christal and Whitehead (2001) with the modifications suggested by Whitehead *et al.* (2012) which uses the GPS-recorded positions of the identification photographs. The dataset was restricted to only Q>3 photographs as in Arnbom (1987). When more than one photograph of the same individual was taken within 10 minutes, the location of the first was taken. Only focal photographs with at least five other identifications taken within 2 hours, of which at least one had to be taken before the selected photograph and one after it, were considered, while still excluding photographs taken at the same time as the focal photograph. The before and after identifications were used to estimate the mean track of the unit, from quadratic regressions of latitude against time and longitude against time. From this track, the left/right and forwards/backwards displacement of the focal identification were calculated from the mean track of the unit (Figure 4-1), with left and forwards displacements being positive, and right and backwards displacements being negative. Displacements greater than 2 kilometers, which appear to result from issues in the track-fitting regressions, were excluded. These measures were used to determine whether individuals were consistently to one side (left/right) or ahead or behind (front/back) of their unit relative to the mean track of the unit. Sign tests were used to determine if the measures for individuals were consistently positive or negative. Only individuals for whom we had calculated displacements from more than 10 focal identifications were included in the individual analysis. The standard deviations of these left/right displacements was considered as the measure of the spatial dispersion of units themselves. These standard deviations were calculated for each unit studied for each year sighted. Travel speeds of the units within each year were also calculated using these measures. Finally, I used the unit-year values to conduct a one-way analysis of variance in order to test if units differed consistently in their spatial spread or travel speed.

Defining Associations between Units

Given that it is difficult to determine the spatial range and behavioral cues which may indicate interactions between members of different units of sperm whales, I quantified associations between members of different units using three different metrics for association of increasing spatio-temporal coordination: Date (identified on the same day), 2hr (identified within 2hrs of one another), and Clustered (identified within the same cluster). Three different sampling periods were also used: 1) Year, a yearly sampling period. This focuses on long term associations between units and eliminates the autocorrelation between sequential days when units are sighted together for short periods; 2) Day, sampling was actually done diurnally with identifications only taken during daylight hours. In addition, a daily sampling interval removes demographic effects (Whitehead and Dufault 1999); and 3) 2 hours, which is the approximate duration of two dive cycles in this species. This interval provides more samples while maintaining independence and has proven useful in previous work on this species (Christal *et al.* 1998; Christal and Whitehead 2001). Three combinations of sampling period and association measure are uninformative: Date-Date and 2hr-2hr in which the sampling period is the measure of association, and 2hr-Date in which the measure of association is longer than the sampling period. As a result, these were not used.

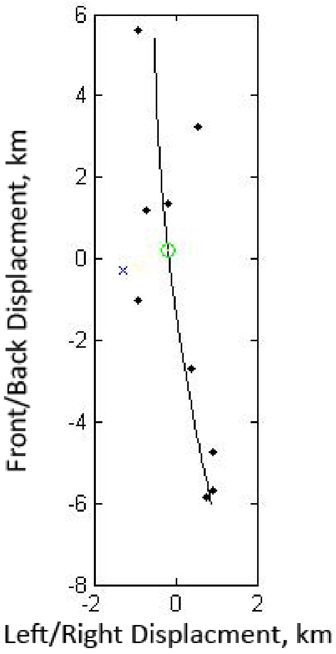


Figure 4-1: Illustration of regression technique for determining the relative position of focal identification. Positions of identifications within 2 hours are shown (black diamonds) and a quadratic position-time regression is fitted through them. The expected position of the focal identification, given its time, is marked by a 'O' on the line, and the 'X' its actual location when taken. The displacement is the horizontal distance between the 'O' and the 'X'. Scales are in kilometers.

Social differentiation was also calculated between units using the methods as above but using each combination of sampling period and measure of association. In addition, a permutation test, as in Bejder *et al.* (1998) with modifications described by Whitehead *et al.* (2005), in which observed associations among individuals, are permuted within the three sampling periods, controlling for the number of associates of each individual in each period, was used to test for preferred/avoided associations with the null hypothesis that animals associate randomly. A further modification was to fix the number of trials (attempts to switch a part of a matrix of associations) rather than the number of actual switches (as recommended by Miklós and Podani (2004). The association matrix between units across years (2005-2010) was permuted 10,000 times as this stabilized the *p* values, and each permutation included 1000 trials. Finally, average-linkage hierarchical clustering analysis was used to examine the associations between units. The cophenetic correlation coefficient (CCC) was calculated to determine how well the dendrogram represented the data. A CCC of over 0.8 is considered a "good" representation of the associations (Bridge 1993). I used modularity (as defined in Newman 2004) to identify significant divisions within the population. "Type 1" modularity or "modularity-G" (Whitehead 2008a; Whitehead 2009) was used as it controls for differences in gregariousness. A Q of greater than 0.3 suggests that the population has a modular structure (Newman 2004).

Matrix Comparisons

Mantel Z-tests (Mantel 1967; Schnell *et al.* 1985) and matrix correlation coefficients between matrices of associations were calculated in order to determine which association matrices were correlated. A test variant, the Rr-test, was also used as it controls for individual gregariousness by replacing the values of association with their within-row ranks (*i.e.* within-individual ranks; Hemelrijk 1990).

The calculation of the HWI, social differentiation, hierarchical clustering analysis, Mantel Z-tests; as well as the Rr-tests described above were carried out using *SOCPROG* 2.4 (Whitehead 2009) in *MATLAB* 7.12 (The Mathworks, Inc., MA, USA).

RESULTS

Over the course of this study, I have spent sufficient time (>9 days) with nine units to be able to conduct these analyses: units A, D, F, J, N, R, T, U and V (CHAPTER 2).

SOCIAL DIFFERENTIATION WITHIN UNITS

In most cases, units have relatively diverse social relationships with a mean value for *S* of 0.80 (SE = 0.05, range = 0.59 – 1.14) among adult females (Table 4-2). Including the calves in the analysis increases values for *S* across all units as the strength of mother-calf bonds affect this analysis (across unit mean = 0.91, SE = 0.03, range = 0.68-1.17). Although units varied in size, social differentiation does not correlate with the number of individuals in a unit (without calves: r=0.11, p=0.77; with calves: r=0.36, p=0.34). Additionally, there was no indication that units have consistently different social differentiation across years (One-way ANOVA: F = 0.312, df = 7, p = 0.94); however power for this analysis was low (0.05) and this result should be interpreted cautiously.

Table 4-2 Social differentiation for all units across all years (2005-2010) both including calves (bottom) and excluding calves (top). HWI – Half-weight index of association, composition including adults (A) and calves (C), IDs is the number of identifications of members of each unit, and S – social differentiation.

Unit No Calves	Mean HWI	Composition	Days	IDs	S	SE
A	0.10	7	31	992	0.706	0.113
D	0.09	5	29	620	0.955	0.127
F	0.10	6	97	1947	0.589	0.082
J	0.20	4	27	821	0.700	0.166
N	0.03	6	9	257	0.965	0.168
R	0.08	8	21	653	1.142	0.089
T	0.11	6	24	1021	0.714	0.112
U	0.13	3	27	493	0.730	0.310
V	0.13	9	10	413	0.622	0.187
With Calves						
A	0.13	7A 4C	31	1911	0.891	0.102
D	0.14	5A 2C	29	1131	1.054	0.074
F	0.13	6A 3C	97	3140	0.898	0.044
J	0.20	4A 1C	27	932	0.682	0.120
N	0.08	7A 2C	9	495	1.089	0.057
R	0.08	8A 1C	21	708	1.17	0.073
T	0.15	6A 2C	24	1449	0.791	0.076
U	0.20	3A 1C	27	606	0.776	0.183
V	0.09	9A 3C	10	441	0.852	0.093

Table 4-3: Spatial spread of individuals within units of sperm whales as estimated using the standard deviation of the left/right displacement of identifications taken at dive locations from the estimated mean trackline of the unit's movement.

Unit	Unit Size	Number of Focal Identifications	Spread (SD of left/right displacement, km)	Speed (km/h)
A	9	188	0.41	2.16
D	7	61	0.57	2.84
F	9	405	0.51	2.21
J	4	129	0.47	2.82
N	8	29	0.51	2.45
R	8	88	0.46	2.79
T	8	230	0.51	2.60
U	4	77	0.54	2.33
V	9	93	0.45	2.74
Across Units		**1376**	**0.49**	**2.46**

SPATIAL SPREAD OF INDIVIDUALS AND UNITS

Displacements were calculated for 1376 focal identifications across 97 days fieldwork. Forty-one individuals had greater than 10 focal identifications from which to analyse individual position relative to the mean of the unit. None of the sign tests could reject the null that animals were close to the mean track of the unit, such that no animal was consistently ahead or behind, or to the left or right, of their unit members. Nor was there an indication that displacements about the track line differed among units (One-way ANOVA: F = 0.92 , df = 6, p = 0.52); however, the power for this analysis (0.05) was low and variation in spatial spread between units should be interpreted from table 4-3. Being based on displacement from a mean trackline, this measure of spread might have been confounded with unit size, but there is no significant correlation between the standard deviation of the left/right displacement and unit size (r=-0.364; n=9; p=0.335). Travel speed does not correlate with unit size either (r=-0.241; n=9; p=0.533) and speeds of the nine units were also similar all ranging between 2.16 and 2.82 km/h and did not vary consistently between units across years (One-way ANOVA: F = 1.33, df = 7, p = 0.32); however, the power for this analysis (0.05) was also low and variation in travel speeds between units should be interpreted from table 4-3. Therefore, it appears that the spatial spread of individuals within units and their travel speeds are similar among all of the units and no individual has a particular position relative to the other unit members. Although it should be noted that these measures were collected at the surface and it is unclear how well these correlate with speeds and spreads at depth.

SOCIAL RELATIONSHIPS BETWEEN UNITS

As would be expected, all of the various combinations of sampling period and association measure result in highly correlated matrices of association, even when comparing the most conservative, short term measure of association between clusters (identified together in a cluster within 2 hours, 2h-CLUSTERED) against the most permissive, long term ones (identified on the same day within a year, YEAR-DAY; matrix correlation coefficient = 0.45). Estimates of social differentiation between units and permutation test results across sampling periods and association measures are shown in figure 2. Social differentiation between units is also high with estimates ranging from 0.51 to 1.11. In most cases, permutation tests confirm that these diverse associations differ from random and that preferred and avoided association exists between units. The exceptions were the case of DAY-2h in which the sparse matrix could not be permuted using the standard algorithms and YEAR-DAY which the null hypothesis that the units associate randomly could not be rejected. Focusing on the most conservative dataset, 2h–CLUSTERED (top, left of figure 4-2), there is one large set of associating units that includes units A, D, F, J, and U. Within this set there are two pairs of units with stronger bonds: F & U, and A & D. The other four units are less connected, but a third pair of Unit T and Unit V is also often associated. Figure 4-3 shows the average linkage hierarchical cluster dendrogram for the resulting associations from the 2h-CLUSTERED matrix. Modularity-G highlights the three pairs of units. Patterns of association did not differ whether Q6 identifications were included or excluded.

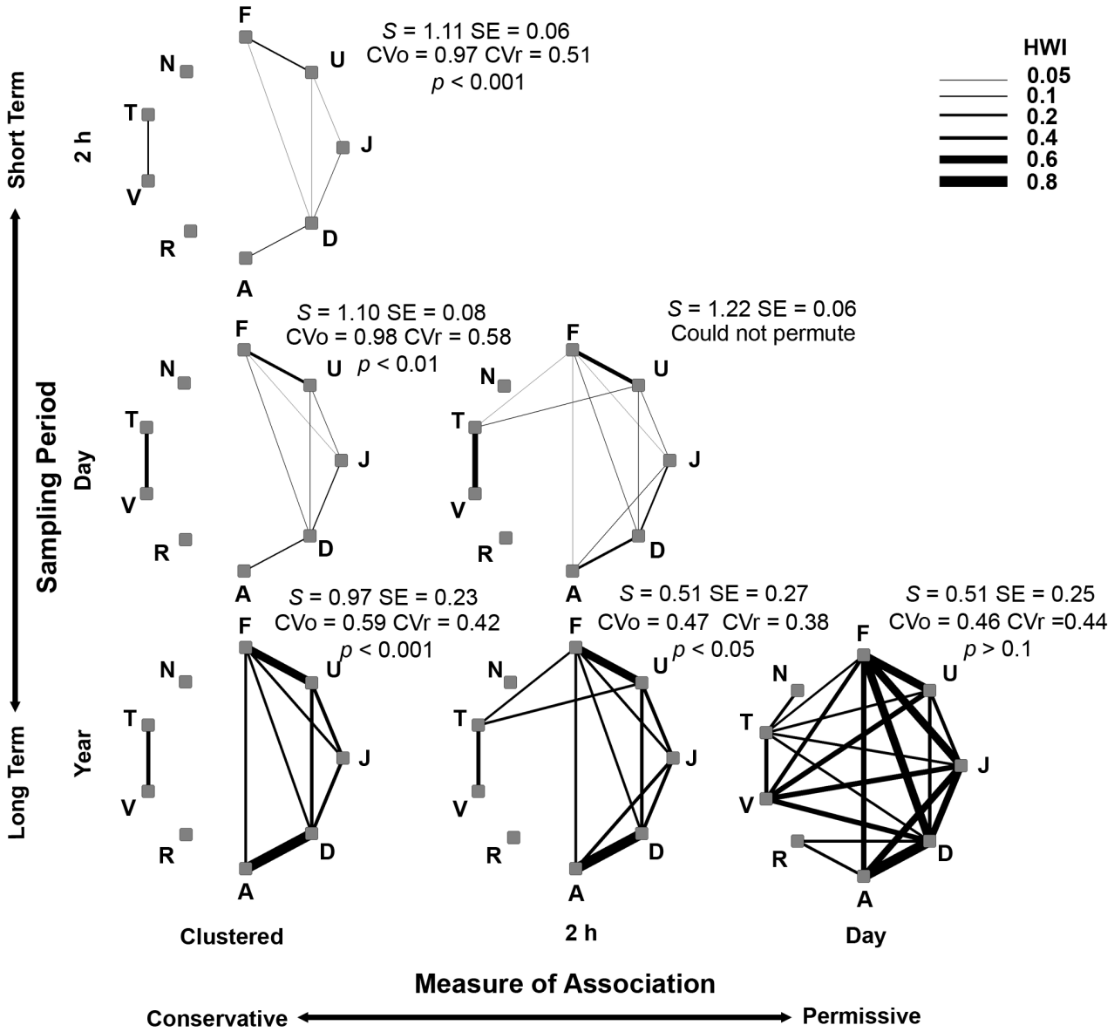


Figure 4-2: Sociograms portraying the relationships amongst the nine social units based on HWI of association across 2005-2010. Estimates for social differentiation (*S)* and results of permutation test for preferred/avoided relationships between units presented with each sociogram (CVo = CV observed data, CVr = CV randomized data).

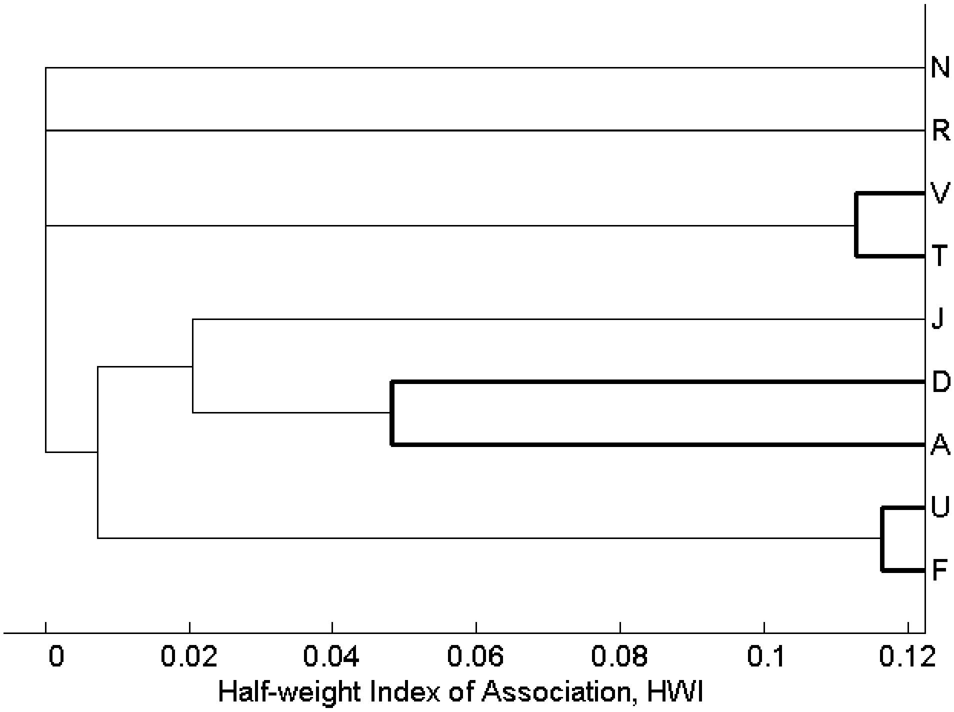


Figure 4-3: Average-linkage hierarchical clustering dendrogram for all units using the associations calculated using a 2 hour sampling interval and identified in the same cluster. This is a good representation as has a cophenetic correlation coefficient of 0.98018. Bolded branches are clusters created by a maximum modularity-G (controlling for gregariousness as in (Whitehead 2008a; Whitehead 2009)) of 0.701 at HWI = 0.0205.

LONG-TERM PATTERNS

For two units (F & U), data were available from a decade prior to the onset of this study with which to compare patterns of association over a longer period. On 12 of 19 days in which members of Unit F were sighted in 1995 and 1996, members of Unit U were also sighted. On 9 of those days, members of both units were associated in the same cluster. Association matrices (2h-CLUSTERED) including only the adult females of units F & U sighted in both time periods do not correlate (Mantel Z-test: matrix correlation coefficient = 0.17, p = 0.26; Rr-Test: matrix correlation coefficient = -0.08, p = 0.63). Patterns of association between adult unit members in the 1995-1996 seasons and the 2005-2010 fieldwork (Figure 4-4) differed in some respects. Figure 4-5 shows the average linkage hierarchical cluster dendrogram for the resulting associations from the 2h-CLUSTERED matrix for individuals of units F and U between 2005-2010. Modularity-G splits the individuals into the two units. Accordingly, I found that relationships within units are significantly stronger than relationships between units in 2005-2010 (Mantel test: t= 2.11, p=0.018 – one-tailed test), while I could not reject the null hypothesis that relationships between and within the two units were similar in 1995-1996 (Mantel test: t= 0.634, p=0.737). Sample size may play a role in this second test as the data set in 2005-2010 is significantly larger. The 7 adults are sampled on average 91.3 times (range: 20-163) in 2005-2010, but only an average of 12.9 times (range: 8-19) in the 1995-1996 dataset. The strongest bond between units in 1995-1996 was between 'Pinchy' (#5560) of The Group of Seven and 'Fork' (#5151) of The Utensils, but was between 'Fingers' (#5722) of the Group of Seven and 'Knife' (#5562) of the Utensils in 2005-2010. While very few data were available for the other units (<11 identifications for any unit), members of another strongly bonded pair of units, two individuals from Unit V and one of Unit T, were identified within a minute of one another in 1995, but were not clustered together.

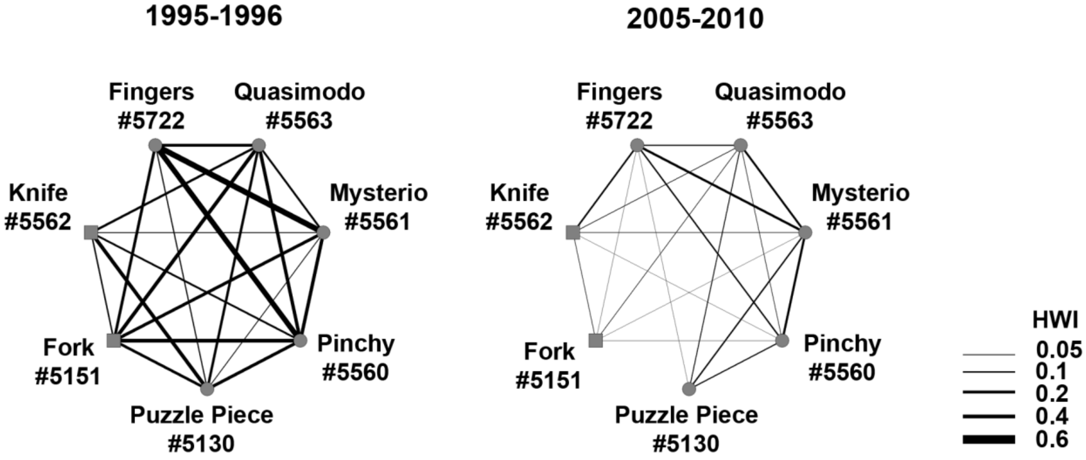


Figure 4-4: Sociograms portraying the relationships between the members of Units F and U. Plots based on 2h-CLUSTERED, HWI matrix of association pooled across years within both the 1995-1996 and 2005-2010 time periods. Members of Unit U shown as square nodes and Unit F shown as circles.

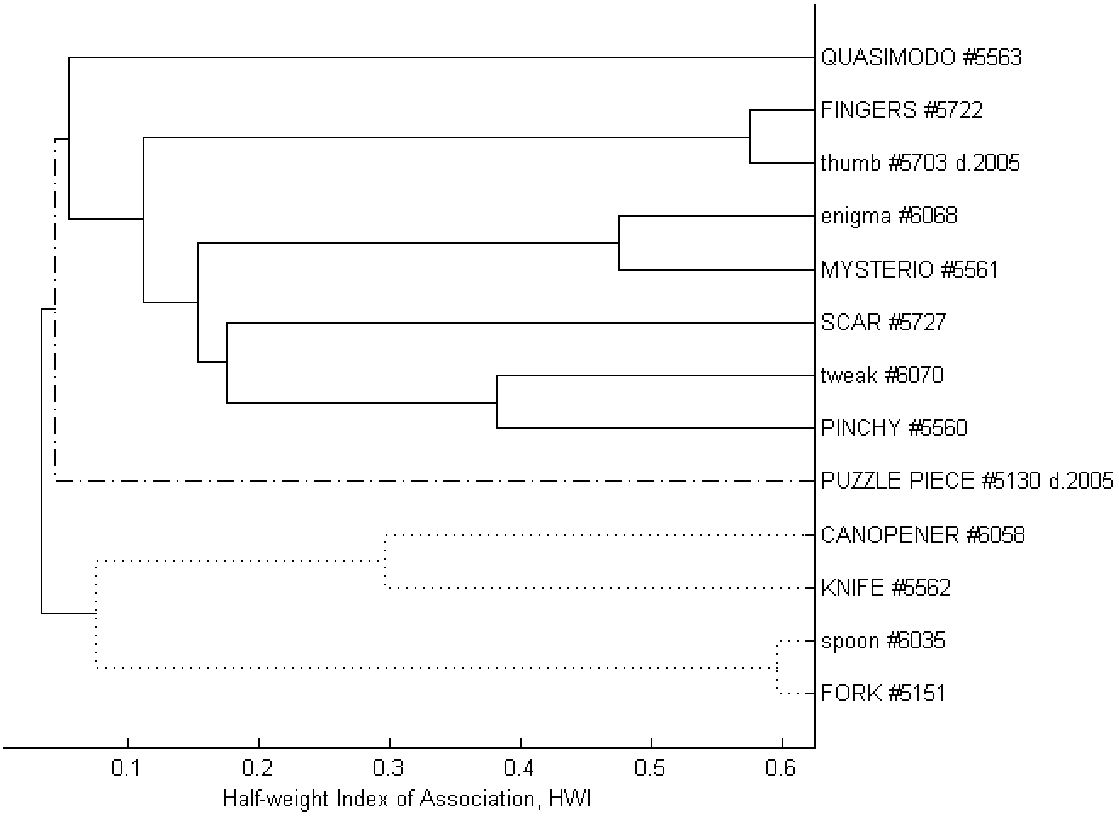


Figure 4-5: Average-linkage hierarchical cluster dendrogram of the 2h-CLUSTERED HWI matrix of association between the members of Units F and U between 2005-2010. Adults labeled with all uppercase and calves in lowercase. In all cases, adults and calves which are closely link are mother-offspring pairs. A maximum modularity-G (controlling for gregariousness as in (Whitehead 2008a); 2009) of 0.29 at HWI=0.044 splits the individuals into distinct units. This dendrogram has a cophenetic correlation coefficient of 0.93418 suggesting a good representation. Links among Unit U shown in dashed and Unit F shown in solid lines. 'Puzzle Piece' (#5130 – highlighted by a dash-dot line), an adult female who disappeared after the 2005 season, is split from either cluster since she was not associated with any individuals since 2005, the first year of the study.

DISCUSSION

Sperm whales have a diversity of relationships across the multiple tiers in their hierarchically-organized social structure. At its base are the strong mother calf bonds, which remain strong well beyond weaning (CHAPTER 3). These bonds along with preferred babysitters for the calves (Gero *et al.* 2009), and a communal, shared responsibility in protecting the young (Whitehead 1996a; Gero *et al.* 2009) result in a diverse social network within units. Gero *et al.* (2008) showed that patterns of variation in strength of relationships within one well-studied unit correlated with relatedness; and here, I demonstrate that this diversity of relationships is common among all nine units studied. These units have levels of social differentiation among relationships within units that are considered “high” based on existing standards (Whitehead 2008b; Whitehead 2008a). Whether units are small or large, members are not interchangeable, but are unique individuals, each with differing gregariousness and preferred associations.

These varied social relationships do not appear to much affect spatial relationships among individuals within sperm whale units while at the surface. Individuals are not equivalent and traits as different as age, dive ability, gregariousness, social roles, or motivation, among others, affect their spatial relationships within a group (Couzin *et al.* 2002; Couzin *et al.* 2005; Bode *et al.* 2011b). However, among the units of sperm whales tested here, there was no significant deviation from the mean trackline of the unit by any individuals. Generally, position within-groups is influenced by feeding competition, predation threat, and dominance (Hall and Fedigan 1997; Peterson *et al.* 2002; Hirsch 2007; King and Sueur 2011) and can have evolutionary and ecological consequences (Krause 1994; Krause and Ruxton 2002). While not explicitly tested, these results could suggest a lack of dominance among female unit members given that dominance often affects spatial relationships within groups particularly in relation to foraging (Hemelrijk 2000; Hirsch 2007). Dominance has not been well studied among wild cetaceans, but it is thought that among females it is generally of little biological consequence (Whitehead and Mann 2000). The lack of spatial structuring of individuals within units may also indicate that additional foraging benefits do not exist for particular locations in the unit. Patterns of front-to-back depletion of food patches have been shown in several species such that it creates a preferred position at the front of the group (Janson 1990; Hall and Fedigan 1997; Di Bitetti and Janson 2001; Rowcliffe *et al.* 2004). The reduced importance of the “finder share” may be a result of sperm whales not being able to monopolize and exclude others from prey patches in a three-dimensional ocean and may also be due to individuals being able to eavesdrop on each other’s echolocation, as is observed in bats (Balcombe and Fenton 1988), such that hiding the discovery of prey is unlikely. As for predator threat, given that the communal protection of calves appears to be the evolutionary force driving sociality in this species (Best 1979; Best *et al.* 1984; Whitehead 1996a), one would expect that mothers with their calves would be found in the safest location in the center of the unit where predator threat is at its lowest (Hamilton 1971; Bumann *et al.* 1997). My results do not find that any individuals are spatially positioned in the middle of units any more than any other individuals. The communal vigilance by the adult females in the units and staggering of foraging dives in order to have adults at the surface to protect the calves creates a situation in which it is likely that calves are protected specifically when predators are detected (Whitehead 1996a). Sperm whale adults have been known to form a stereotyped "marguerite" defense formation surrounding the calves during attack (Nishiwaki 1962; Pitman *et al.* 2001) and to cease foraging quickly and gather closely at the surface to stand up against attackers and place calves in safeguarded positions (Brennan and Rodriguez 1994; Pitman and Chivers 1999). Lastly, these findings may also indicate a lack of positional leadership, in that no specific individual leads the unit's movement from the front while others follow. This is in contrast to female African elephants (*Loxodonta africana*), a terrestrial mammal which shares many socio-ecological similarities with sperm whales (Weilgart *et al.* 1996), in which one elder female, or matriarch, plays a key role in coordinating group movements (McComb *et al.* 2001; Moss 2001; McComb *et al.* 2011; Moss and Lee 2011). However, one needs to be cautious given that leadership and the mechanism in which it operates can be distinct such that a particular animal may be dictating movement by alternative means, such as the use of acoustic signals for example, while not physically leading the unit around (Bode *et al.* 2012).

Spatial spread at the surface appears similar across units. These findings are consistent with Whitehead *et al.* (2012) who found that spatial spread of units across study sites in different oceans were all similar even though units in the Pacific are generally larger than those in the Atlantic (Jaquet and Gendron 2009). This spacing may reflect the optimal distance to take advantage of by-product mutualisms when foraging (Whitehead 1989) or over which to maintain communication for unit coordination. In addition, all of the nine units appear to travel at approximately the same speed through the waters off Dominica. Mean horizontal speeds ranging between 2.16 and 2.84 km/h are consistent with mean travel speeds from other study areas which range between 1.9 and 4.6 km/h (summarized in Whitehead 2003). It appears that both large males at high altitudes and females and immature in units travel at similar speeds when foraging whether they are successfully capturing prey or not but differ only in the pattern of their movements and the amount of area they cover (Whitehead 1996b; Jaquet and Whitehead 1999; Whitehead 2003; Whitehead *et al.* 2008).

Table 4-4: Associations between units in clusters and when males are present. Bottom, left triangle of the matrix displays the number of days on which both units were sighted followed by the number of those days in brackets on which males were also sighted with the females or nearby. Shaded diagonal gives the total number of days on which each unit was sighted and the number of clusters across the 2005-2010 time period (days/clusters). Top right triangle of the matrix gives the number of clusters in which at least one member of each unit was associated. Bolded cells indicated pairs of units identified by modularity-G and average-linkage hierarchical cluster analysis.

Units	A	D	F	J	N	R	T	U	V
A	31/311	**4**	0	0	0	0	0	0	0
D	**16 (3)**	29/167	3	3	0	0	0	3	0
F	2	4 (3)	97/906	2	0	0	0	**35**	0
J	3 (1)	9 (4)	5 (3)	27/208	0	0	0	1	0
N	0	0	0	0	9/71	0	0	0	0
R	1	1	0	0	0	21/168	0	0	0
T	0	1 (1)	1 (1)	1 (1)	1	0	24/323	0	**7**
U	0	3 (3)	**24 (4)**	3 (3)	0	0	1 (1)	28/153	0
V	0	1 (1)	2 (1)	1 (1)	0	0	**6 (3)**	2 (2)	10/100

Apart from rare occasions or when mature males are around (males aggregate units of females which would otherwise not be associated, CHAPTER 2), only members of three pairs of units (F-U, A-D, and T-V) formed clusters with members of different units (Table 4-4). In all other cases, although multiple units might have been occupying the same area, individuals only clustered with members of their own unit. This is consistent with the finding that Pacific units preferred unit members to others when gathered in groups (Christal and Whitehead 2001). Perhaps most intriguingly, while patterns of association within units are diverse and appear to change over time (CHAPTER 3), long-term patterns of association between units appear consistent over time. Members of Unit T and Unit V were seen together once in 1995 and the two adult female members of unit U were seen with unit F females on 12 different days in 1995 and 1996. Unit U has been identified in 15 different years since 1990. Although generally observed alone as a separate social unit, members of U have been sighted in clusters with members of F in 6 of those years. This long-term preference between social units appears similar to that found in “bond groups” of African Elephants (Moss and Poole 1983; Moss and Lee 2011). Elephant society is also organized into small matrilineal families who care for each other’s young, each group has a homerange which overlaps with those of other families. Two or more elephant families which share some portion of their homerange and spend much of their time together while coordinating their behavior are called a “bond group”. Unlike the elephants, however, I know very little about each of the sperm whale units’ homeranges beyond my study site or to what degree they overlap with those of other units, but ongoing genetic analysis will reveal if there is any genetic relatedness between units F and U, or the other pairs of units who seem to share this “bonded” long term relationship. What is apparent is that the relationship between these units goes beyond preferred associations among adult members. Both dependent calves from Unit F, ‘Enigma’ and ‘Tweak’, were often babysat by members of Unit U. This would suggest that the boundary for altruistic or cooperative allocare behavior may extend beyond the stable, matrilineal social unit to members of long-term, preferred bond groups. These association patterns would also indicate that female sperm whales have the ability to identify a large number of conspecifics which are not regularly encountered and discriminate preferred units with which to associate. Therefore, females are likely able recall the interaction histories and accumulate social knowledge over long time periods, drawing another parallel with African elephants who share this ability (McComb *et al.* 2000). Thus, there are both mutualistic and non-mutualistic forms of groups among sperm whales (Connor 2000). In some cases, whales gather to form groups for reasons which benefit the individuals, such as for increased numbers of babysitters, and so preferences between units exist; while other times groups form due to external influences like the presence of mature males. So, while group formation is temporary, preferred membership seems to be stable across decades. More time will be needed to elucidate the details of what influences the patterns of formation of mutualistic groups and the trade-offs between ecological costs and social benefits (Clutton-Brock and Harvey 1977; Emlen and Oring 1977).

Social preferences based on direct personal knowledge create complexity and diversity in the types of relationships formed at multiple levels of sperm whale social structure and across various time scales. Individuals show preferences for each other across hours, days, and years and units form strong long-term bonds across decades. Given that sperm whale vocal clans in the Pacific appear to mark divisions between sperm whale cultures which include thousands of animals; this species, along with other long-lived, socially complex animals, may have the ability to develop knowledge of a large number of conspecifics, spread across large spatial and temporal scales.

CHAPTER 5

VARIATION IN INDIVIDUAL VOCAL REPERTOIRE WITHIN THREE UNITS OF SPERM WHALES

The value of identity of course is that so often with it comes purpose.

~Richard R. Grant

INTRODUCTION

When social associations between individuals are organized into hierarchical levels of nested groups, various forms of recognition are important to mediate interactions between various levels of social structure (Sherman *et al.* 1997). In order for individuals or groups to identify themselves there must be enough variation in the signal to allow for individual- or group-level distinction. Hierarchical cues of identity are common among birds in which the general form of the song itself identifies species, while variations within that form identify the singer as an individual (Becker 1982; Falls 1982). More broadly, the correlation between social complexity and greater variation in communicative signals is demonstrated in several different taxa (Freeberg *et al.* 2012) including: bats (Wilkinson 2003), primates (Maestripieri 2005; McComb and Semple 2005) and birds (Freeberg and Harvey 2008).

Among cetaceans, variation in a species' communication signal correlates with the level of social association most significant in their society (Tyack 1986; Tyack and Sayigh 1997). Humpback whales (*Megaptera novaeangliae),* which appear to have only weak preferences among social partners, exhibit only population level variation of songs (Payne and Guinee 1983), while bottlenose dolphins (*Tursiops* spp.) have strong and consistent individual-level variation in their signature whistles which presumably facilitates their complex fission-fusion social structure (Caldwell and Caldwell 1965; Quick and Janik 2012). Killer whales are another interesting case as they show strong pod-specific dialects (Ford 1991; Miller and Bain 2000; Yurk *et al.* 2002).

The sperm whale (*Physeter macrocephalus*, Linnaeus 1758) lives in a multileveled society (Whitehead *et al.* 2012). This species communication system includes 'codas', stereotyped patterns of 3-20 clicks (Watkins and Schevill 1977; Weilgart and Whitehead 1997). Distinct coda dialects appear to act as vocal markers of clans, which include thousands of individuals that share a similar dialect and which may be the largest example of cooperative non-kin groups outside humans (Rendell and Whitehead 2003b). There is also important social stratification within clans. Clans are made up of units, the primary level of the sperm whales' social structure. Units contain mature females and their dependent offspring. The females are often but not always related (Richard *et al.* 1996a; Mesnick 2001) and unit membership is stable over long time periods (Whitehead *et al.* 1991; Christal *et al.* 1998). Rendell (2003) suggested that there is some variation in coda repertoire between units within at least one of the sympatric clans in the Eastern Tropical Pacific, while Gero (CHAPTER 6) shows that units in the Atlantic have distinct repertoires within the Eastern Caribbean Clan.

Within units, matrilineal relationships structure associations among individuals (Gero *et al.* 2008; CHAPTER 3). Furthermore, these individual-level relationships within units are dynamic, changing with age, reproductive status, and social role (CHAPTER 3). This all indicates that the whales must be adept at identifying one another individually. Just how this recognition is achieved is unclear. Watkins and colleagues hypothesized that different coda types functioned in individual recognition (Watkins and Schevill 1977; Watkins *et al.* 1985); however, more recent research suggests that individuals within units share common coda repertoires (Moore *et al.* 1993; Rendell and Whitehead 2004; Schulz *et al.* 2011). The most detailed study on individual repertoires to date showed a more complex picture in which a mother and her dependent calf had distinctive coda repertoires compared with the other adult and subadult unit members (Schulz *et al.* 2011). Schulz *et al.* (2011) suggested that mothers, which have a greater need for individual recognition, may alter their repertoire to be more distinct to assist the relationship with their calf, but revert to the common unit repertoire when they have weaned their calves.

Further variation among individual sperm whales can be found in the way individuals produce a specific coda type. In the same unit studied by Schulz *et al.* (2011), Antunes *et al.* (2011) found individually-specific characteristics in the '5R' coda type which were robust across recording days, but not in the other most common types in the unit's repertoire. Taken together these two studies suggest that sperm whales have specific cues to identify not only themselves as individuals using their 5R codas, but also their social roles by varying their coda repertoire when rearing a dependent calf.

Given the complexity of social interactions between individuals within units, and the possibility that sperm whales may also use codas to mark for higher levels of social structure, variation in coda usage and production at the level of the individual demands closer examination to understand how the variation at higher levels arises. In this study, I address fine-scale variation in coda repertoires between individual unit members. Recordings were made of codas produced by three well-studied units of sperm whales which have been tracked across years (2005-2010) as a part of a longitudinal study off sperm whale behavior off the coast of the island of Dominica in the eastern Caribbean. Specifically, I examine individual coda repertoires (patterns of usage of various coda types), as well as differences in the way specific coda types are made by different individuals within units (or accents). Additionally, I test whether repertoire or accent similarity correlates with social associations among unit members. Finally, changes in the composition of these units have allowed us to test the hypothesis that females alter their vocal repertoire with the birth of new calves and then revert to a shared common repertoire following weaning.

METHODS

FIELD METHODS

My study area covered approximately 2000 km^2 along the entire west (leeward) coast of the island of Dominica (N15.30 W61.40). Social units of sperm whales were tracked both acoustically and visually by observers on one of three platforms (a dedicated 12m auxiliary sailing vessel, a dedicated 5m outboard skiff, or an 18m whale-watch vessel). Observations were made over 324 days of effort in the winters of 2005 through 2010 for a total of 2549 hours with whales (Table 5-1). On heavier weather days during season when operating from the small outboard skiff, if the skiff was unable to operate, the research team worked from the larger whale-watch vessel. These whale watch tours focused their search effort on sperm whales. As a result, the methods remained the same across all three platforms, with the work on heavy weather days during skiff seasons being restricted only by the length of time spent at sea by the whale watch vessel.

Table 5-1: Effort across years

Year	Start Date	End Date	Days Effort	Platform
2005	January 14	April 13	62	Sailing only
2006	January 17	February 11	21	Whalewatch only
2007	January 28	February 28	30	Skiff and Whalewatch
2008	February 8	May 8	75	All
2009	January 11	March 29	64	Skiff and Whalewatch
2010	January 20	April 18	72	Sailing only

Clusters of whales ("cluster" is defined later) visible at the surface were approached, during daylight hours only, in order to collect photographs for identification purposes (Arnbom 1987). If a calf was present in a cluster, dorsal fin pictures of the calf from alongside the animals were taken before moving behind the adults in order to photograph distinct markings on the trailing edge of their flukes, which are raised from the water at the start of deep foraging dives. Samples of sloughed skin samples were collected in the slicks of individuals after identification for genetic determination of sex, haplotype, and pairwise relatedness, (Whitehead *et al.* 1990; Amos *et al.* 1992; Richard *et al.* 1996a; Richard *et al.* 1996b).

After identification photographs were collected, digital acoustic recordings were made for two purposes: 1) to record the onset of the echolocation "usual" clicks of singleton whales (*i.e.* a cluster containing only one whale) for measuring that individual's echolocation click inter-pulse interval, and 2) to record coda output for clusters of all sizes while initiating dives. Codas were also recorded when the whales were socializing. Vocalizations were recorded using one of several recording setups: In 2005, we used a Fostex VF-160 multitrack recorder (44.1 kHz sampling rate) and a custom built towed hydrophone (Benthos AQ-4 elements, frequency response: 0.1-30kHz); no recordings were made during the short 2006 season; in 2007 and 2009, we used a Zoom H4 portable field recorder (48 kHz sampling rate) and a Cetacean Research Technology C55 hydrophone (frequency response: 0.02-44kHz); during the 2008 and 2010 seasons, we used the custom built towed hydrophone (Benthos AQ-4 elements, frequency response: 0.1-30kHz) and computer based recording system using the International Fund for Animal Welfare's LOGGER software (48 kHz sampling rate). Variation in the frequency responses of the different recording systems is not important given that only the temporal patterning of clicks was used in this analysis.

ANALYSES

Defining Units and Association between Individuals

Units were delineated as in previous work based on photoidentifications and association data collected over the six years of this study (CHAPTER 4). A unit was defined as a set of individuals for which each pair was observed clustered together during two different years. Associations across years suggest stable, long-term companionship as defined by Whitehead *et al.* (1991). Associations between individuals were quantified using the half-weight index (HWI) of association as this best accommodates my methods (Cairns and Schwager 1987) and we used a two hour sampling period (CHAPTER 4). Individuals were considered cluster members if they were within approximately 3 adult-body lengths of any other cluster member (~40m "chain rule") and their behavior was coordinated (Whitehead 2003). Here, I used these association datasets to ask whether individuals with similar repertoires associated more often by calculating matrix correlation coefficients between the association matrices and matrices of repertoire similarity across pairs of individuals using Mantel tests with 10000 permutations (Mantel 1967; Schnell *et al.* 1985). In addition, for one unit, pairwise genetic relatedness was available from a previous study (Gero *et al.* 2008) and used to test whether vocal similarity correlates with genetic relatedness.

I analysed recordings from three different units: Units F (5 adults 2 calves: 44 recordings on 27 different days over 4 years), Unit J (4 adults 1 calf; 21 recordings on 8 different days over 4 years), and Unit U (3 adults 1 calf; 18 recordings on seven different days over 3 years). Unit F was the same unit studied by Schulz *et al.* (2011) and Antunes *et al.* (2011), and my larger set of recordings includes those used in those two studies. These three units had larger sample sizes and distinct inter-pulse intervals which allowed for assignment of vocalizations to individuals using the methods below.

Assigning Codas to Individuals

The multi-pulsed structure of a sperm whale click is made up of a set of uniformly spaced pulses with decaying amplitude which result from the sound undergoing a series of reverberations within the nasal-complex of the whales (Norris and Harvey 1972; Møhl *et al.* 2003). The interpulse interval (IPI) can be measured with the aid of a computer by simply taking the time lag between pulses. By the nature of the sound's path, the time lag has a direct relationship with the size of the spermaceti organ (Gordon 1991; Rhinelander and Dawson 2004; Teloni *et al.* 2007). This in turn can, and has been, used to accurately measure individual animals using an equation which relates the IPI, and thus the length of the spermaceti, to actual body length (Adler-Frenchel 1980; Gordon 1991; Leaper *et al.* 1992; Pavan *et al.* 2000; Drouot *et al.* 2004; Rhinelander and Dawson 2004; Teloni *et al.* 2007; Growcott *et al.* 2011; Schulz *et al.* 2011).

Here, I use measurements of IPI in order to attribute vocalizations to individuals based on analyses developed by Schulz *et al.* (2011) with some minor modifications. Three steps were required to identify and assign vocalizations to individuals. In the first, recordings of the first few minutes of echolocation clicks of photoidentified singletons were used to define the echolocation click IPI for that individual. I used *Rainbow Click* software (developed by the International Fund for Animal Welfare, see Gillespie 1997; Leaper *et al.* 2000; Jaquet *et al.* 2001; Rendell and Whitehead 2004) to identify and export waveforms of echolocation click trains. The IPIs of the clicks were then calculated using a modified version of custom-written MATLAB routines which require approval of each click by an observer (Schulz *et al.* 2011). While the pulsed structure of the received click varies with the relative aspect of the whale to the hydrophone (Zimmer *et al.* 2005), previous studies (Gordon 1991; Goold 1996; Rhinelander and Dawson 2004; Teloni *et al.* 2007; Schulz *et al.* 2011) have also used recordings made of the clicks during the first few minutes after a single animal dives. This places the hydrophone such that it is "on-axis" and therefore at an aspect most favorable to the accurate reception of the pulse structure (Zimmer *et al.* 2005). Any click deemed to be "off-axis" based on visual inspection, and those for which there was a clear non-biological transient, such as wave and engine nose or hydrophone knocking, were omitted from further analyses. After approval, the routines calculated three estimates of the IPI: 1) the time-delay giving the maximum waveform cross-correlation, 2) the median time-delay among those giving the five largest positive cross-correlation values, and 3) the time-delay of the peak closest to the midpoint between the peaks which are at least 30% of the height of the maximum cross-correlation. I then calculated a single mode over all three measures for all the clicks analyzed in a recording and if greater than 50% of the clicks were within 0.05msec of that mode, then I took that mode to be the measured IPI for that individual for that recording. The final echolocation click IPI for each whale was calculated by taking the mode of the IPIs across its recordings over different days within a year. Echolocation click IPIs were calculated for each individual within each unit for each year from 2005-2010. The result of this initial step was a library of echolocation click IPIs which had been attributed to identified individuals for a given year.

Coda recordings were then analyzed using *Rainbow Click* software to determine the coda inter-click interval (ICI, the time between the onset of one click and the onset of the next click) for all codas recorded. The coda clicks were marked and codas defined manually by a trained observer (SG analyzed all recordings) and the timing of the clicks within codas calculated by the software. Each coda could then be represented by the set of ICIs, either using absolute time intervals (Absolute ICI) or proportions relative to the total coda length (Standardized ICI, which conserves rhythm but discards tempo of codas as in Moore *et al.* 1993). Rare long coda types (>10 clicks; <5% of all codas recorded) were excluded from the analysis.

I then analyzed the coda recordings in a similar manner using the *Matlab* routines to determine the coda click IPI for each coda. Each coda was assigned an IPI by taking the mode over all three measures (as above) for all clicks within that coda. Just as when analyzing the IPI of echolocation clicks, only audible codas which had a clear structure were used such that codas that were off-axis or in which there was a clear non-biological transient were omitted from analyses. Finally, equipped with the library of echolocation click IPIs, I assigned codas to individual whales when its modal echolocation click IPI (derived from the recordings taken when the individuals were alone) was within 0.05 msec of the modal coda click IPI of a whale which was present at the time of recording and at least 0.1 msec different from the modal coda click IPI of every other whale present at the time of the recording. The details of how these cut-offs were determined are given in Schulz *et al.* (2011). In general, clusters of whales were hundreds to thousands of meters apart; and thus, only members of the photoidentified cluster were within a few hundred meters of the hydrophone and therefore recorded, given that codas are only clearly audible through near-surface hydrophones at ranges of a few hundred meters or less.

Measures of Similarity between Repertoires

To quantify similarity between repertoires of individuals, I used seven different measures: three categorical and four continuous measures. First, I assigned codas to categorical type using *k*-means cluster analysis using both absolute and standardized ICI measures as described in Rendell and Whitehead (2003a; 2004) with modifications as in Schulz *et al.* (2011). Given that previous work has highlighted the problems in determining the appropriate number of clusters into which each coda size (4-click, 5-click, etc.) are to be grouped (*k*) using non-arbitrary methods (see Rendell and Whitehead 2003a), I determined *k* in three different ways. The first two used stopping rules based on Variance Ratio Criteria (VRC; Calinski and Harabasz 1974) by taking either the lowest local maxima or the absolute maxima of the VRC as *k* increases (Schreer *et al.* 1998; Rendell and Whitehead 2003a). After first visually interpreting the plotted data, I also categorized codas based on a third set of values for *k*. This "conservative" set of *k* values differed from the lowest local maxima method primarily by increasing number of clusters attributed to the 4 and 5-click coda sets, which have proven to be problematic in similar analyses (Rendell and Whitehead 2003b). As a result, VRC methods had fewer coda types but increased variability within coda types, whereas the "conservative" method split clusters into more coda types but each had a higher similarity between codas within them. Coda types were given names based on the patterning of the clicks following previous nomenclature (Weilgart and Whitehead 1997; Rendell and Whitehead 2003b; Schulz *et al.* 2011). For example, a '5R' coda is one in which five clicks are regularly spaced, while a '1+1+3' coda sounds like "click-[PAUSE]-click-[PAUSE]-click-click-click" with longer gaps between the first two clicks followed by three clicks in quick succession. For categorical measures of similarity, two codas were given a similarity of 1 if they were assigned to the same type and were given a similarity of 0 if they were assigned to different types.

For the continuous measures, the multivariate similarity of two codas with the same number of clicks was measured using either the infinity-norm distance or Euclidean distance, a basal similarity of 0.001, 0.01, 0.1 or 1.0, and either ICI measure using the equation below, as in previous work (Rendell and Whitehead 2003a; Rendell and Whitehead 2003b; Schulz *et al.* 2011).

$$S_{AB} = \frac{\sum_{i=1}^{n_A} \sum_{\substack{j=1 \\ l_j=l_i}}^{n_B} \frac{b}{b + d_{ij}}}{n_A n_B}$$

where S_{AB} is the similarity between repertoires *A* and *B* each with n_A and n_B codas, respectively; l_i and l_j are the number of clicks in coda *i* from repertoire *A* and the number of clicks in coda *j* in repertoire *B*; *b* is the basal similarity and d_{ij} is the distances between ICI vectors using either of the measures. The multivariate similarity between two codas containing different numbers of clicks was zero.

Differences between Repertoires

Matrix correlations and Mantel tests with 10000 permutations (Mantel 1967; Schnell *et al.* 1985) were then calculated on two different data sets to examine differences in repertoire. First, in order to test the null hypothesis that coda repertoires do not differ between individuals within units, I tested whether pair-wise similarities were higher between two days' recordings of the same individual (Same individual, Different Days - SIDD) compared with two days' recordings of different individuals (Different individuals, Different Days - DIDD). Each day's recordings were treated independently in an attempt to account for any autocorrelation in coda production within recording days. To do so, I tested the matrix of pairwise similarities of each days recordings against a 1/0 matrix with 1 coding for SIDD and 0 coding for DIDD. If individuals have distinct repertoires, then the expectation is a significantly positive correlation between these matrices. Secondly, in order to see if coda repertoires of individuals differed between years, I calculated the mean similarity between recordings of a focal individual within the same year and between years for all individuals in all three units. Unfortunately, sample sizes within individuals within years were too small to conduct Mantel tests. All matrix correlations and Mantel tests, here and above, were carried out using *SOCPROG* 2.4 (Whitehead 2009) in *MATLAB* 7.12 (The Mathworks, Inc., MA, USA).

Patterns of Similarity between Individuals

Similarity matrices were used to construct average-linkage clustering dendrograms using the similarity results and tested their robustness using 1000 bootstrap replicates. At each bootstrap iteration, the codas from each repertoire were randomly sampled with replacement prior to calculating the pairwise repertoire similarities. For each branch, I counted the proportion of replicates in which the branch was reproduced. The cophenetic correlation coefficient (CCC) was also calculated to indicate how well the dendrogram represented the data. A CCC of over 0.8 is considered a "good" representation of the associations (Bridge 1993).

Subsets and Testing within Coda Types:

These analyses were repeated on restricted datasets: only 4-click codas (5 coda types), only 5-click codas (4 coda types), the 1+1+3 variant codas (2 coda types), only the '5R' type codas, only the '1+1+3slow' codas, and only the '1+1+3' codas. Note that for the last three datasets there is only one coda type and so I used only the multivariate techniques.

Therefore, these tests examine similarity within a coda type used by different individuals. For example, it would test whether different individuals make the '5R' coda in consistently different ways.

RESULTS

The results did not vary greatly when using any of the three k-means methods or any of the combination of multivariate techniques (Absolute ICIs or standardized ICIs and regardless of the distances norms used or basal similarity). As a result, and for simplicity, I present only the categorical results using the clusters determined by the conservative values for *k* and the multivariate results of the standardized ICIs, infinity norm distances, and with a basal similarity of 0.001, for consistency with previous studies (Moore *et al.* 1993; Rendell and Whitehead 2003a).

PATTERNS ACROSS THE THREE UNITS

Coda repertoire differs between individual members of all three units (Table 5-2). This is true for all subsets of the repertoire for which I was able to test with the exception of the '1+1+3' coda type. General patterns emerging from all three units are that individuals differ in their overall repertoires, and their accent on the '5R' codas, but not their accent on the '1+1+3' codas (Table 5-2). While I was not able to test the significance explicitly due to sample size, the mean similarities within and between years of an individual's repertoire (Table 5-3) would suggest that individuals do not much change their vocal repertoire between years, at least over the six year duration of this study (2005-2010). Juveniles and calves appear to use more coda types (Mean adult females = 8 types, mean juveniles/calves = 12 types). In particular, calves in two of the three units used the 3+1 when none of the adults from any of the units did so even once. Finally, for all three units, I found no relationship between social association and vocal similarity for either the full repertoire or any of the repertoire subsets or specific coda types (Table 5-4).

Unit F: 'The Group of Seven'

Unit F, or 'The Group of Seven', has at its base five adult females, who have been consistent associates since at least 1995 (Gero *et al.* 2007). In addition, there is an immature male, 'Scar' (#5727), who, based on his length, was between 8 and 10 years old in 2005 (Schulz 2007), making him between 13 and 15 in 2010. There have also been several changes in the composition of the unit over the course of this study. One female ('Fingers' #5722) lost her calf ('Thumb' #5703) after the 2005 season, the adult female 'Puzzle Piece' (#5130) disappeared between the 2005 and 2006 seasons and has not been sighted since, and two new calves have been born: 'Enigma' (male, #6068) to 'Mysterio' (#5561) in 2005 and 'Tweak' (male, #6070) to 'Pinchy' (#5560) in 2007. As sample size was low for the two new calves, their vocal production was merged to look at differences between adults and calves.

Table 5-2: Mean repertoire similarities within individuals and between individuals and results of one-tailed Mantel tests of a null hypothesis that repertoire similarity between recordings of the same individual on different days is the same as that between recordings of different individuals on different days. Only Unit F had sufficient sample size to conduct the analysis for the 4-click coda dataset and Unit J did not have sufficient sample size for the '5R' test. Multivariate similarity using standardized ICIs, infinity-norm distances, and b=0.001. Categorical similarity using conservative values for *k*. Significant tests (at *p*<0.05) bolded.

Unit	Repertoire	Multivariate Similarity				Categorical Similarity			
		Within	Between	Matrix Correl.	*p*	Within	Between	Matrix Correl.	*p*
F	**Full**	0.027	0.007	**0.50**	**<0.002**	0.474	0.228	**0.32**	**<0.001**
	5-Click Only	0.028	0.021	**0.24**	**<0.001**	0.444	0.367	**0.09**	**0.03**
	4-Click Only	0.054	0.023	**0.61**	**<0.001**	0.840	0.365	**0.53**	**0.004**
	5R Only	0.029	0.021	**0.30**	**0.04**		One Coda Type		
	1+1+3 Both	0.031	0.025	**0.18**	**<0.001**	0.520	0.484	0.05	0.10
	1+1+3slow	0.045	0.031	**0.55**	**<0.001**		One Coda Type		
	1+1+3	0.045	0.038	0.09	0.08		One Coda Type		
J	**Full**	0.027	0.021	**0.20**	**0.003**	0.369	0.331	0.07	0.13
	5-Click Only	0.029	0.026	**0.12**	**0.046**	0.402	0.416	-0.02	0.57
	1+1+3 Both	0.031	0.028	**0.19**	**0.02**	0.471	0.496	0.06	0.22
	1+1+3slow	0.042	0.035	**0.24**	**0.005**		One Coda Type		
	1+1+3	0.042	0.041	0.03	0.35		One Coda Type		
U	**Full**	0.023	0.010	**0.61**	**<0.001**	0.381	0.194	**0.54**	**<0.001**
	5-Click Only	0.035	0.018	**0.63**	**<0.001**	0.629	0.391	**0.38**	**<0.001**
	5R Only	0.042	0.025	**0.55**	**<0.001**	One Coda Type			
	1+1+3 Both	0.038	0.017	**0.79**	**0.002**	0.875	0.567	**0.58**	**0.002**
	1+1+3slow	0.042	0.020	**0.80**	**0.007**	One Coda Type			
	1+1+3	0.018	0.025	-0.32	1.0	One Coda Type			

I recorded a total of 1065 codas from members of the Group of Seven. As a unit, their repertoire is dominated by 4 different coda types: the '1+1+3', '1+3D', '1+1+3slow' and the '7D', in descending order (Figure 5-1). The dendrogram in figure 5-1 provides a good representation of the similarity of repertoires between individuals as it has a cophenetic correlation coefficient of 0.9418. Most adults, and the juvenile male, shared the '1+1+3' variants or the '5R' coda types as greater than 10% of their production. The two exceptions are Fingers, an adult female, and Thumb the calf from the 2005 season. Fingers' repertoire differs in that she rarely used the '1+1+3' codas or the '5R' type, but made a large number of the other two predominant coda types for this unit (1+3D and 7D).

Table 5-3: Mean full repertoire similarity of individuals within and between years. **Multivariate similarity using standardized ICIs, infinity-norm distances, and b=0.001. Categorical similarity using conservative values for *k*.**

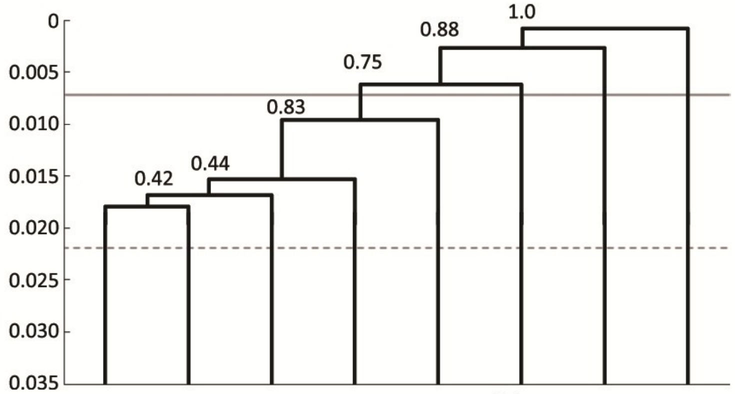
Full Repertoire			**Multivariate**		**Categorical**	
Unit	**Individual**	**Years**	**Within Year**	**Between Years**	**Within Year**	**Between Years**
F	**Unit Means**		0.022	0.021	0.438	0.461
	SE		0.001	0.001	0.021	0.007
	Pinchy	4	0.018	0.025	0.317	0.437
	Mysterio	3	0.029	0.021	0.425	0.405
	Fingers	4	0.043	0.041	0.612	0.649
	Scar	3	0.015	0.015	0.400	0.354
	Tweak	3	0.006	0.004	0.265	0.322
J	**Unit Means**		0.024	0.024	0.376	0.338
	SE		0.002	0.001	0.033	0.017
	Jocasta	3	0.017	0.019	0.243	0.319
	Oedipus	4	0.032	0.033	0.465	0.451
	Sophocles	2	0.013	0.014	0.236	0.237
	Laius	4	0.036	0.030	0.561	0.345
U	**Unit Means**		0.017	0.019	0.312	0.328
	SE		0.003	0.001	0.040	0.011
	Fork	2	0.010	0.016	0.282	0.315
	Knife	2	0.032	0.034	0.507	0.528
	Spoon	2	0.007	0.007	0.147	0.140

However, these coda types were not exclusively made by Fingers. Two other adult females (Puzzle Piece and Mysterio) and the calves produced the 1+3D, and Scar and Mysterio produced the 7D. In this latter case, the 7D was also a predominant coda type in Mysterio's repertoire. Interestingly, the two new calves' merged vocal repertoire differed from that of Thumb. Thumb was a young of the year in 2005 when recordings of him were made, while the other two calves (both also male) were older ranging in age from 1 and 5 between 2008 and 2010 when their codas were recorded. The three calves did share a unique coda type which only calves made, the 3+1 type.

Table 5-4: Matrix correlations comparing social association (HWI) within units with vocal similarity across years (2005-2010) and the results of Mantel tests with a null hypothesis that individual repertoire similarity is unrelated to social association.

		Multivariate Similarity		Categorical Similarity	
Unit	**Repertoire**	**Matrix Correlation**	***p***	**Matrix Correlation**	***p***
F	**Full**	-0.10	0.66	-0.29	0.93
	5-Click Only	-0.28	0.94	-0.32	0.98
	4-Click Only	0.13	0.38	0.06	0.49
	5R Only	0.19	0.34	One Coda Type	
	1+1+3 Both	-0.36	0.88	-0.42	0.96
	1+1+3slow	-0.38	0.86	One Coda Type	
	1+1+3	0.12	0.34	One Coda Type	
J	**Full**	0.00	0.36	0.12	0.22
	5-Click Only	0.36	0.29	0.59	0.17
	1+1+3 Both	0.13	0.29	0.18	0.38
	1+1+3slow	0.23	0.30	One Coda Type	
	1+1+3	-0.37	0.75	One Coda Type	
U	**Full**	0.00	0.53	-0.04	0.54
	5-Click Only	-0.71	0.58	0.11	0.58
	5R Only	-0.47	0.74	One Coda Type	
	1+1+3 Both	-0.77	1.0	0.98	0.33
	1+1+3slow	-0.92	1.0	One Coda Type	
	1+1+3	-0.24	0.68	One Coda Type	

Social association between individuals within this unit was found to be independent of vocal similarity (Table 5-3). For this unit only, pairwise relatedness data were available in addition to social association. When all individuals except the two new calves were included (no skin sample was available for the two new calves), genetic relatedness correlated quite strongly but not statistically significantly with repertoire similarity (matrix correlation = 0.40, *p* = 0.10); however, when Puzzle Piece (the adult female who disappeared after the first year and for which the sample was smaller) is removed there is a strong and significant correlation between repertoire similarity and pairwise relatedness (matrix correlation = 0.83, *p* = 0.003; Figure 5-2).



Coda Length	Coda Type	Puzzle	Scar	Pinchy	Mysterio	Quasi	Calves Merged	Fingers	Thumb	Total Codas by Type
		A	JM	A	A	A	C	A	C	
3	3R	0	0	0	0	0	2	0	0	**2**
	2+1	0	0	0	0	0	12	0	0	**12**
4	4R	0	0	0	0	0	8	0	0	**8**
	1+3	0	0	0	1	0	4	12	0	**17**
	1+3D	10	0	0	10	0	2	157	0	**179**
	1+1+2	0	0	0	1	0	3	1	0	**5**
	3+1	0	0	0	0	0	26	0	1	**27**
5	5R	0	36	18	7	0	13	0	0	**74**
	1+1+3slow	0	31	58	59	4	16	0	0	**168**
	1+1+3	18	102	46	36	5	51	6	0	**264**
	2+1+1+1	0	1	0	0	0	6	0	11	**18**
6	6R	0	12	0	0	0	5	0	0	**17**
	6S	0	4	0	0	0	2	0	17	**23**
	1+1+4	0	4	0	3	0	3	18	0	**28**
7	7R	0	5	6	0	2	3	0	0	**16**
	7S	0	1	0	0	0	2	0	20	**23**
	7D	0	1	0	18	0	0	98	0	**117**
8	8R	0	5	7	0	2	1	0	1	**16**
	8S	0	4	2	0	0	0	0	6	**12**
	8D	0	4	0	1	1	1	8	0	**15**
9	9R	0	4	2	0	0	0	0	0	**6**
	9S	0	2	2	0	0	0	0	4	**8**
	9D	0	0	0	0	3	0	0	0	**3**
10	10R	0	0	1	0	0	0	0	0	**1**
	1+9	0	1	0	0	1	0	0	0	**2**
	9+1	0	1	2	0	0	0	0	1	**4**
Total Codas by Individual		28	218	144	136	18	160	300	61	1065
Recordings Total - Days - Years		5-4-1	16-10-3	14-13-4	10-8-3	4-3-2	11-5-3	22-13-4	4-4-1	44-27-4

Figure 5-1: Coda repertoires of individuals in Unit F compared using infinity-norm distances of standardized inter-click intervals with a basal similarity of 0.001 (top) and conservative *k*-means classification methods (bottom). Numbers next to branches of the dendrogram indicate the proportion of the 1000 bootstrap replicates in which that branch was reproduced. A cophenetic correlation coefficient of 0.9418 suggests this is a good representation. Horizontal rules indicate the mean between (solid) and within (dotted) individual similarities. Letters denote age class (A – Adult, JM – Juvenile Male, C – Calf). Numbers in the table indicate the frequency with which each individual coda type was produced by each individual. Shaded numbers indicate that the coda type made up at least 10% of the individual's coda production. For the nomenclature: "R" indicates a coda with regular ICIs, "+" indicates a longer gaps between clicks, "S" indicates increasing ICIs throughout the coda, "D" indicates decreasing ICIs throughout the coda, and "slow" indicates a variant of the coda type above it in which the last set of clicks had relatively longer, but still equal to each other, ICIs than its predecessor. Numbers below each column are the total number of codas recorded from each individual, as well as the total number of recordings, recording days, and years per unit.

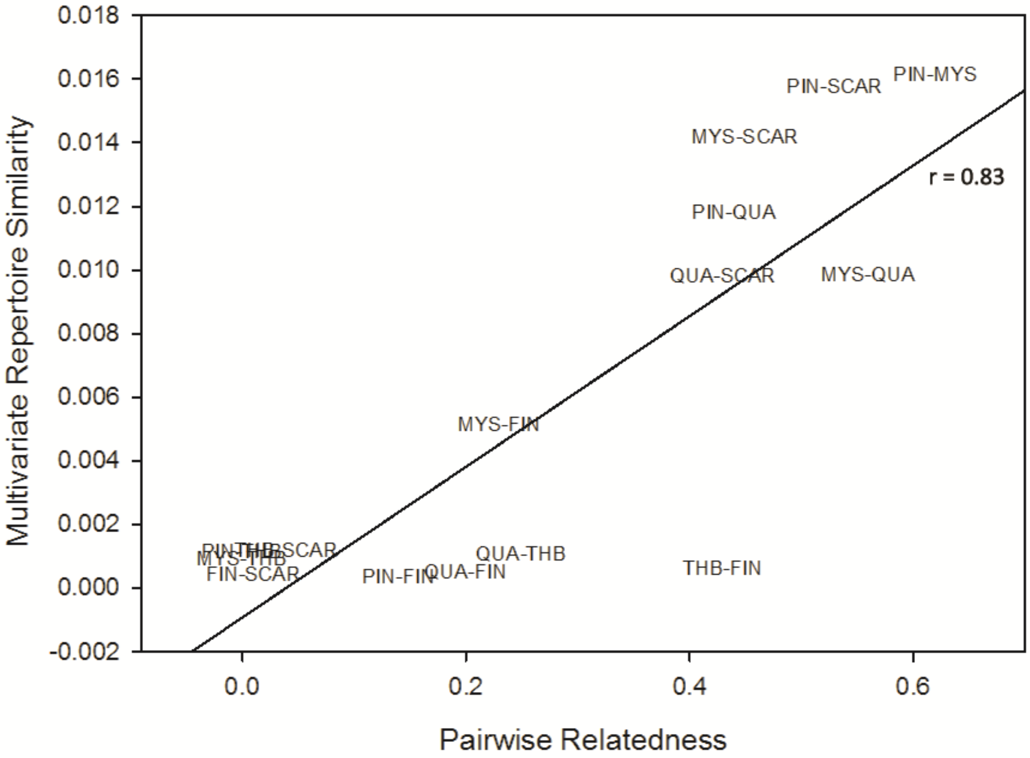


Figure 5-2: Plot comparing pairwise genetic relatedness of dyads from Unit F with the dyad's corresponding multivariate repertoire similarity of their full repertoires based on standardized ICIs, infinity norm distances, and a basal similarity of b=0.001. Note that Fingers, 'FIN', has local vocal similarity and genetic relatedness with other members of the unit.

Unit J: 'Jocasta's Unit'

Unit J is a small unit of only four adults and one calf. When first encountered in 2007, 'Oedipus' (#5978) was still suckling from 'Jocasta' (#5987) and 'Sophocles' (#5979) and 'Laius' (#5981) often escorted Oedipus. Between the 2009 and 2010 seasons, 'Antigone' (#59871) was born. While this calf appeared to make suckling attempts on both Oedipus and Laius, it was most often escorted and nursed by Jocasta, so as a result maternity is uncertain.

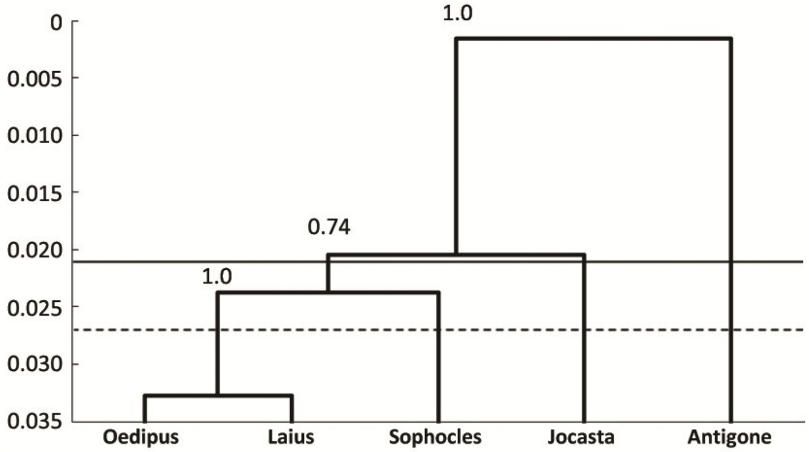
I recorded a total of 387 codas from Unit J, the bulk (91%) of which were '1+1+3' variants or the '5R' coda. While individual repertoires within this unit were more similar to each other than among individuals in Unit F, they still differed significantly both categorically and using multivariate methods. The dendrogram in figure 5-3 provides a good representation of the similarity of repertoires between individuals as it has a cophenetic correlation coefficient of 0.9972. All individuals used these coda types with the exception of the calf, Antigone, who made the ‘3+1’ coda and the 2+1+1+1; however, I only had a very small sample from the calf in this unit. Patterns of association within the unit did not correlate with vocal similarity (Table 5-3) and coda repertoire of all the individuals remained similar between years (Table 5-2).

Unit U: ‘The Utensils’

Unit U, or The Utensils, is a small unit of 2 adult females, a juvenile female, and one male calf. ‘Fork’ (#5151) is ‘Spoon’s’ (#6035) mother. As of 2010, Spoon was still dependent on Fork and still occasionally suckled. The unit also contains ‘Canopener’ (#6058), an independent juvenile female, and ‘Knife’ (#5562), the other adult female. Maternity for Canopener is still uncertain, but her size would suggest that Knife would likely be the mother given that Fork still has a dependent calf.

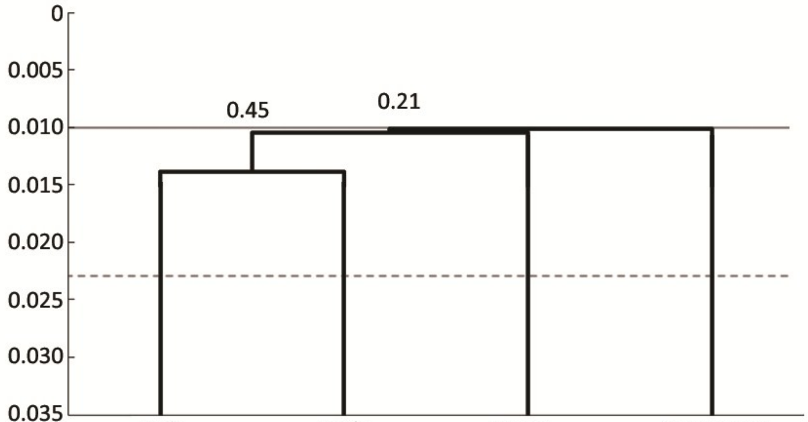
I recorded 255 codas from members of Unit U. There were two predominant coda types: ‘5R’ and ‘1+1+3’ (Figure 5-4). While Mantel tests for differences between individual repertoires were significant (Table 5-1), the cophenetic correlation coefficient of 0.4749 suggests the dendrogram is not a good representation of the differences in repertoires. This is supported by the low bootstrap values for the branches of the dendrogram (Figure 5-4).

As with the other two units, individual repertoires within Unit U did not differ between years (Table 5-2) and did not correlate with association (Table 5-3).



Coda Length	Coda Type	Oedipus	Laius	Sophocles	Jocasta	Antigone	Total Codas by Type
		A	A	A	A	C	
4	4R	0	0	2	1	0	**3**
	1+3	1	0	0	0	0	**1**
	1+3D	1	0	0	0	0	**1**
	1+1+2	1	0	0	0	0	**1**
	3+1	0	0	0	0	3	**3**
5	5R	1	2	9	10	0	**22**
	1+1+3slow	58	41	27	30	0	**156**
	1+1+3	71	35	48	20	0	**174**
	2+1+1+1	0	0	4	0	1	**5**
6	6R	1	2	2	1	0	**6**
	6S	0	0	2	0	0	**2**
	1+1+4	0	0	1	0	0	**1**
7	7R	1	0	0	0	0	**1**
8	8R	0	0	1	1	0	**2**
	8S	0	0	1	1	0	**2**
	8D	0	0	1	0	0	**1**
9	9R	1	0	2	0	0	**3**
	9S	0	0	1	0	0	**1**
	9D	0	0	1	0	0	**1**
10	10R	0	0	1	0	0	**1**
Total Codas by Individual		**136**	**80**	**103**	**64**	**4**	**387**
Recordings Total – Days - Years		**13 - 6 - 4**	**11 - 6 - 4**	**9 - 3 - 2**	**6 - 6 - 3**	**1 - 1 - 1**	**21 - 8 - 4**

Figure 5-3: Coda repertoires of individuals in Unit J compared using infinity-norm distances of standardized inter-click intervals with a basal similarity of 0.001 (top) and conservative *k*-means classification methods (bottom). A cophenetic correlation coefficient of 0.9972 suggests this is a good representation. All notations are as in Figure 1.



Coda Length	Coda Type	Fork A	Knife A	Spoon C	Canopener A	Total Codas by Type
4	**4R**	0	0	3	1	**4**
	1+3	0	0	0	1	**1**
	1+1+2	0	1	1	0	**2**
5	**5R**	23	16	20	23	**82**
	1+1+3slow	0	53	19	18	**90**
	1+1+3	0	3	14	5	**22**
	2+1+1+1	0	0	2	0	**2**
6	**6R**	0	1	9	9	**19**
	6S	0	0	0	1	**1**
	1+1+4	1	0	1	1	**3**
7	**7R**	0	0	3	0	**3**
	7S	2	0	1	0	**3**
8	**8R**	4	1	1	0	**6**
	8S	3	0	1	0	**4**
	8D	0	0	1	0	**1**
9	**9R**	2	1	0	2	**5**
	9S	0	0	2	1	**3**
	9D	1	0	1	0	**2**
10	**10R**	0	0	0	2	**2**
Total Codas by Individual		**36**	**76**	**79**	**64**	**255**
Recordings Total - Days - Years		**5-4-2**	**8-5-2**	**8-3-2**	**8-4-2**	**18-7-3**

Figure 5-4: Coda repertoires of individuals in Unit U compared using infinity-norm distances of standardized inter-click intervals with a basal similarity of 0.001 (top) and conservative *k*-means classification methods (bottom). A cophenetic correlation coefficient of 0.4749 suggests this dendrogram is not a good representation of the differences in the repertoires. All notations are as in Figure 1.

DISCUSSION

I have found some consistent patterns in individual-level coda repertoires across three social units. I have also found that within units, individuals produce '5R' codas in distinctive ways, but cannot be distinguished in their production of the 1+1+3 codas, extending previous findings from a single unit (Antunes *et al.* 2011). Furthermore, these differences appear to be consistent across years, as an individual's coda repertoire is similar between years. It is important to note that the six years of this study represent only a small part of a sperm whale's lifespan (>80 years, Whitehead 2003) and so the absence of variability across years for adult females should be interpreted with caution. However, my results are consistent with a similar degree of temporal stability found in the repertoires of social units (not individuals) in the Pacific (Rendell and Whitehead 2005).

In contrast to what has previously been hypothesized, mothers do not generally vary their coda repertoires with the birth of a new calf. Females who have had a calf during this study kept their vocal repertoires consistent. Vocal repertoire appears to be stable across years, even for individuals whose repertoire differs substantially from that of her unit's. Schulz *et al.* (2011) based their maternal repertoire variation hypothesis on a single year's (2005) recordings of a mother-calf pair from Unit F, Fingers and Thumb. Fingers and Thumb had the most distinct repertoires while the other females and the juvenile male shared a common unit repertoire based on the '5R' and '1+1+3' codas (Schulz *et al.* 2011). With multiple years of data, I can conclude now that Fingers did not vary her repertoire following the death of her calf, but rather had a consistently atypical repertoire for her unit. This is consistent across years and across social roles (Table 5-5). Fingers has played several roles in Unit F since the beginning of this study. In 2005, she was Thumb's new mother (Thumb was estimated to be less than 4 months old when first encountered, Gero *et al.* 2008). After his death, Fingers was the primary babysitter for Mysterio's new calf, Enigma, until Pinchy also had a new calf in late 2007 at which point the concurrent mothers babysat for each other (CHAPTER 3). Even through the changes in social role, Fingers' coda repertoire remained distinct from the other females in her unit. Fingers is also a genetic outlier, being the least related of the 5 adult females. Previous genetic analysis suggested that Fingers is likely to be the aunt of the other females in the unit (Gero *et al.* 2008; Gero and Herbinger unpublished data). Her distinct repertoire and her low pairwise relatedness result in a strong correlation between vocal similarity and relatedness among

Table 5-5: Coda repertoire of Fingers across years and social roles

Coda Type	2005 Mother	2008 No Role	2009 No Role	2010 No Role	Total Codas by Type
1+1+2	1	0	0	0	**1**
1+3	5	2	0	5	**12**
1+3D	38	23	16	80	**157**
1+1+3	0	2	0	4	**6**
1+1+4	0	0	0	18	**18**
7D	0	0	0	98	**98**
8D	0	0	0	8	**8**
Total by Year	**44**	**27**	**16**	**213**	**300**

individuals in Unit F. This could suggest that there is more strict vertical transmission of coda repertoires and individuals learn from their mothers rather than from other members of the unit; however the merits of this hypothesis should be tested for several calves across units before drawing any firm conclusions. Interestingly, while Fingers' coda repertoire is an outlier, she is well integrated socially and often participates in allocare (Gero *et al.* 2008, CHAPTER 3). In contrast, Quasimodo, an adult female who appears to be socially peripheralized (Gero *et al.* 2008, CHAPTER 3), has a repertoire which is more similar to the other adult females in the unit. Given the social and behavioral complexity of this species (Rendell and Whitehead 2001; Rendell and Whitehead 2003b; Whitehead *et al.* 2012; CHAPTERS 3 and 4), it is likely that individuals are dissimilar, or similar, in a number of largely-independent behavioral dimensions (Krause *et al.* 2010; Réale *et al.* 2010). Though distinct acoustically, Fingers is not distinct socially; while for Quasimodo the pattern is reversed.

It is also interesting that the young of year calf recorded in 2005 in Unit F, Fingers' son Thumb, differed more greatly from the common unit repertoire than did the older calves recorded between 2008 and 2010. This provides some insight into the ontogeny of an individual's coda repertoire by suggesting that calves may converge on the unit's common coda types within a few years. Unfortunately, the limits of this methodology made it difficult to distinguish between the two older calves in Unit F. The pulsed structure of their echolocation and coda clicks was not as clear as among the adults and the differences in their sizes, and thus IPIs, was minimal and highly inconsistent. As a result, assignment of codas to the different calves made in the same recording was not possible and dramatically reduced the sample of these two individuals.

It has been suggested that an individual's accent on the '5R' coda might serve as an individual identifier (Antunes *et al.* 2011), and my findings of significant variation between individuals within this coda type in two further units lends support to this notion. However, I found that the rate of social association among pairs of individuals did not correlate with their overall repertoire similarity or similarity in accent for any of the coda types investigated, including the '5R' codas. This suggests that individuals do not use self-similarity in the '5R' coda to determine preferred social partners.

In contrast, I found no significant differences between the '1+1+3' codas produced by different individuals which is also in agreement with Antunes *et al.* (2011). This coda is consistently stereotyped across units studied in the eastern Caribbean (CHAPTER 5). The 1+1+3 type codas have only ever been recorded in the Caribbean and the tempo appears to have remained consistent for over 30 years (Moore *et al.* 1993; Antunes 2009). This coda may therefore function in identifying the population in the Eastern Caribbean, as coda repertoires appear to be geographically structured in the Atlantic (Antunes 2009), perhaps allopatric analogs of the vocal clans in the Pacific.

These results suggest that there have been selective pressures for the development of both individual- and group-specific vocal cues in sperm whales. Living in cooperative, stable social units in which individuals have preferred associates creates a selective environment which favors individual recognition (Crowley *et al.* 1996; Tibbetts and Dale 2007). The variability in coda repertoire and accents demonstrated here would suggest that the whales are likely able to distinguish among individuals, but this has not been explicitly tested. It has previously been suggested that individuals could simply use IPI to discriminate between individuals among the few members of a unit (Whitehead 2003), just as I have in this study. However, others (Antunes 2009) have argued that the utility of IPI as a signal of identity may be limited by changing IPI with size as individuals grow (Gordon 1991), that units are larger in other areas (Whitehead *et al.* 2012) making overlap more likely, and that the clarity of the IPI signal is highly dependent on the producer's aspect relative to the receiver. While aspect-related clarity may present some issues, it is likely that the whales are far better at discerning IPI than any of these statistical processes, and thus overlap in larger groups may also not be a significant problem. Additionally, individual growth rates are slow enough to allow other unit members the chance to adapt to changing IPIs. Undoubtedly, it will be difficult to determine just which cue receivers use for individual, unit, or clan recognition or to determine if whales use this information at all. This will require experimental approaches involving playbacks of codas to individuals whose vocal repertoire and social associations are well-known.

CHAPTER 6

DISTINCT VOCAL REPERTOIRES OF UNITS OF SPERM WHALES WITHIN A VOCAL CLAN IN THE NORTH ATLANTIC

Language is the road map of a culture. It tells you where its people come from and where they are going.

~Rita Mae Brown

INTRODUCTION

Species which live in large and highly organized societies should exhibit complex communicative signals to discriminate among the various tiers of their social structure (Philips and Austad 1990; Freeberg 2010; Freeberg *et al.* 2012). The link between vocal complexity and sociality has been highlighted among primates (Maestripieri 2005; McComb and Semple 2005), and recent evidence suggests that social complexity drives increasing signaling complexity (Freeberg *et al.* 2012). Substantial social complexity has been identified in a number of mammalian species across a wide range of taxa including primates, elephants, and cetaceans (Moss and Poole 1983; Smuts *et al.* 1987; Connor 2000; Wittemyer *et al.* 2005; Strier 2007; Whitehead *et al.* 2012). In these situations, I expect communicative signals to mark social entities, and vocalizations are particularly suited to this role (Philips and Austad 1990; Freeberg *et al.* 2012). But if vocalizations are to function as population, group, or individual identifiers among these species, individuals should be able to hear, learn and recognize the calls of their conspecifics.

While common in songbirds, vocal learning is rare among mammals; however, the cetaceans are well known for their vocal imitation and learning abilities (Janik and Slater 1997). The ocean environment, which varies greatly over long spatial and temporal scales and less over smaller ones in comparison to terrestrial systems (Steele 1985), gives the cetaceans an environment in which social learning is favoured over individual learning or genetic determination of behavior (Whitehead 2007). High mobility, made possible by low travel costs (Williams 1999), and large ranges (Stevick *et al.* 2011) may partially explain their extensive vocal learning capabilities compared with most terrestrial mammals (Tyack and Sayigh 1997). Vocal learning may have evolved in order to facilitate social decisions by allowing cetaceans to recognize the signals of a wide number of conspecifics and neighboring social groups encountered in their large ranges (Deecke *et al.* 2010). This link between large ranging patterns, encounters with less-known individuals across tiers of a multileveled social structure, and vocal learning is evident in the African elephant (*Loxodonta africana*). Elephants have the ability to learn and recognize the vocal signals of an extensive range of well-known and lesser known individuals and social groups across multiple levels of social structure and over large spatial and temporal scales (McComb *et al.* 2000; McComb and Semple 2005; Poole *et al.* 2005; Soltis *et al.* 2005). The ocean is a good medium for sound transmission, making vocal markers for social structures even more likely among cetaceans by potentially allowing identification to occur over large distances (Tyack 1986; Connor *et al.* 1998).

The coevolution of functionally diverse communication systems and complex societies among cetaceans has perhaps best been studied among killer whales (*Orcinus orca*). Among fish-eating 'resident' killer whales, matrilines, within which both sexes remain their whole lives, associate into 'pods' with other matrilines which share a similar socially learned traditional dialect. Several genetically related 'pods' which share some similar vocalizations are grouped into 'clans' and several clans make up vocally distinct communities which use distinct, although sometimes overlapping, geographic areas but never mix socially (Ford 1991; Ford 2002b; Ford 2002a; Ford and Ellis 2006; Deecke *et al.* 2010; Ivkovich *et al.* 2010). Vocal learning seems to occur between pods but the clan boundary may be acting as the barrier to horizontal transmission of vocal culture (Deecke *et al.* 2000).

The sperm whale (*Physeter macrocephalus,* Linnaeus 1758) shares some parallels with the life histories and social structures of both the killer whales and African elephants. One or more matrilines form 'social units' whose female membership is stable across decades, while maturing males leave their natal unit (Whitehead *et al.* 1991; Mesnick 2001). Units range widely and regularly travel up to 2000 kilometers (Whitehead *et al.* 2008). Sperm whales produce a number of stereotyped social calls termed 'codas' that are patterns of 3-20 clicks. Codas appear to function in social communication in that they are often overlapped and exchanged between individuals (Schulz *et al.* 2008). Thousands of individuals across dozens of units which all share a distinct coda dialect have been defined as 'vocal clans'(Rendell and Whitehead 2003b). In the Eastern Tropical Pacific, there are sympatric vocal clans and patterns of association between units are predominantly limited to within a clan (Rendell and Whitehead 2003b). In the Atlantic, however, coda repertoire appears to differ geographically and only one repertoire is heard in any given area (Antunes 2009; Whitehead *et al.* 2012).

While killer whale vocal repertoire is a clear marker of the levels of their social structure, to date we have only acoustically distinguished large cultural groups, the vocal clans, in sperm whales, and at ocean-basin scales. The existence of vocal markers of cultural identity makes this species' communication system of particular interest, but preliminary work suggests little variation between coda repertoires of individuals in the same social unit (Schulz *et al.* 2011). For a highly social species living in a multilevel society, why have such a varied communication system, if it only serves to facilitate broad scale social interactions between cultures? Given that units show preferences in their associations with one another (CHAPTER 4), if coda repertoires function in social identification, we would expect the coda repertoires of different units to be distinguishable. Units could be distinguishable in two obvious ways: 1) by their repertoire of codas (*i.e.* variation in the presence, absence, and pattern of usage of various coda types), or 2) by an accent on given coda types (*i.e.* variation in the acoustic characteristics of specific coda types which might be shared among some units). Here, I investigate similarity among the coda repertoires of nine social units from the Eastern Caribbean across a six year study (2005-2010). Specifically, I test if units whose ranges overlap, and which frequently interact, have distinct coda repertoires by examining variation in both the pattern of coda usage (repertoire) and in the way specific coda types are produced (accents). Following from this, I investigate the relationship between these measures of vocal similarity and social associations among units.

METHODS

FIELD METHODS

Social units of female and immature sperm whales were located and followed both acoustically using either a directional hydrophone, a towed hydrophone or both, and visually, by observers on one of three platforms (a dedicated 12m auxiliary sailing vessel, a dedicated 5m outboard skiff, or an 18m whale-watch vessel) in an area that covered approximately 2000 km^2 along the entire west (leeward) coast of the island of Dominica (N15.30 W61.40), in waters sheltered from the trade winds. Research was conducted in the winters of 2005 through 2010 for a total of 2549 hours with whales across 324 days of effort (Table 6-1). On heavier weather days, when the skiff was unable to operate, the research team worked from onboard the larger whale-watch vessel. Whale watch tours focused their search effort on sperm whales using hydrophones. As a result, methods remained the same across all three platforms, with the work on those days being restricted only by the length of time spent at sea by the whale watch vessel.

Table 6-1: Effort across years

Year	Start Date	End Date	Days Effort	Platform
2005	January 14	April 13	62	Sailing only
2006	January 17	February 11	21	Whalewatch only
2007	January 28	February 28	30	Skiff and Whalewatch
2008	February 8	May 8	75	All
2009	January 11	March 29	64	Skiff and Whalewatch
2010	January 20	April 18	72	Sailing only

During daylight hours, clusters of individuals visible at the surface were approached and photographs were taken to identify individuals. If a calf was present in a given cluster, priority was given to taking dorsal fin pictures of the calf from alongside the animals, before moving behind the adults in the cluster in order to photograph distinct markings on the trailing edge of their flukes for individual identification purposes (Arnbom 1987).

After animals dove and identification photographs were taken, digital acoustic recordings were made behind individuals in order to record coda output for clusters while initiating dives or when socializing. Vocalizations were recorded using one of several recording setups: In 2005, we used a Fostex VF-160 multitrack recorder (44.1 kHz sampling rate) and a custom built towed hydrophone (Benthos AQ-4 elements, frequency response: 0.1-30kHz); no recordings were made during the short 2006 season; in the 2007 and 2009, we used a Zoom H4 portable field recorder (48 kHz sampling rate) and a Cetacean Research Technology C55 hydrophone (frequency response: 0.02-44kHz); during the 2008 and 2010 seasons, we used the custom-built towed hydrophone (Benthos AQ-4 elements, frequency response: 0.1-30kHz) and computer based recording system as a part of the International Fund for Animal Welfare's (IFAW) LOGGER software package (48 kHz sampling rate). As I use only the temporal patterning of clicks in this analysis, variation in the frequency responses of the recording systems used is not important.

ANALYSES

Coda Analysis

Analyses followed those by Schulz and colleagues (2011) with some minor modifications. I analyzed the coda recordings using *Rainbow Click* software (developed by IFAW, see Gillespie 1997; Leaper *et al.* 2000) to determine the coda inter-click intervals (ICI, the times between the onset of each click and the onset of the next click) for all codas recorded. Clicks were marked and codas defined by a trained observer (SG analyzed all recordings) and the timing of the clicks within codas calculated. Each coda can then be represented by the ICI, either using absolute time intervals (Absolute ICI) or proportions relative to the total coda length (Standardized ICI; conserves rhythm but discards tempo of codas as in Moore *et al.* 1993)). Codas that were overlapped by a clear non-biological transient, such as wave and engine nose or hydrophone knocking, were omitted from analyses. Rare long coda types (>10 clicks; <5% of all codas recorded) were also excluded from the analysis. While most recordings (83% of codas recorded) were made on days when only one unit was identified; on 8 different days (10% of recording days, 17% of codas recorded), we encountered different units at different times and so recordings were made of different units on the same day. Only recordings made when the clusters included members of only one unit were used on these days. Trackline data (GPS) showed that clusters of whales were usually hundreds to thousands of meters from each other; and thus, only members of the photoidentified cluster were recorded, given that codas are only clearly audible through near-surface hydrophones at ranges of a few hundred meters or less.

Measuring Similarity between Repertoires:

I used seven measures to examine similarity between repertoires: three categorical and four different continuous measures. For the categorical methods, I assigned codas to categorical type using k-means cluster analysis as described in Rendell and Whitehead (2003a; 2004) with modifications as in Schulz (2011) using both ICI measures. Given that deciding on the number of clusters into which each coda size (4-click, 5-click, etc.) are to be grouped (*k*) using non-arbitrary methods presents problems (see Rendell and Whitehead 2003a), I determined *k* in three different ways. The first two used stopping rules based on Variance Ratio Criteria (VRC; Calinski and Harabasz 1974) by taking either the lowest local maxima or the absolute maxima of the VRC as *k* increases (Schreer *et al.* 1998; Rendell and Whitehead 2003a). I also categorized codas based on a third set of values for *k* based on visual observation of the plotted data. This "conservative" set of *k* values differed from the lowest local maxima method primarily by the number of clusters attributed to the 4 and 5-

click coda sets, which have proven to be problematic in similar analyses (Rendell and Whitehead 2003b). The "conservative" values for *k* created more coda types such that each type had higher similarity between codas within each cluster, while VRC methods had fewer coda types but greater variability between codas in each type. Coda types were given names based on the patterning of the clicks following previous nomenclature (Weilgart and Whitehead 1997; Rendell and Whitehead 2003b; Schulz *et al.* 2011). For example, a '5R' coda is one in which five clicks are regularly spaced, while a '1+1+3' coda sounds like "click-[PAUSE]-click-[PAUSE]-click-click-click" with longer gaps between the first two clicks followed by three clicks in quick succession. For categorical measures of similarity, two codas were given a similarity of 1 if they were assigned to the same type and were given a similarity of 0 if they were assigned to different types.

For the continuous measures, the multivariate similarity of two codas with the same number of clicks was measured using either the infinity-norm distance or Euclidean distance norms, a basal similarity of 0.001, 0.01, 0.1 or 1.0, and either ICI measure as in previous work (Rendell and Whitehead 2003a; Rendell and Whitehead 2003b; Schulz *et al.* 2011). The multivariate similarity between two codas containing different numbers of clicks was zero.

Differences between Repertoires:

To determine whether coda repertoires were significantly different between units, I treated each day's recordings as a replicate for a given unit's repertoire and tested whether pair-wise similarities were higher between two days' recordings of the same unit compared with two days' recordings of different units. This accounts for autocorrelation of coda production within recording days. Mantel tests (Mantel 1967; Schnell *et al.* 1985) with 10000 permutations and matrix correlations were calculated between a pair-wise similarity matrix of the days' repertoires, as calculated using each of the multiple methods described above, and a matrix coded with 0 for different unit, different day, or 1 for same unit, different day. If units have distinct repertoires, then the expectation is a significantly positive correlation between these matrices.

Patterns of Similarity between Units

To visualize the patterns of vocal similarity between units, I constructed average-linkage clustering dendrograms using the similarity results for all methods and estimated their robustness using 1000 bootstrap replicates. At each bootstrap iteration, the codas from each repertoire were randomly sampled with replacement prior to calculating the pairwise repertoire similarities and building the hierarchical clustering linkages. For each branch, I counted the proportion of replicates in which the branch was reproduced. The cophenetic correlation coefficient (CCC) was calculated to determine how well the dendrogram represented the data. A CCC of over 0.8 is considered a "good" representation of the associations (Bridge 1993).

Subsets and Testing within Coda Types:

This entire analysis was repeated on restricted datasets: only 4-click codas (6 coda types), only 5-click codas (4 coda types), The 1+1+3 variant codas (2 coda types), only the '5R' type codas, only the '1+1+3slow' codas, and only the '1+1+3' codas. Note that for the last three datasets there is only one coda type and so I used only the multivariate techniques. Therefore, these tests examine similarity within a coda type used by different units. For example, it would test whether different units make the 5R coda in consistently different ways.

Defining Units and Association between Them:

Units were delineated as in previous work based on photoidentifications and association data collected over the six years of the study (CHAPTER 4). Given that it is difficult to determine the spatial range and behavioral cues which may indicate interactions between members of different units of sperm whales; in chapter 4, I quantified associations between members of different units using three different metrics for association of increasing spatial coordination (clustered, identified within 2 hours, identified on the same day) and three different sampling periods of increasing duration (2 hours, Day, Year). I used these datasets to calculate matrix correlation coefficients between the matrices of association between units and the matrices of repertoire similarity using Mantel tests (Mantel 1967; Schnell *et al.* 1985)in order to determine whether coda repertoire similarity correlated with rate of social association among units. Mantel tests, here and from above, were carried out using *SOCPROG* 2.4 (Whitehead 2009) in *MATLAB* 7.12 (The Mathworks, Inc., MA, USA).

RESULTS

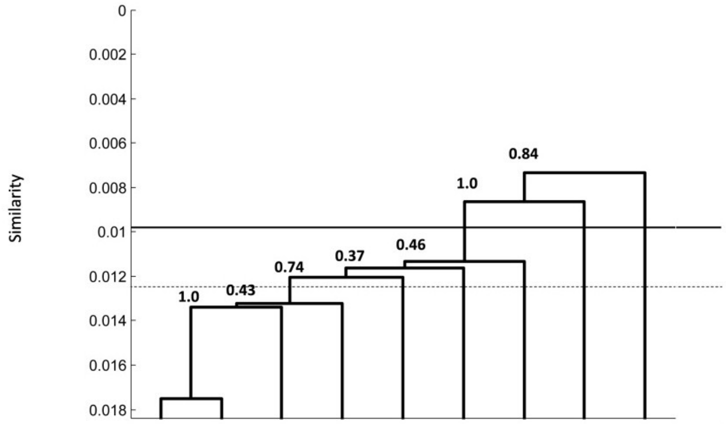
Over the course of this study, I had made sufficient recordings (>10 recordings over more than 4 days) across years for 9 units in order to be able to conduct these analyses: units A, D, F, J, N, R, T, U, and V (Figure 6-1). I attributed 4125 codas to those 9 units across 164 recordings in 5 different years. Codas were categorized into 28 types with one type '1+1+3' and its 'slow' variant making up more than 50% of the codas recorded. Adding the next most common type, '5R', encapsulates 65% of all codas. And overall, 4-click and 5-click codas made up just over 79% of all codas.

As would be expected, matrices of similarity produced by the different techniques were highly correlated (Mantel Tests: correlation coefficients range: 0.86-0.99, all $p<0.001$). Thus, the results did not vary greatly when using any of the three k-means methods or any of the combination of multivariate techniques used (Absolute ICIs or standardized ICIs and regardless of the distances norms used or basal similarity). As a result, and for simplicity, I present only the categorical results using the clusters determined by the conservative values for k and the multivariate results of the standardized ICIs, infinity norm distances, and with a basal similarity of 0.001, for consistency with previous studies (Moore *et al.* 1993; Rendell and Whitehead 2003a).

Differences in Repertoires:

All units have two or more coda types which each make up more than 10% of their coda production (shaded boxes in figure 6-1). In most cases, these are 5-click coda types, either variants of the '1+1+3' or the '5R' coda. The three most distinct repertoires (units N, A, F) also have a 4-click coda type as one which is greater than 10% of their coda production. Unit F is the only unit to commonly use a fourth type, '7D'. The inclusion of these additional types creates much of the structure in the dendrogram from the cluster analysis (Figure 6-1).

Highly significant Mantel tests confirm that recordings of the same unit on different days are more similar than recordings of different units on different days (Table 6-2). This is true for all subsets and for within coda types, with two exceptions: the categorical similarity between the two variants of the '1+1+3' coda, showing that all units made similar proportions of these two variants, and the multivariate similarity of the '1+1+3' coda type, showing that this coda type was highly stereotyped across units. These results show that units not only differ in the full coda repertoire which they use, but they also consistently produce the '5R' and '1+1+3slow' coda types differently.



Coda Length	Coda Type	J	R	T	D	V	U	N	A	F	Total Codas by Type
3	**3R**	1	0	1	0	2	0	7	5	2	**18**
	1+2	0	1	0	0	1	0	0	12	0	**14**
	2+1	1	0	0	0	0	0	1	0	12	**14**
4	**4R**	4	0	1	1	3	5	0	61	10	**85**
	1+3	2	1	0	2	38	1	3	2	19	**68**
	1+3D	1	1	0	1	5	0	1	1	186	**196**
	1+3fast	0	0	0	0	3	0	69	1	0	**73**
	3+1	3	3	0	3	3	0	0	1	29	**42**
	1+1+2	1	0	3	2	2	2	1	0	11	**22**
5	**5R**	23	29	49	78	35	95	36	21	75	**441**
	1+1+3slow	182	91	196	129	163	95	112	49	180	**1197**
	1+1+3	257	116	45	57	132	22	38	65	308	**1040**
	2+1+1+1	6	3	2	6	39	3	1	6	34	**100**
6	**1+1+4**	1	4	0	1	6	3	0	5	40	**60**
	6R	8	7	5	13	19	20	3	11	23	**109**
	6S	4	5	5	12	0	3	1	5	24	**59**
7	**7R**	4	4	10	12	15	3	1	8	20	**77**
	7D	0	6	0	0	5	0	0	5	138	**154**
	7S	1	3	1	5	3	4	0	5	24	**46**
8	**8R**	3	6	14	4	22	6	8	1	21	**85**
	8D	1	5	1	0	4	1	2	2	16	**32**
	8S	3	3	4	3	6	4	3	1	12	**39**
9	**9R**	5	2	16	2	9	5	8	0	6	**53**
	9D	2	3	1	0	6	2	0	4	3	**21**
	9S	1	4	9	4	5	3	0	1	9	**36**
10	**10R**	1	2	13	0	2	2	1	0	2	**23**
	1+9	0	3	1	0	3	0	0	0	2	**9**
	9+1	0	1	5	1	0	0	0	1	4	**12**
Total Codas by Unit		**515**	**303**	**382**	**336**	**531**	**279**	**296**	**273**	**1210**	**4125**
Recordings Total - Days - Years		**21-8-4**	**10-5-1**	**17-12-2**	**14-10-3**	**20-6-1**	**12-7-3**	**11-4-2**	**15-8-4**	**44-27-4**	**164-78/87-5**

Figure 6-1: Coda repertoires of units of sperm whales recorded off Dominica compared using infinity-norm distances of standardized inter-click intervals with a basal similarity of 0.001 (top) and conservative *k*-means classification methods (bottom). Numbers next to branches of the dendrogram indicate the proportion of the 1000 bootstrap replicates in which that branch was reproduced. This is a good representation as the dendrogram has a cophenetic correlation coefficient of 0.8346. Horizontal rules indicate the mean between (solid) and within (dotted) unit similarities. Letters denote units. Numbers in the table indicate the frequency with which each individual coda type was produced by each unit. Shaded numbers indicate that the coda type made up at least 10% of the unit's coda production. For the nomenclature: "R" indicates a coda with regular ICIs, "+" indicates a longer gaps between clicks, "S" indicates increasing ICIs throughout the coda, "D" indicates decreasing ICIs throughout the coda, "slow" indicates a variant of the coda type above it in which the last set of clicks had relatively longer, but still equal to each other, ICIs than its predecessor, and "fast" indicates a variant with relatively shorter ICIs than its predecessor. Numbers below each column are the total number of codas recorded from each unit, as well as the total number of recordings, recording days, and years per unit. On 8 days recordings where made of different units and so that day was counted once as a recording day for each unit in the unit totals, therefore there is a difference in the two totals for days (Unique Calendar Days/Unit Days).

Table 6-2: Results of Mantel tests of the null hypothesis that repertoire similarity between recordings of the same unit on different days is the same as that between recordings of different units on different days. Multivariate similarity using standardized ICIs, infinity-norm distances, and b=0.001. Categorical similarity using conservative values for *k*. Non-significant tests bolded

	Multivariate Similarity				Categorical Similarity			
Repertoire	**Same Unit**	**Different Units**	**Matrix Correlation**	***p***	**Same Unit**	**Different Units**	**Matrix Correlation**	***p***
Full	0.0126	0.0095	0.13	<0.001	0.2015	0.1616	0.10	0.006
5-Click Only	0.0223	0.0204	0.10	0.001	0.3897	0.3512	0.07	0.015
4-Click Only	0.0462	0.0107	0.82	<0.001	0.6794	0.0665	0.87	<0.001
5R Only	0.0298	0.0266	0.17	0.003		One Coda Type		
1+1+3 Both	0.0270	0.0249	0.10	<0.001	0.5570	0.5337	0.03	**0.109**
1+1+3slow	0.0335	0.0307	0.16	<0.001		One Coda Type		
1+1+3	0.0394	0.0371	0.07	**0.095**		One Coda Type		

While all units commonly use both of the two '1+1+3' variants, units appear to consistently produce the '1+1+3slow' differently, but the '1+1+3' in a similar way. Much of the variation in the '1+1+3slow' coda may be the result of the similarity index responding differently to structurally different coda types, primarily regular versus irregular types. When comparing across methods for the *k*-means categorization, the '1+1+3slow' codas are primarily (~70%) lumped in with the '5R' when using the VRC methods while the conservative method splits this large cluster (Table 6-3). The '1+1+3slow' is an intermediate between the '5R' and the '1+1+3' (Figure 6-2) and this division between them may be an arbitrary statistical one and not a biological one. When using the categories determined by the lowest maxima of the VRC methods and the '5R' and '1+1+3slow' coda types are lumped together as one type, they still have significant variation between units (matrix correlation = 0.35, $p < 0.001$), while the '1+1+3' is borderline for a one-way test (matrix correlation = 0.09, $p = 0.03$).

Interestingly, each of the three most vocally distinct units uses a different 4-click coda type (Unit N: '1+3fast', Unit F: '1+3D', and Unit A the '4R'); which results in a high matrix correlation coefficient and a significant mantel test for the categorical similarity of 4-click codas. These coda types, which are not exclusive to the unit but are used far more frequently by each of these units, appear to not be the result of a short period of aberration as each was made by the respective unit across years. It is more difficult to understand whether the distinct coda type is made in each case by a single member of the unit with a distinctive individual repertoire, rather than being part of a shared repertoire. Individual-specific coda repertoires were only available for one of these units, Unit F (CHAPTER 5).

Three of the adult females in the unit used the 1+3D coda type in different years and a calf from this unit produced it twice, suggesting it is shared, but it is also the case that one of the three females produced it more frequently and consistently than the other two in every year.

Table 6-3: Differences in categorization of 5 click codas between methods of *k*-means indicate that the majority (~70%) of the '1+1+3slow' codas from the conservative classification are lumped in with the '5R' type using VRC methods.

	Method		
Coda Types	**Conservative values for *k***	**Lowest Maxima of VRC**	**Absolute Maxima of VRC**
5R	441	1286	1285
1+1+3slow	1197	0	0
1+1+3	1040	1372	1373
2+1+1+1	100	120	120

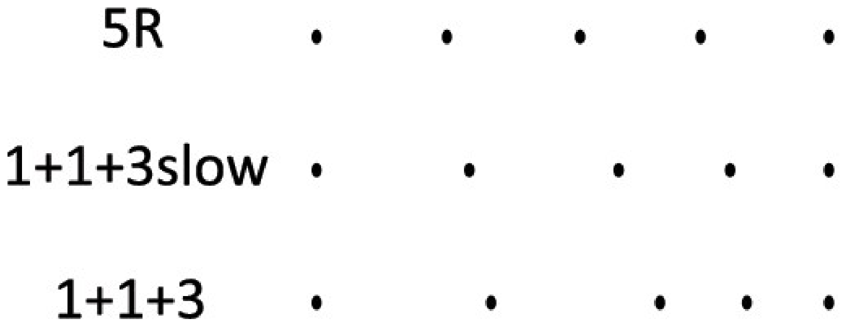


Figure 6-2: Relative time patterns of the clicks in '5R', '1+1+3slow' and '1+1+3' coda types as defined by the conservative k-means method on standardized ICIs.

Patterns of Vocal Similarity between Units:

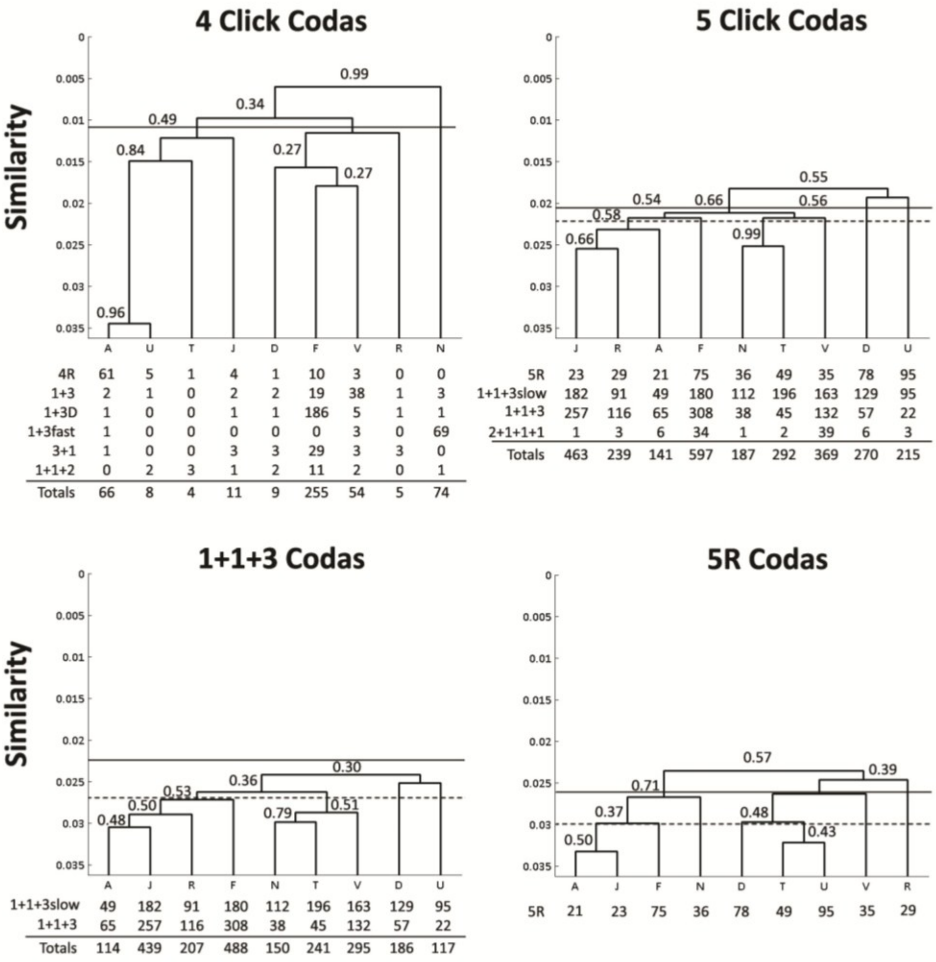
Patterns of similarity among unit repertoires portrayed by the cluster analysis dendrograms suggest that units' vocal repertoires do not group into distinct clusters (Figure 6-1). Apart from a pair of units (J & R), whose repertoires are three times more similar as each is to the most distinct repertoire (Unit F), the average-linkage cluster dendrogram shows a cascading pattern suggesting little distinction between units T,D,V,U and N. There is strong bootstrap support for splitting Units A and F from the rest of the units, but less support of the linkages between the remaining units, excepting some moderate support (Bootstap value of 0.74) for distinguishing units J, R, T, D from V, U, N.

Patterns of Similarity within Coda Lengths and Types:

Restricting within coda lengths or types results in different patterns of linkages between units, most of which only have moderate bootstrap support (Figure 6-3). Units J and R which are most similar across the full repertoires are less similar when restricting to only the 5R coda type or all 4-click codas, but remain relatively similar when considering all 5-click codas and the '1+1+3' codas, suggesting they are distinctive in the way they produce these coda types. While there appears to be some clustering of units upon inspection, overall bootstrap support is weak.

Relationship between Coda Repertoire and Social Association between Units:

Mantel tests found no indication that the patterns of association correlated with similarity of full vocal repertoires (Table 6-4). There was much variability in vocal similarity among units which were never associated, but plotted data indicated a weak inverse relationship of association with vocal similarity, in that units which associated more across time had lower vocal similarity; however, this relationship was not statistically significant (Figure 6-4). While the 4-click codas appeared to distinguish between units based on previous analyses, if the dataset was restricted to the 4-click codas, there was no relationship with social association. If the dataset was restricted to only include the most common coda length, 5 clicks, then correlation coefficients were larger and Mantel tests suggested that there is a significant inverse relationship between association within clusters and vocal similarity over both the short term (Clustered within 2 hours: matrix correlation coefficient = -0.26, p = 0.04) and long term (Clustered Across Years: matrix correlation coefficient = -0.33, p = 0.03). However, including only units which were observed associated (non-zero index of associations), I found that this weak correlation reverses in the restricted datasets (Figure 6-3). This appeared to be largely driven by variation in the '1+1+3' coda types as the correlation coefficients were similar in magnitude for these coda types as for all 5-click codas (Table 6-4).



	A	U	T	J	D	F	V	R	N
4R	61	5	1	4	1	10	3	0	0
1+3	2	1	0	2	2	19	38	1	3
1+3D	1	0	0	1	1	186	5	1	1
1+3fast	1	0	0	0	0	0	3	0	69
3+1	1	0	0	3	3	29	3	3	0
1+1+2	0	2	3	1	2	11	2	0	1
Totals	66	8	4	11	9	255	54	5	74

	J	R	A	F	N	T	V	D	U
5R	23	29	21	75	36	49	35	78	95
1+1+3slow	182	91	49	180	112	196	163	129	95
1+1+3	257	116	65	308	38	45	132	57	22
2+1+1+1	1	3	6	34	1	2	39	6	3
Totals	463	239	141	597	187	292	369	270	215

	A	J	R	F	N	T	V	D	U
1+1+3slow	49	182	91	180	112	196	163	129	95
1+1+3	65	257	116	308	38	45	132	57	22
Totals	114	439	207	488	150	241	295	186	117

	A	J	F	N	D	T	U	V	R
5R	21	23	75	36	78	49	95	35	29

Figure 6-3: Restricted coda repertoires of sperm whale units compared using infinity-norm distances of standardized inter-click intervals with a basal similarity of 0.001 (top) and conservative *k*-means classification methods (bottom). Letters denote units. Dendrograms of 4-Click codas, 5-Click codas, 1+1+3variants, and 5R have cophenetic correlation coefficients or 0.9359, 0.7396, 0.6825, and 0.5576, respectively. Therefore, only the dendrogram of 4-click codas is a good representation of the data. In order to have all of the scales of the y-axes the same for comparison, the within unit similarity (denoted by a dashed line in all other dendrograms) for the 4-click coda types (within unit mean = 0.046) does not appear as it is greater than the y-axis. All other notation is as in Figure 6-1.

Table 6-4: Matrix correlation coefficients and resulting Mantel test *p*-values for comparisons between various matrices of association among social units and their vocal similarity. The null hypothesis is that the rate of association among units and their vocal similarity are unrelated.

Sampling Period-Association	Repertoire Set	Matrix Correlation Coefficient	*p*
2h-Clustered	All Codas	-0.10	0.25
Date-Clustered	All Codas	-0.07	0.32
Year-Clustered	All Codas	-0.20	0.16
Year-Date	All Codas	-0.07	0.41
Year-2h	All Codas	-0.18	0.22
Date-2h	All Codas	-0.07	0.33
2h-Clustered	5-Clicks Only	-0.26	0.04*
Date-Clustered	5-Clicks Only	-0.20	0.09
Year-Clustered	5-Clicks Only	-0.33	0.03*
Year-Date	5-Clicks Only	-0.14	0.28
Year-2h	5-Clicks Only	-0.31	0.05
Date-2h	5-Clicks Only	-0.18	0.14
2h-Clustered	4-Clicks Only	-0.05	0.44
Date-Clustered	4-Clicks Only	-0.04	0.49
Year-Clustered	4-Clicks Only	-0.04	0.45
Year-Date	4-Clicks Only	0.06	0.66
Year-2h	4-Clicks Only	0.01	0.59
Date-2h	4-Clicks Only	-0.03	0.53
2h-Clustered	5R	-0.02	0.48
Date-Clustered	5R	0.04	0.57
Year-Clustered	5R	-0.09	0.29
Year-Date	5R	0.12	0.71
Year-2h	5R	-0.04	0.39
Date-2h	5R	0.03	0.59
2h-Clustered	1+1+3 & 1+1+3slow	-0.25	0.06
Date-Clustered	1+1+3 & 1+1+3slow	-0.19	0.14
Year-Clustered	1+1+3 & 1+1+3slow	-0.26	0.07
Year-Date	1+1+3 & 1+1+3slow	-0.09	0.36
Year-2h	1+1+3 & 1+1+3slow	-0.26	0.07
Date-2h	1+1+3 & 1+1+3slow	-0.17	0.13

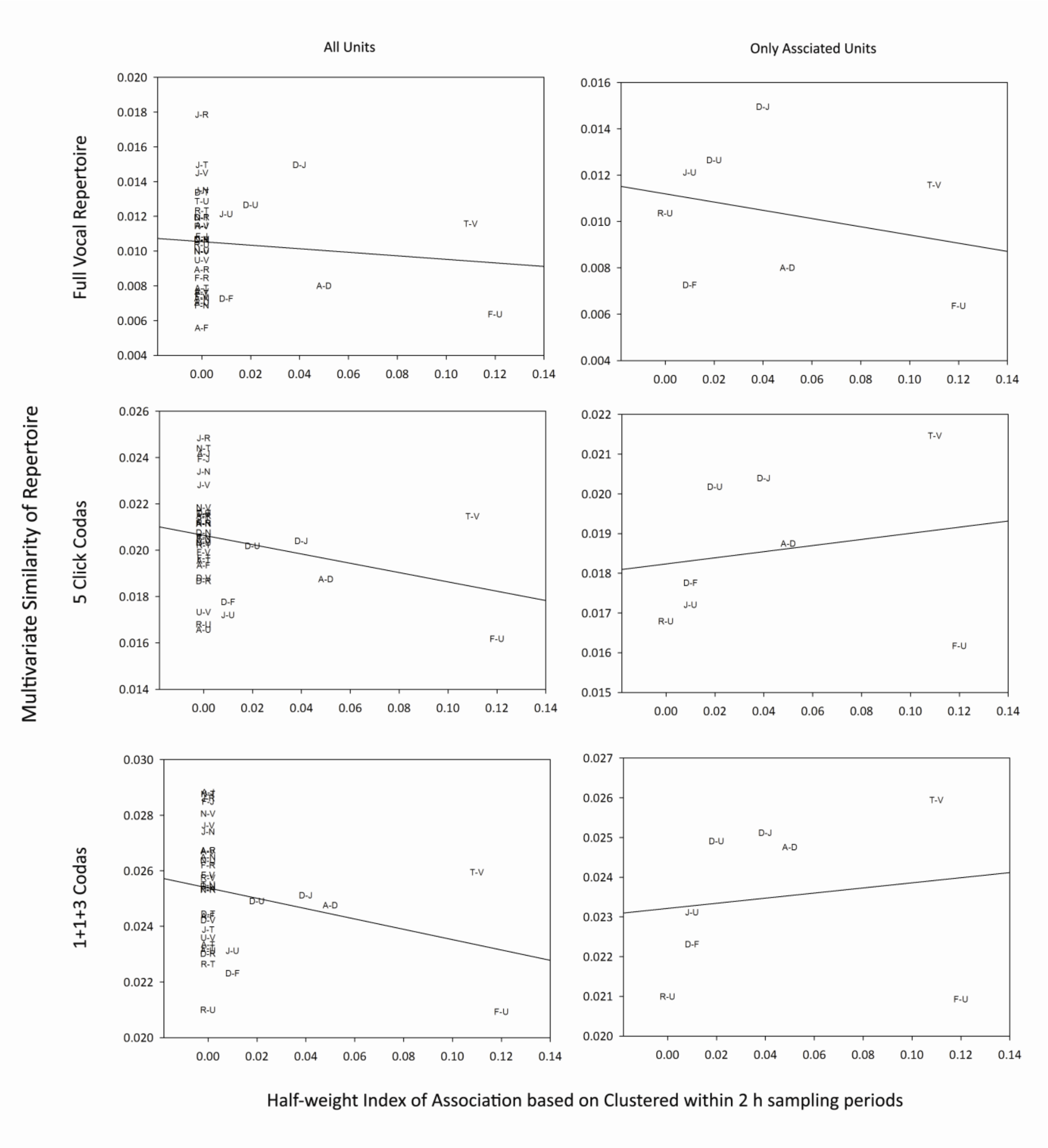


Figure 6-4: Plots of similarity of full vocal repertoire based on standardized ICIs using infinity-norm distances and a basal similarity of 0.001 against association of units clustered together within a 2 hour sampling interval. Plot including all unit-dyads on the left, and only dyads which were actually observed associated (non-zero HWI) on the right. Letter pairs denote unit-dyad.

DISCUSSION

Social units recorded off Dominica have distinct vocal repertoires, but all of them are dominated by the '1+1+3' and '5R' coda types. Variation at the repertoire level appears to be primarily the result of some units commonly using characteristic 4-click coda types in addition to the two prevalent 5-click coda types used by all units.

While units can be statistically distinguished based on coda repertoire, the mean between-unit similarity across the full repertoire (0.010; Table 6-1) of the social units studied here lines up almost exactly with the between-unit "within clan" mean from the study in the Pacific (0.011; Rendell and Whitehead 2003b). This would suggest that all of the units studied off Dominica are from the same vocal clan, in the sense that the term is used for the Pacific. Finding distinct repertoires among units within clans draws another parallel with killer whale pods, where pods within clans also have distinguishable but not exclusive repertoires (Ford 1991).

Antunes (2009) concluded that vocal repertoires in the North Atlantic appear to be geographically structured having found no evidence of the sympatric clans documented in the Pacific. Among mammals, variation in call repertoire between sympatric or neighboring groups which could potentially interbreed have generally been referred to as dialects, while differences between populations separated by long distances which do not interbreed is referred to as geographic variation and can be explained by drift (Conner 1982). Rendell and Whitehead (2003b) defined a 'vocal clan' among sperm whales following previous work on 'resident' killer whales (Ford 1991) in which all social groups (units in sperm whales, pods in killer whales) which share a vocal repertoire are members of a 'clan'. Rendell and Whitehead (2003b) argue, as Ford (1991) did for the killer whales, that the sympatric clans are evidence of true socially learned vocal dialects which function as markers of a shared cultural heritage and may act as barriers to cooperative and altruistic behavior and thus structure their societies. This is supported by the fact that units preferentially (exclusively in the case of sperm whales) associate with other units which are in the same vocal clan even though in both 'resident' killer whales and Pacific sperm whales units from different clans may use the same waters (Rendell and Whitehead 2003b). When in-group favouritism of this kind occurs, it can increase between-group heterogeneity in behaviour and this is the case among the sympatric clans in the Pacific which also differ in movement patterns, habitat use, and foraging success (Whitehead and Rendell 2004), as well as diet (Marcoux *et* *al.* 2007b) and reproductive success (Marcoux *et al.* 2007a). Importantly, recent work shows that this variation in behavior among clans cannot easily be explained by genetic variation (Rendell *et al.* 2012).

In some respects, Antunes' (2009) findings in the Atlantic do not contradict the functional explanation of vocal clans of Rendell and Whitehead (2003b). Among humans, the correlation between symbolic markers and behavior are strongest when cultures are close in space (McElreath *et al.* 2003). This appears to be the case among sperm whales as well, in that the differences in the coda dialects of sympatric vocal clans in the Pacific are greater than between the coda repertoires of geographic areas in the North Atlantic (Rendell and Whitehead 2003b; Antunes 2009). Therefore our study and that of Antunes (2009) beg the question of, what is a "vocal clan" in the Atlantic? By definition, both geographic variation in repertoires across the North Atlantic and the sympatric dialects of the Pacific fit the basic notion of a "clan" being a collection of units that share a similar coda repertoire (Rendell and Whitehead 2003b). What may differ between "allopatric clans" of the Atlantic and "sympatric clans" of the Pacific are the factors which determine the variation. Does the geographic structure in sperm whale coda repertoires in the Atlantic demonstrate that there is simply geographic variation between segregated populations caused by cultural drift and therefore repertoire differences may have little or no functional value, or do the allopatric clans of the Atlantic still represent cultural groups but the Atlantic simply lacks multicultural areas like those in the Pacific? In short, are allopatric clans functionally different from sympatric clans?

At this stage this issue is hard to address. Whitehead *et al.* (2012) discuss the environmental, social, cultural, and genetic factors that might be affecting populations of sperm whales differently in the Atlantic and Pacific oceans. They conclude that there is likely a complex interaction of differences between oceans which has led to the existence of sympatric clans in the Pacific and allopatric clans in the Atlantic. They suggest that differences in social structure, primarily the increased formation of multi-unit groups due in part to increased predation by killer whales in the Pacific, creates a situation in which finding a suitable group partner with similar traditional foraging behaviors and movement patterns requires vocal markers and thus the evolution of sympatric clans. Understanding whether vocal variation functions in different ways in the Atlantic and Pacific will require playback experiments to gauge the response to in-group versus out-group dialects in both regions.

The absence of evidence of sympatric clans in the Atlantic may simply be due to effort. Whitehead and Rendell (2004) describe one clan's units being found more closely associated with the islands in the Galapagos and having far more convoluted movement patterns, while the offshore unit travelled in straight lines. Although, I found no inshore offshore differences in vocal repertoire off Dominica, this study differed greatly in scale as compared to research in the Pacific. The median distance from the Galapagos Islands for the offshore 'Plus-one clan' was 29km (Whitehead and Rendell 2004), but during my research, the vessel only rarely ventured beyond 20km offshore and the mean distance from the western shore of Dominica during encounters with whales was less than 10km (CHAPTER 2). So perhaps the lack of multiple dialects in my study stems from a lack of covering sufficient distance from the island and this 'Eastern Caribbean 1+1+3 clan' is just the island associated clan in this part of the Caribbean. Antunes (2009) covers more area in his study across the Azorean archipelago and finds greater variation between the repertoires recorded in the Azores than between units off Dominica. Additionally, if we examine more closely the analysis conducted by Antunes (2009), while most of the repertoires recorded in the Gulf of Mexico cluster together in the hierarchical cluster analysis, several repertoires recorded in the Gulf are quite dissimilar from the more commonly recorded ones. This variation within sea is evident in the repertoires recorded in the Sargasso Sea which do not cluster together closely either. Lastly, there is evidence of variation in coda repertoire within the Caribbean Sea. Two groups were recorded off of Panama in 1993 and attributed to the "Caribbean Clan" by Rendell and Whitehead (2003b). While similar to each other, these Western Caribbean repertoires differ from those recorded in this study in the Eastern Caribbean both quantitatively (low multivariate similarities with a small subset of Dominica recordings analyzed by Antunes 2009) and qualitatively, in that the predominant coda types in the Western Caribbean are '6+1+1', '5+2A', '6+1', '2+4', and '5+1' (Rendell and Whitehead 2003b); none of which appeared in any of the repertoires of the units recorded off Dominica (although what Rendell and Whitehead termed the '2+4' may resemble the relatively uncommon '1+1+4' from this study). In addition, the predominant types from the Western Caribbean repertoires are all greater than 6 clicks in length, when all codas 6 clicks or longer combined only make up about 20% of all codas recorded off Dominica. Although these two distinct repertoires have never been recorded in overlapping geographic areas, they are only roughly 2000 km apart. This is well within the spread of Pacific sympatric clans (~5000km) and within travel distances of individuals and units (1000-4000km) observed within the Eastern Tropical Pacific (Whitehead *et al.* 1998; Rendell and Whitehead 2003b; Rendell and Whitehead 2005; Whitehead *et al.* 2008).

Previous fine scale analyses from one of the units in this study (Unit F) suggest that individual differences in the '5R' coda may allow animals to identify each other (Antunes *et al.* 2011). My finding of significant variability between units in the '5R' type is consistent with this. Both individual-level studies found no significant variation among individuals within the '1+1+3' coda types (Schulz 2007; Antunes *et al.* 2011); and among the 5-click codas, the '1+1+3' had the least variation among individuals (Antunes *et al.* 2011). Furthermore, I found that the '1+1+3' coda was did not vary between units. These findings suggest that different classes of coda could serve to identify different levels of social structure. Units approaching other units at sea likely use several cues to identify who they are encountering. While '5R' codas may be used for individual identification, the 4-click and the '1+1+3' codas could function as unit-level identification cues. The '1+1+3' coda, which appears to be similar across units and which is unique to this region, could likewise function as a clan or region level cue. This type of hierarchical recognition is common in bird song, in which the general form of the song identifies the species while variations within it identify individuals (Becker 1982; Falls 1982). Further support for this interpretation is found in the documentation of the 1+1+3 coda type in this region for over the last 30 years. Recordings made in the Eastern Caribbean off islands surrounding Dominica (from Union Island to Guadeloupe; N16.1, W61.86 to N12.66, W61.42) between 1981 and 1987 found that these same coda types dominated the overall merged repertoire for the area ('5R' and '1+1+3' referred to as Type 'C' and 'E' from Moore *et al.* 1993). Additional recordings made off Dominica by Gordon *et al.* (1998) in 1995 and 1996 also show the same predominant coda types. However, some of the individuals in this study were sighted as far back as 1984 and many were identified during the Gordon *et al.* (1998) work (Gero *et al.* 2007; CHAPTER 2). As a result, it is likely that many individuals recorded in this study were alive throughout this period.

CONCLUSIONS:

Units differ both in the types of codas they use, and the accents they place on certain coda types, while other coda types appear to be made consistently by all units. While functional explanations for these hierarchical levels of variation are necessarily speculative, this study suggests that various levels of sperm whale social structure may be acoustically distinguished and raises new questions about the function of vocal clans in different oceans. If sympatric variation in the Pacific and allopatric variation in the Atlantic are functionally different, why exhibit similar complexity in coda repertoires across the same spatial distributions? Clearly further work is needed to elucidate the details of sperm whale vocal complexity and its relationship to culture and social structure. Experimental approaches such as coda playbacks are much more feasible now that the social context is well established and typical coda usage has been outlined. This type of work is difficult among wild cetaceans but would allow us to gain a far better understanding of the communicative function of the various coda types.

CHAPTER 7

CONCLUSIONS

We need another and a wiser and perhaps a more mystical concept of animals…We patronise them for their incompleteness, for their tragic fate of having taken form so far below ourselves. And therein we err, and greatly err. For the animals shall not be measured by man. In a world older and more complete than ours they move finished and complete, gifted with extensions of the senses we have lost or never attained, living by voices we shall never hear. They are not bretheren, they are not underlings; they are other nations, caught with ourselves in the net of life and time, fellow prisoners of the splendour and travail of the Earth.

~Henry Beston, The Outermost House, 1926

SOCIAL AND VOCAL VARIATION ACROSS LEVELS OF SOCIAL STRUCTURE:

Combining this study and its predecessors, I can for the first time compare vocal similarity and social differentiation across levels of social structure in sperm whales (table 7-1 and table 7-2). I have studied social differentiation within and between units in the Eastern Caribbean (CHAPTER 4), as well as, vocal similarity within-individuals (CHAPTER 5), among individuals within units (CHAPTER 5), and between units within a clan in the Caribbean (CHAPTER 6). Previous work has reported on vocal similarity within and between clans in the Eastern Tropical Pacific (ETP; Rendell and Whitehead 2003b), as well as, the social differentiation between individuals within units studied off the Galapagos Islands (Whitehead *et al.* 2012).

VARIATION IN SOCIAL DIFFERENTIATION:

Social relationships between individuals within units as well as between units are more heterogeneous in the eastern Caribbean than off the Galapagos (Table 7-1). The within-unit variation of relationships between individual unit members is highly differentiated in the Atlantic but only minimally so in the Pacific. Given that multi-matrilineal units are common in the Pacific, while not in the Atlantic (Lyrholm *et al.* 1996; Richard *et al.* 1996a; Lyrholm and Gyllensten 1998; Whitehead *et al.* 1998; Lyrholm *et al.* 1999; Mesnick 2001; Gero *et al.* 2008), the low levels of social differentiation within the larger multi-matrilineal units off the Galapagos would suggest that various matrilines living together do not structure within-unit associations between individuals, as relatedness does in the smaller, more closely-related units of the Caribbean (Gero *et al.* 2008). Initially this finding may seem counterintuitive. Why would relationships within units not reflect genetic relatedness off the Galapagos, where differences in relatedness typically have a wider span (often being zero) and where inter-individual relationships within groups are segregated based on unit membership (Christal and Whitehead 2001)? It may be the result of far fewer calves being present in the Galapagos (Whitehead *et al.* 2012). Calves strongly influence social relationships within units (CHAPTER 3), and an absence of strong mother-calf bonds would affect within-unit social differentiation. The lack of calves may be an indirect result of whaling. Whalers in the eastern Pacific, and likely elsewhere, focused primarily on large mature males as spermaceti yield per unit catch was higher (Whitehead *et al.* 1997). The resulting imbalance in the sex ratio appears have lasted well beyond the end of whaling in the 1980s and impacted an area far wider than the whaling grounds (Whitehead *et al.* 1997). These effects lead to reduced breeding opportunities for females and decreased pregnancy rates (Clarke et al. 1980), and thus, fewer calves. Whaling may also have affected social differentiation within units by altering the social structure in the Galapagos (Whitehead *et al.* 2012). If units were forced to merge into multi-matrilineal units due to decreased numbers as a result of heavier whaling in the Pacific (Smith *et al.* 2008), it is likely that bonds between unrelated members of different units would be important to maintain the newly formed units and reduce the effect of relatedness structuring social interactions within units. A note of caution should also be given regarding the interpretation of the results from the Galapagos, although overall levels of effort and data collection were similar in the two studies, the Galapagos population was much larger so there is much less data available for particular individuals.

Between units, the difference between sites is even more dramatic. Relationships between units in the Caribbean are highly differentiated while they are statistically homogenous in the Galapagos (Table 7-1). The most obvious source of this variation between sites is the difference in the formation of temporary multi-unit groups. In the Pacific, units commonly form groups with other units such that multi-unit groups are typically encountered at sea. In contrast, multi-unit groups are less common in the Atlantic, both in the Caribbean (CHAPTER 2) and the Azores (Antunes 2009). Most significantly, while there is evidence of long-term relationships between units in the Caribbean (CHAPTER 4), these appear quite rare among units in the Galapagos (only one pair of units has been identified together across years; Whitehead 2003). Whitehead *et al.* (2012) suggest this may be the result of differing levels of predation threat from killer whales. Units in the Galapagos show little preference for their group partners and form groups more readily as long as the other unit is within their vocal clan (Rendell and Whitehead 2003b), such that the boundary for cooperative anti-predator relationships is clan membership. Additionally, some of this difference might result from a slightly more relaxed definition of unit used in the Galapagos studies. In the Galapagos, units which were identified together more than three times together which were separated by more than 30 days would have been merged into a single unit while in Dominica units were defined based on social associations between individuals across multiple years. This would mean that two units that spent a lot of time together would be merged under the Galapagos definition but not the Dominica one. However, I believe this has only a small contribution to the dramatic differences in social unit differentiation shown in Table 7-1.

Table 7-1: Comparisons of social differentiation across levels of social structure in different oceans. Values are calculated using likelihood methods described in Whitehead (Whitehead 2008a). Standard Errors were estimated based on 1000 bootstrap replicates.

Level of Social Structure	Region	Social Differentiation	Source
Between Individuals, within Units	Eastern Caribbean Galapagos	0.80 ± SE 0.05 0.41 ± SE 0.16	Chapter 4 Whitehead *et al.* 2012
Between Units, within Clans	Eastern Caribbean Clan Galapagos, Regular Clan	1.11 ± SE 0.06 0.00 ± SE 0.09	Chapter 4 Whitehead, Unpublished

Killer whales, however, are rare in the Caribbean (Ward *et al.* 2001) and with lower predation risk units may be able to spend more time alone without the need for the dilution, vigilance, and communal defence benefits provided by larger groups. This would reduce intraspecific competition and the other common issues associated with living in larger groups (Alexander 1974; Connor 2000). Atlantic units could therefore be more selective about which other units to associate with leading to higher levels of social differentiation. This begs the question, what draws units together to form these bond-pairs in the Atlantic? At this point I can only be speculative, given that we know very little either about how ecological factors might affect group formation in this species (although see Antunes 2009) or about the distribution, abundance, or behaviour of their squid prey (although prey species do differ between oceans and dramatic changes in prey abundance may affect social structure, Whitehead 2003; Whitehead and Kahn 1992). However, I suggest the inter-unit preference may be the result of any of the following: 1) if patterns of allocare differ in quality and quantity between units, as suggested by Chapter 2 and by Gero *et al.* (2009), associations between units might be driven by common behaviours surrounding allocare, just as common movement patterns and habitat use within clans facilitate reduced predator risk (Whitehead *et al.* 2012); 2) there may be a kin-bias in selecting bond-group partners, as has been shown among African elephants (*Loxodonta africana;* Moss and Poole 1983; Moss and Lee 2011), and determining the genetic relatedness between units will be an important step in future studies; and/or 3) the potential for smaller ranges within the Caribbean may also affect social differentiation simply by allowing units to coexist in the same area more regularly. I should note that these hypotheses are not necessarily mutually exclusive and the result likely stems from a complex combination of differences between ocean basins and populations.

This variation in differentiation between oceans may also indicate that the most significant social boundary in the Pacific is the clan, while in the Atlantic it may be the unit itself. This may follow from the fact that there are no sympatric clans in the Atlantic and vocal repertoire differs geographically (Antunes 2009). Should this difference in social boundaries exist, one would expect that the variability in vocal marker of membership would be greatest where recognition of identity is most important, *i.e.* the variation in vocal repertoire would be greatest at the level of clan in the Pacific, but not in the Atlantic where clans are geographically structured.

VARIATION IN VOCAL SIMILARITY:

As would be expected, vocal similarity between entities within structures decreases as we move up the hierarchical levels of social structure and include increasingly more individuals. However, there is a ten-fold decrease in similarity when we move from units within clans to between clans, which supports the theory that broadcasting clan identity is important in the Pacific.

The vocal similarities between units within the eastern Caribbean and between units within clans in the Eastern Tropical Pacific are very comparable (Table 7-2). The apparent absence of sympatric clans in the Atlantic makes it difficult to determine the importance of clan identity to units in the Caribbean. Studies on the margins of neighbouring geographic areas where allopatric clans border each other would be particularly revealing and would allow us to test for the social segregation seen among clans in the Pacific.

Interestingly, in the Atlantic, vocal repertoires of different individuals within the same unit are not much more similar than the repertoires of different units suggesting that advertising unit identity is as important as advertising individual identity or perhaps that individual identity is not advertised by a whale's entire coda repertoire, given that different coda types may serve different functions. Codas which function for individual identity, as has been hypothesised for the '5R' coda by Antunes *et al.* (2011) and supported in Chapter 5, would face selective pressures to become more distinct and variable between individuals; while selection would stabilize codas across individuals which serve functions at higher levels of social structure, as appears to be the case for the 1+1+3 coda in the Caribbean (CHAPTERS 5 & 6). For example, signals of clan membership must be recognizable by individuals and groups who spend little time together. As a result, opposing selective forces are acting across the full vocal repertoire.

An obvious omission in Table 7-2 is a measure of similarity between individuals within units from the Pacific. This would allow for comparisons within particular coda types, help elucidate the details of coda function, and support or reject the hypotheses proposed here.

Table 7-2: Comparisons of vocal similarity across levels of social structure. Mean similarities are based on multivariate methods using standardized ICIs, infinity-norm distances and a basal similarity of 0.001. No measures of SE were published for estimates from the Eastern Tropical Pacific.

Level of Social Structure	Region	Similarity	Aspect which Varies	Source
Within Individuals, Between Recordings	Eastern Caribbean	0.026 ± SE 0.001		Chapter 5
Within Units, Between Individuals	Eastern Caribbean	0.013 ± SE 0.001	IPI, accent on '5R' codas, or coda repertoire	Chapter 5
Within Clans, Between Units/Groups	Eastern Caribbean ETP	0.010 ± SE 0.0001 0.011	Coda repertoire or Group-specific 4-click codas	Chapter 6 Rendell and Whitehead 2003b
Within Oceans, Between Clans	ETP	0.001	Full Coda Repertoire	Rendell and Whitehead 2003b

Overall, it would appear that sperm whales in the Caribbean live in a much more individualized society than their counterparts in the Pacific. Social relationships between unit members are dynamic, and long-term relationships between units may be based on social preferences through direct personal knowledge. In contrast, the society in the Pacific may be more structured at the cultural level, in an 'Us versus Them' fashion. This may be the result of a society devastated by whaling, such that the social structure in the Atlantic reflects what might have existed prior to whaling, or the response to differing environments in which broad recognition of clan membership is important in the Pacific to facilitate grouping formation in a high risk environment in which individual units may range more widely and not form preferred associations.

In summary, sperm whale behaviour is not homogenous. Social and vocal behaviour vary between individuals and among the units they make up. The link between coda communication and social structure was previously shown among sperm whales at ocean basin scales among the vocal clans in the Pacific (Rendell and Whitehead 2003b), but these findings also show that sperm whale social and vocal variation is a balance between the importance of individuality and conformity within units and clans. An individual's behavioural phenotype is a complex interaction between selection for distinct individuality and group-level conformity.

BROAD LESSONS FROM SPERM WHALE SOCIETY:

Over the last eight years, through my masters and doctorate research, it has been a privilege to study the sperm whales of Dominica. It has really been the first time that anyone has come to know these leviathans from the deep as individuals, as brothers and sisters or as mothers and babysitters. They are truly a community of families each with their own behavioural traits and each with a unique story; but which all live together as neighbours in overlapping homeranges in the eastern Caribbean Sea.

Over the course of this study, I have learned several broad, simple lessons from observing these animals:

LESSON 1: LOVE YOUR MOTHER

As in all other mammalian societies, the mother-calf bond is a critical part of sperm whale life. This study has shown that the strength of this bond endures well beyond weaning (CHAPTER 3) and previous work shows that mother-calf relationships create structure within units (Gero *et al.* 2008; Gero *et al.* 2009). New mothers appear to go through a short period of social isolation (~1 year) as they spend the majority of their time either with their dependent calf or at depth feeding to meet the energetic requirements of nursing. They remain connected to the rest of the unit primarily through their calves' social relationships (CHAPTER 3). Mothers cycle in and out of the center of a unit's social network as they give birth, nurse, wean, and babysit. Continued work with more units will allow for the testing of patterns identified in Chapter 3 within this population. In addition, more detailed studies at the individual-level are needed from both around the Atlantic and in the Pacific in order to provide regional and clan level comparisons.

While a mother's social patterns change with the birth of new calves, their vocal repertoire does not. In chapter 5, I tested Schulz *et al.'s* (2011) maternal repertoire variation hypothesis and found no supporting results. While several females gave birth to new calves during the six year study, none shifted their repertoire to be more distinct. The predominant coda types used by an individual whale across years and social role appear to remain consistent (CHAPTER 5), even if the individual is an acoustic outlier within their unit. It is more likely that mothers are individually identified based on cues within coda types as with other individuals, and in that regard this work (CHAPTER 5) supports findings by Antunes *et al.* (2011) which suggested that the '5R' might serve this function.

LESSON 2: SPEND TIME WITH YOUR OLDER SIBLINGS BECAUSE EVENTUALLY THEY MOVE AWAY

This study has allowed us to study a young male as he separates from his natal unit. We now know that this juvenile has learned his natal dialect (CHAPTER 5 and Schulz *et al.* 2011) and that the birth of a sibling may be a cue which initiates or promotes the separation (CHAPTER 3). Previous collaborative work of mine showed that the young males are often playful with the young calves (Gero *et al.* 2008; Gero *et al.* 2009), and at least in the case of Scar, his interest in his newest half-brother certainly suggests that the kin bonds are important even to individuals who will not live out their lives within the unit (CHAPTER 3). Many of the calves in this study are males, and further research will allow us to make comparisons across individuals as more young males reach maturity and separate from their unit. The continuation of this research program will allow us to learn more from the infrequent, but apparently repeated, visits from mature and adolescent males (CHATPER 2).

LESSON 3: LEARN FROM YOUR GRANDMOTHERS' EXPERIENCE:

Unlike African elephants (Moss and Lee 2011), there does not appear to be any kind of elder female sperm whale physically leading the units around (CHAPTER 4). Nonetheless, it is clear that socially learned behavioural traditions are important in the lives of sperm whales (Rendell and Whitehead 2001). Young sperm whales are not born with an innate coda repertoire as it appears that calves initially use different coda types than their adult unit-mates and converge on the unit's common repertoire within a few years (CHAPTER 5). Even though individuals and units exhibit distinguishable differences between their coda repertoires, overall, social units of whales living in the Caribbean seems to converge on a common general coda repertoire (CHAPTER 6). While the 9 units studied have distinguishable repertoires, they produce one specific coda type, the '1+1+3', in a stereotyped manner that has been commonly used in the area for at least the last 30 years (CHAPTER 6). These units have an overall repertoire similarity which meets the definition of a vocal clan as in the Pacific (Rendell and Whitehead 2003b). Given the findings in the Pacific which suggests that coda dialects mark significant divisions among sympatric clans which differ in habitat use, diet, movement patterns as well as foraging and reproductive success (Rendell and Whitehead 2003b; Whitehead and Rendell 2004; Marcoux *et al.* 2007a; Marcoux *et al.* 2007b; Rendell *et al.* 2012), it raises the question of whether units, rather than clans, differ in their habitat use, movement, diet and foraging success within a clan in an area in which only one repertoire has been identified?

LESSON 4: BE A GOOD NEIGHBOUR

Perhaps the most interesting finding of this entire thesis is the discovery of "bond-pairs" of social units, whose membership is stable across decades (CHAPTER 4). This finding indicates that there is a whole other level of social structure and interactions still yet to be studied. Not only are these relationships preferential, but they are also mutualistic. Each family unit probably benefits by having members of the other babysit their calves. This expands the ambit for altruistic and cooperative behaviours from close kin within a stable social unit to include individuals who are encountered somewhat frequently but not regularly and sometimes separated by long periods of time. This hints at large-scale cooperation. Further work is needed to establish the genetic relationships between bond-pairs and how preferred partners identify each other and across what scales. Do bond-pairs hear and recognize each other at a distance and actively move towards each other, or are these mutualistic groups formed only when two well-connected units happen upon each other simply out of having large portions of their homeranges which overlap? Studies using satellite telemetry to outline each unit's homerange are needed. Furthermore, the detailed understanding of each unit's and individual's repertoire outlined here will increase the likelihood of success from coda playback experiments aimed at elucidating the function of coda types.

LESSON 5: SHARE THE BURDEN OF YOUR RESPONSIBILITIES BY WORKING TOGETHER:

This study has shown that social relationships within the natal unit are dynamic and that relationships among bonded units may last decades (CHAPTERS 3 & 4). Ultimately, in an empty ocean, sperm whale mothers must count on others to help raise their calves (CHAPTER 3). Allocare of the calves creates variability in the social networks within units of sperm whales (CHAPTER3) and between them (CHAPTER 4). Mutualistic groups may form in order to increase the number of potential babysitters so that calves may be attended by members of other units during periods when these groups form. Studies of this detail in the Pacific would provide a valuable comparison of social life within units.

LESSON 6: BE AN INDIVIDUAL

My research has shown that sperm whales have personalities. Individual whales have differing patterns of association between their fellow unit members (CHAPTER 3). The social dynamics within social units, which have typically been treated as the base level of social structure, are more complex than previously thought. Some individuals are highly gregarious and centrally connected in their unit's social network, while others are peripheralized.

There is also individual level vocal variation that allows us, and presumably the whales themselves, to distinguishing between individuals (CHAPTER 5). While there is enough variation within individual coda repertoires to distinguish among them, it is still unclear what cues receivers use to recognize individuals. Experimental approaches using coda playbacks are needed to elucidate the details of individual recognition.

CONSERVATION AT THE LEVEL OF THE INDIVIDUAL:

The levels of variation among individuals highlighted in this study clearly indicate that each individual whale plays a unique role in a dynamic nested social network. What then does this mean for conservation? Traditionally, conservation has focused on managing declining populations due to anthropogenic threats or dramatic environmental changes and management has focused on abundance and distribution of individuals in order to maintain sufficient genetic diversity in order for the species to survive. Sperm whales are managed based on vaguely defined stocks which cover large areas of ocean (Donovan 1991). However, arguments are being made increasingly that management must operate on more biologically meaningful levels in order to preserve phenotypic variation as well as genetic diversity (*e.g.* de Guia and Saitoh 2007) This study suggests that individuals play an important role in the observable behavioural variation among sperm whales, but can we really expect to conserve individual variation by protecting every single whale from the inevitable damage interactions with humanity will cause?

To answer that question, we need to ask, why we want to protect sperm whales in the first place? On an evolutionary timeline, sperm whales are among the oldest of the toothed whales. They have lived in the oceans for longer than modern humans have walked upright. Some have argued that this evolutionary distinctness is a currency worth preserving (Isaac *et al.* 2007; Collen *et al.* 2011). Sperm whales are recognized as a monotypic family, well separated even from their closest relatives the Kogiidae (pygmy and dwarf sperm whales; Mchedlidze 2002).

Over a modern timeline, this species is clearly a significant part of the ocean ecosystem given the amount of biomass they consume (Kanwisher and Ridgway 1983) and the generally top-down regulation of marine food webs (Worm and Myers 2003). In addition, they link the deep ocean to the surface (Watwood *et al.* 2006) which allows their defecation to play a role as a carbon sink (Lavery *et al.* 2010).

More directly, these families I have been working with over the last eight years have known each other for far longer just by living in the same neighborhood. We know that these families have lived in the area for decades (CHAPTER 2), and that their ancestors where there likely even for centuries based on their life cycle (Whitehead 2003). While mature male sperm whales range widely, social units of females have much smaller ranges creating a scenario where genetic exchange between communities occurs primarily via male dispersal (Lyrholm *et al.* 1999; Engelhaupt *et al.* 2009). Interestingly, the social boundaries between clans which differ behaviourally and are marked by acoustic signals of membership fit existing definitions of ethnic boundaries among humans (Van den Berghe 1981). In this case, the cultural unit containing multiple lineal groups (mainly patrilineal in humans according to Van den Berghe, but matrilineal in the case of sperm whales) is maintained while one sex (males in sperm whales while generally females in humans) is transferred between groups within cultures as well as across cultural boundaries. As a result, many have suggested the primary management unit be communities of female units regardless of the genetic mixing created by the wide dispersal of males (Dufault *et al.* 1999; Gero *et al.* 2007). In some ways, units of sperm whales are citizens of their part of the ocean as much as any of us are of our natal countries. They were born there, learnt their local dialect and the rules of the natal unit's culture from their mothers and grandmothers. Given that this within-population variation makes species more adaptive and resilient, should preserving this variation between communities not be a part of our conservation schemes? Whitehead (Whitehead *et al.* 2004; Whitehead 2010) advocated for the inclusion of cultural groups into definitions of management units. Certainly, the stability of and distinctness of the 1+1+3 codas produced by all of the social units in this study (CHAPTERS 5 & 6), as well as their high resighting rates, and apparent small ranges (CHAPTER 2) makes this community distinct from those in other parts of the world (Whitehead *et al.* 2012). Their ocean nation has lived parallel to ours, mostly unnoticed, for generations and the weight of their shared history in the waters off Dominica, should greatly affect our goals as managers, policy makers, and conservationists.

Studies of animal social networks and the interconnectedness of individuals across communities is highlighting the different, and important, roles seemingly interchangeable individuals play (McComb *et al.* 2001; Lusseau and Newman 2004; Williams and Lusseau 2006; Lusseau 2007; Krause *et al.* 2010; Schürch *et al.* 2010; Sueur *et al.* 2010; Bode *et al.* 2011a; McComb *et al.* 2011; Bode *et al.* 2012; Cantor *et al.* 2012; Foster *et al.* 2012). However, the individual differences found in this work indicate that individuals are not interchangeable. Among killer whales, another matrilineal cetacean, simulations showed that the targeted removals of single individuals greatly affected a community's social network (Williams and Lusseau 2006). But given the little resources available, limited understanding of the subject species, and inadequate public education on the issues, conserving individuals seems like a monumental goal.

So, perhaps individual level conservation has nothing to do with the species we are interested in protecting at all, but entirely to do with ourselves as individuals. As an individual, I should make myself the agent upon which the growth of a new conservation-minded regime must depend. What changes can I make to change that state of the oceans? What can I do for Unit F? How will I ensure that Enigma, a calf today, fathers his young in a healthy ocean? My parents' generation sent people to the Moon, and robots to Mars, but we will be here to save the oceans. This generation, my generation, is the ocean generation. And now is the time to start. Now. It is critically important because lives are at stake. Rich complex lives of long-lived individuals with families. A multicultural nation of ocean dwellers we hardly know and from whom we are only starting to learn about their social complexity, the communicative potential of their coda dialects, and their lives in the deep ocean.

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