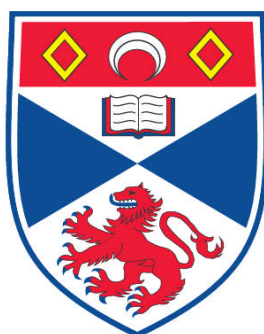


**VARIATION IN SPERM WHALE (*PHYSETER MACROCEPHALUS*)
CODA VOCALIZATIONS AND SOCIAL STRUCTURE IN THE
NORTH ATLANTIC OCEAN**

Ricardo Nuno Calado Antunes

**A Thesis Submitted for the Degree of PhD
at the
University of St. Andrews**



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School of Biology
University of St.Andrews



Variation in sperm whale (*Physeter macrocephalus*) coda vocalizations and social structure in the North Atlantic Ocean

A thesis submitted as part of the requirements for the degree of
Doctor of Philosophy (Biology)

March 2009

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Abstract

This study aimed at complementing studies of sperm whale social and vocal behaviour that were restricted to the Pacific Ocean.

The characteristic multi-pulsed structure of sperm whale clicks allows for estimation of whales' size from measurements of the inter-pulse intervals (IPI). I have developed two new automatic methods for IPI estimation from clicks recorded during foraging dives. When compared to other previously developed methods, the newly developed method that averages several clicks' autocorrelation function showed the best performance amongst the automatic methods.

Previous studies did not support individual identity advertisement among social unit members as the function for the sperm whale communication signals called codas. I tested within coda type variation for individual specific patterns and found that, while some coda types do not allow for individual discrimination, one did so. This variation suggests that different coda types may have distinct functions.

Analysis of social structure in the Azores found that, similar to the Eastern Tropical Pacific, sperm whales form long term social units of about 12 individuals. Unlike the Pacific Ocean, Azorean social units do not form temporary groups with other units, suggesting differences in the costs and benefits of group formation. I argue that these are due to differences in terms of predation pressure and intraspecific competition between the Azores and the Pacific study sites.

The variation of coda repertoires in the Atlantic also showed a pattern dissimilar to that previously documented in the Eastern Tropical Pacific. In the North Atlantic, coda repertoire variation is mostly geographic, which is parsimoniously explained by random drift of culturally transmitted coda repertoires. No sympatric vocal clans with distinct dialects were found as has been noted in the Pacific. Drawing upon the differences found in social structure I argue that selection for maximization of differences between units with similar foraging strategies may have led to the Pacific vocal clans.

The differences between oceans suggest that sperm whales may adaptively adjust their behaviour according to experienced ecological conditions.

Declarations

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CHAPTER 1

General introduction

1.1. Introduction

1.1.1. Animal social structure

Conspecifics are an important part of the environment of the great majority of animal species. Examples include animals that occupy the same space or aggregate in the same food patch, parents and offspring in early stages of life, and animals that maintain long term social relationships throughout their lives. Interactions among co-occurring conspecifics can be mutually beneficial, such as between offspring and a care providing parent, or disadvantageous to either or both interactants, for example when animals compete for resources.

Social structure is the synthesis of interactions among individuals. Hinde's (1976) concept of social structure treats it as the top of a three level framework. At the bottom of this framework is the quality and nature of the interactions among individuals, with interactions occurring when the presence and/or the behaviour of one individual, affects that of another. These interactions can take many forms, such as instances of nursing of offspring, grooming and agonistic encounters. At the second level are the social relationships among individuals; the content, quality and patterning of the interactions between a pair of individuals defines their relationship. The social structure of a group of animals is then made up of the content, quality and patterning of relationships among them and this makes up the top level (Whitehead, 2008).

Interactions among individuals, the basis of Hinde's framework, are often hidden from a scientist's perception, particularly in more cryptic species. An alternative is to use spatio-temporal associations of individuals instead of interactions as the fundamental element of social structure.

Animals are usually considered to be "*associated*" when they are in conditions where interactions can take place. Associations have the advantage that, being state variables, they can more easily be measured instantaneously as opposed to interactions, which may require longer periods of observation (Whitehead, 2008).

Cetaceans spend a large proportion of their lives submerged and are a prime example of a taxon where behavioural interactions among animals are difficult to observe. Thus the study of social structure in this group is usually based on measuring associations among individuals. In the study of both interactions and associations, the identification and recognition of individual animals is essential. In cetacean studies, individuals are usually identified using conspicuous marks and shapes on the animal's body, normally through the use of photographic techniques that allow a permanent record of sightings and associations of individuals. These techniques have proven themselves in numerous studies of social structure in these highly social species (*e.g.* Bigg *et al.*, 1990; Christal *et al.*, 1998; Karczmarski *et al.*, 2005).

Social structure can affect aspects of a species' biology such as gene flow (Whitehead, 1998), habitat use (Baird & Dill, 1996; Ersts & Rosenbaum, 2003), the spread of diseases (Lee, 1994; Guimarães *et al.*, 2007) and the manner in which information is retained and transmitted among individuals (McComb *et al.*, 2001; Wittemyer *et al.*, 2005) and therefore deserves consideration. In turn, social structure is also affected by ecological factors such as predation pressure and availability of resources (Whitehead, 2008).

Predation pressure can be minimized by the presence of conspecifics because the probability of a single animal being predated upon may be reduced by the presence of conspecifics (dilution effect). The presence of other individuals may also reduce vigilance requirements for any one individual (and consequently increase time to forage), enhance group defence (*e.g.* mobbing in birds) and confuse predators and these further contribute to reducing predation pressure. The presence of conspecifics may also provide an advantage in acquiring and defending resources such as food and may provide useful information to individuals deciding where to settle and forage by indicating the presence of suitable conditions. Cooperative hunting for prey can be another advantage provided by the presence of conspecifics (Barnard, 2004). These potential advantages can act as a force that brings animals together, potentially leading to group formation. However, group formation may also involve disadvantages. A group may be more conspicuous to predators than single individuals, and in some cases predators may preferentially, or uniquely, prey upon

groups, in which case predation pressure may be higher for groups compared to single individuals. Conspecifics usually have similar resource requirements, including food, reproductive partners and shelter, and the presence of other individuals may increase the competition for these resources. The balance of the advantages and disadvantages of proximity to conspecifics will affect the quality and nature of interactions among individuals, and consequently influence the social structure.

Correlation between various ecological factors and social structure has been reported in several studies. For example Faulkes *et al.* (1997) investigated the relationship between phylogeny, ecology and sociality in 15 species of African mole-rats that live in a range of different ecological conditions, and exhibit differences in social structure. They found that more complex social systems occur in habitats with low geophyte density and high variability in rainfall, suggesting that environmental constraints are a determining factor in the evolution of social structure. Intraspecific variation in social structure has also been correlated with ecological differences. For example, Wittemeyer *et al.* (2005) observed that the cohesion of African savannah elephant (*Loxodonta africana*) family units was little altered with different ecological conditions, whereas the formation of aggregations of these family units was significantly reduced in dry seasons in comparison to wet seasons.

1.1.2. Recognition using communication signals

Living in groups may require the coordination of activities among group members. This may be facilitated by transfer of information among group members through the use of communication signals. Animals may use communication signals for sexual partner coordination (*e.g.* lordosis in female cats), pair-bond maintenance (*e.g.* tail twining in dusky titi monkeys; *Callicebus moloch*; Bradbury & Vehrencamp, 1998), appeasement and affiliation (*e.g.* grooming in primates; Bradbury & Vehrencamp, 1998), coordination of movement (*e.g.* movement initiation calls in African Savannah elephants; Payne, 2003) and in the sharing of environmental information (*e.g.* vervet monkey, *Cercopithecus aethiops*, warning calls; Cheney & Seyfarth, 1990). In addition to these functions, communication signals may also be used to facilitate recognition. Recognition involves the discrimination of specific individuals and/or groups, among a domain of non-target individuals or groups (Bradbury & Vehrencamp, 1998; Sherman *et al.*, 1997).

Group recognition can be achieved by familiarization with each group member's individual specific signals, but may also be achieved through the use of group specific signals. Screech calls of greater spear-nosed bats (*Phyllostomus hastatus*) provide an example of the latter. These calls show

differences among groups, but not among individuals (Boughman, 1997). Playback studies have shown that greater spear-nosed bats can discriminate between the calls of their own group mates and those of other bats, but show no evidence of discrimination between individuals (Boughman & Wilkinson, 1998). Individual-level signal recognition is always based on learned familiarization and memorization (through imprinting for example), and requires prior experience with specific individuals (Bradbury & Vehrencamp 1998, Tibbetts & Dale 2007) and thus may be more likely to arise within groups of animals with long term social relationships.

Individual recognition is thought to have an important role in the evolution of cooperation and in particular of altruism (Crowley *et al.*, 1996). The evolution of helping behaviour in which individuals increase another's fitness at the expense of its own immediate fitness, is often explained in terms of an increase in inclusive fitness by providing aid to offspring or other relatives (Hamilton, 1964), or the later reciprocation of helping behaviour by unrelated individuals (Trivers, 1971). Recognition of the target of help by the provider is therefore an important aspect of the evolution of this behaviour, by allowing differential provision of help to kin and reciprocators.

Individual recognition is also thought to facilitate the stabilization of linear dominance hierarchies by allowing individuals to keep track of the outcome of previous interactions with previous members of the hierarchy (Barnard & Burk, 1979; Dugatkin & Earley, 2004).

1.1.3. Sperm whale life history and social structure

The sperm whale (*Physeter macrocephalus*) is the largest species of the toothed whales (sub-order Odontoceti), with females growing up to 12.5m (15 metric tons) and males up to 18.3m (60 metric tons) (Best, 1979; Rice, 1989). Usually found in waters deeper than 200m in all oceans, it has the second widest distribution of any marine mammal, exceeded only by the orca (*Orcinus orca*), although female sperm whales usually only occur between parallels 40° North and South (Rice, 1989).

Within this wide range, sperm whale distribution is not uniform however. Whalers were the first to recognize the existence of areas where sperm whales were concentrated, or 'grounds' (Townsend, 1935). The factors that determine these concentrations are still poorly understood, not least because of the inaccessibility of the mesopelagic realm in which members of the species forage. Several studies have suggested factors such as the continental shelf break, oceanic fronts where water masses meet, cyclonic eddies, and warm-core rings as determinants of sperm whale

distribution (Waring *et al.*, 1993; André, 1997; Griffin, 1999; Biggs *et al.*, 2000; Gregr & Trites, 2001; Waring *et al.*, 2001; Whitehead, 2003) but there is no consensus on the relative importance of these factors. Jaquet (1996) argued that the correlation between sperm whale distribution and oceanography is scale dependent, and that at larger scales it is mostly determined by primary production which may determine the food available to sperm whales.

In most parts of the world sperm whales appear to feed on meso and bathypelagic cephalopods with mantle lengths between 0.2 and 1.0m (Clarke, 1962; Berzin, 1972; Clarke, 1980; Kawakami, 1980; Rice, 1989; Santos *et al.*, 1999). Fish between 0.3 and 3m long have also been found in sperm whales stomachs, particularly at higher latitudes (Kawakami, 1980; Rice, 1989). To catch prey, sperm whales engage in foraging dives that can take them as deep as 1000m (Whitehead, 2003). The global population of sperm whales is estimated to consume about a 100 million metric tons of prey per year, a number that underlines the species' ecological importance.

The sperm whale's long life span (Rice, 1989) allows the formation of long-term social bonds among individuals (Christal *et al.*, 1998). Studies on the social organisation of sperm whales in the Pacific Ocean have shown that female sperm whales and their immature offspring live in long-term stable social units of 10 to 12 individuals with only occasional movements of individuals among units. In the Pacific these units form temporary multi-unit groups that typically last for periods of days before disassociating (Christal *et al.*, 1998; Coakes & Whitehead, 2004; Jaquet & Gendron, in Press). Gero (2005) found that within sperm whale social units, individuals have preferred associations and avoidances.

Male sperm whales disperse from their maternal units at about the age of 6 to form what are called '*bachelor groups*' with other males of similar age (Best, 1979). As they age and grow, males are found in smaller groups and at higher latitudes, a trend that culminates in a solitary life in polar latitudes which are outside the range of females. Sexually mature males travel to lower latitudes for breeding, often transferring between oceans (Ivashin, 1981). It is suggested that they rove between female units/groups in search of females in oestrus (Best, 1979; Whitehead, 1993; Christal & Whitehead, 1997; Whitehead & Weilgart, 2000; Whitehead, 2003). The factors that govern the range and timing of movements of mature males and the extent to which they return to their natal seas to breed is unknown.

These patterns of female philopatry and male dispersal are displayed in the species' genetic

population structure. Studies using microsatellites suggest that globally sperm whales present low diversity in the bi-parental nuclear genome and little variation among ocean basins due to breeding outside maternal units and male-mediated transfer of genetic material over long ranges and across oceans (Lyrholm *et al.*, 1999; Engelhaupt, 2004). Analysis of the variation in the maternally inherited mitochondrial genome showed low levels of diversity on a global scale, but marked variation among ocean basins, indicating that females do not switch basins (Lyrholm & Gyllensten, 1988). Genetic analysis has also shown that although sperm whale units/groups often contain highly related individuals, they typically also include unrelated individuals, and often more than one matriline is present (Bond, 1999; Mesnick, 2001; Engelhaupt, 2004).

1.1.4 Sperm whale vocalizations

One of the unique features of the sperm whale is the spermaceti organ, an oil filled anatomical structure located in its nose, that makes up to 25 - 33% of the animal's body (Rice, 1989). Different theories about the function of the sperm whale's hypertrophied nasal complex have been put forward (Carrier *et al.*, 2002; Clarke, 1970, 1978), but the most convincing and generally accepted is that of Norris & Harvey (1972) which describes it as a sound producing organ – the largest in the animal kingdom. Other studies have further developed the Norris & Harvey theory on the mechanism of sound production (Cranford, 1999; Møhl *et al.*, 2003). According to these, sperm whales produce sound by forcing air through a lip-like structure that produces a sound pulse. This sound pulse propagates inside the spermaceti organ until it is reflected from the air sacs located at the frontal and distal ends of the oil case. This process produces a series of decaying pulses, one from each reflection cycle, which propagate to the lower part of the spermaceti organ, the junk. This is thought to function as an acoustic lens, collimating the sound and transmitting it to the water in front of the whale. Despite an initial description of sperm whale clicks which reported a lack of directionality (Watkins, 1980; Watkins *et al.*, 1985), subsequent studies demonstrated that they are in fact highly directional, and have source levels as high as 223 dB re 1 μ Pa @ 1m, the highest biologically produced source levels that have been recorded from any animal (Zimmer *et al.*, 2005a). The click sounds that are produced by this mechanism are short (0.1 – 30 ms in duration; Whitehead, 2003) and broadband, and often have an intrinsic structure composed of regular decaying pulses, resulting from the multiple reflections inside the spermaceti. The time interval between consecutive pulses, the inter-pulse interval (IPI), is proportional to the length of the spermaceti organ, and therefore to the whale's size, allowing acoustic measurement of sperm whale

lengths (Norris & Harvey, 1972; Adler-Fenchel 1980; Gordon 1991; Goold, 1996; Rhinelanders & Dawson, 2004).

The evolution of such a large sound-producing organ suggests that sound production must have an important function in the life of the sperm whale. Echolocation, either for prey finding or navigation is likely an important use of sound, especially during the long foraging dives that can take the whales down to depths of several hundred metres, well below the euphotic zone. During these foraging dives, sperm whales produce regular sequences of clicks at rates of between 0.5 and 1 s⁻¹ (Whitehead & Weilgart, 1990; Gordon, 1991; Goold & Jones, 1995; Jaquet *et al.*, 2001; Madsen *et al.*, 2002b).

1.1.5. Sperm whale codas

Occasionally sperm whales produce series of clicks with stereotyped timings called codas. The term codas was first used by Watkins & Schevill (1977), to name the “temporal repetitive pulse patterns” that sometimes can be heard at the end of longer sequences of sperm whale clicks. These were the same sounds previously mentioned by Backus & Schevill (1966) as “sequences of clicks which are repeated several times”. Watkins & Schevill (1977), described codas as stereotyped series of 3 to 40 clicks, lasting between 0.5 and 1.5 seconds. By using an array of hydrophones, which allowed them to estimate the location of the vocalizing whales, they described what seemed to be an exchange of codas between two spatially separated whales.

Neither Watkins & Schevill (1977) nor Watkins (1977) refer to the sex of the whales recorded. Mullins *et al.* (1988) did not report any codas from two male sperm whales tracked off Nova Scotia, but some authors report hearing codas from mature males (Pavan *et al.*, 2000, Karlsen *et al.*, 2001), and others report codas at latitudes where only mature males occur (Gordon *et al.*, 1992). In the Azores, where both mature male individuals and female groups occur (Clarke, 1956), Antunes (2000) reported codas produced by whales with estimated lengths between 7 and 13 metres, a range that does not include the larger mature males, and the smaller calves. Marcoux *et al.* (2006) found that codas recorded in the tropical and subtropical South Pacific Ocean were almost entirely produced by mature females.

The observation of preferred associations and avoidances among sperm whale social unit members (Gero, 2005) suggests that sperm whales have individualized relationships within units. This may require ways by which animals recognize individuals in order to adjust their behaviour

accordingly. Chemical signalling is unlikely to be used because Odontocetes do not have a well developed sense of smell (Morgane & Jacobs, 1972) and signals would disperse in a slow and unpredictable way in the aquatic environment. Visual cues could potentially be used at short distances during daylight periods but the transmission of identity through acoustic signals is better suited for instantaneous long range communication. Codas have been proposed to function for communication and identification of unit membership, and are the most likely signals to be used for individual identification and recognition. Backus & Schevill (1966), noted that the temporal pattern and repetition rate of coda sequences were not adequate for echolocation and suggested that codas have a communicative function. Watkins & Schevill (1977) hypothesised that the function of codas could be to signal the individuals' identity to conspecifics. However, Weilgart & Whitehead (1993) dismissed the individual identification theory on the basis that the number of coda types was considerably less than the number of whales present in their study area, that different whales produced the same coda types, and that individuals often produced more than one coda type. Others (Watkins *et al.*, 1985; Moore *et al.*, 1993; Rendell & Whitehead, 2004) also observed coda types that were shared by different individuals. More recently, Schulz (2007) has studied the individual coda repertoires from a single social unit from Dominica and found that, apart from one adult female and her calf, all of the other five individuals mainly produced the same two coda types at similar frequencies, providing further evidence that codas do not function exclusively for individual identification, and recognition is not possible using coda type repertoires.

Although the precise function of codas is unclear, evidence points to communication and social bonding as their main function (Watkins & Schevill, 1977; Whitehead & Weilgart, 1991; Schulz, 2007; Chapter 3). This suggests that individuals within a unit must share a common signal code for communication to be effective. Unit members share elements of their coda repertoire, and engage in antiphonal coda exchanges suggesting sharing of a signal code (Schulz, 2007). Unless there is a large genetic component to the coding scheme, or it corresponds to an adaptation to the physical environment, sharing of repertoires suggests convergence of vocal signals by social learning during interaction with other whales.

Observations on the vocalizations of three stranded sperm whale calves, of different ages and in rehabilitation, have shown an increasing resemblance to codas in the older ones (Watkins *et al.*, 1988), suggesting a developmental process. Acoustic communication is the most likely modality for medium to long range communication underwater, and therefore mother-calf

communication is likely to take the form of acoustic signals. An immediate post-birth need for localization and coordination between a calf and its mother that forages at depth for long periods in a featureless environment, suggests that signals and coding schemes used for this purpose may have a strong inherited component. Schulz (2007) found that within a sperm whale social unit, the mother and calf coda type repertoires were distinct from other unit members, supporting the idea of specific mother-calf communication signals. However, sperm whale calves, and in particular females who have a low probability of dispersing from the natal social unit, may also require a communication scheme for coordination with other social unit members. The temporal stability of coda repertoires (Rendell & Whitehead, 2005a) suggests that if female sperm whale calves remain in their natal units, they may acquire a coda repertoire that is functional within the unit from other unit members, because the unit may already possess a functional common repertoire. This repertoire acquisition may arise through a developmental process mediated by genetic determination, but the long term social environment within units also provides the conditions for social learning to take place. Learning the typical vocal repertoire of the maternal units might also prove useful in the case where whales later transfer between units, as happens occasionally in the Pacific (Christal *et al.*, 1998), because units preferentially associate with others having similar vocal repertoires, and therefore transfers are likely between units with similar repertoires.

Gordon (1987) suggested that codas could vary geographically and some differences are found between distinct geographical locations. The most common coda types found in the Caribbean have longer intervals at the beginning (Moore *et al.*, 1993), while in the Galápagos the last intervals seem to be longer (Weilgart & Whitehead, 1993). In contrast however, a coda type made of five equally spaced clicks (5 regular) has been found in the NW Atlantic (Watkins & Schevill, 1977), Caribbean (Moore *et al.*, 1993) and Pacific (Rendell & Whitehead, 2003), and was the most common type in the Azores (Antunes, 2000) and the Galapagos (Weilgart & Whitehead, 1993). In the Mediterranean, most codas seem to fit the type called 3+1 (three evenly spaced clicks, followed by a final click with a longer interval; Borsani *et al.*, 1997; Pavan *et al.*, 2000), although other types have been found (Drout & Gannier, 1999).

Weilgart & Whitehead (1997) found group-dialects and geographical variation in coda repertoires of the Pacific, and proposed that codas are learnt within matrilineal social groups and reflect family relationships. Further analysis by Rendell & Whitehead (2003b) found that sperm whale social units in the Pacific could be grouped into vocal clans based on their coda repertoires.

Because vocal clans were often sympatric and shared most nuclear DNA haplotypes, they suggested that vocal clans are the result of culturally transmitted behaviour. Additional studies have reported differences between clans in terms of habitat use, foraging and reproductive success, indicating that clan membership likely has consequences for individual fitness (Marcoux *et al.*, 2007a; 2007b; Whitehead, 2003; Whitehead & Rendell, 2004). Rendell & Whitehead (2005a) found geographical variation in coda repertoires within clans, with similarity among repertoires showing a negative trend with increasing distance. They also found that coda repertoires seem to be temporally stable for periods of at least six years.

Animal communication coding schemes and consequently their signals, result from the interplay of inherited traits and the physical and social environment (Bradbury & Veherencamp, 1998). The extent to which each of these components contributes to the resulting communication signals is variable. It is generally agreed that to ensure a good match between sender and receiver coding schemes, developing animals that have neither the time nor the opportunity to learn, rely heavily on heritable acquisition of signals and codes (Bradbury & Veherencamp, 1998). For example anurans produce species specific sounds without prior experience with conspecifics (Gerhardt, 1994). Other species seem to rely mostly on learning to develop a functional coding scheme. For example, differences in contact call dialects of yellow-naped amazon parrots (*Amazona auropalliata*) are maintained by dispersing birds matching their calls to those of the roost they disperse into, even in the presence of high levels of gene flow across dialect boundaries (Wright, 1996; Wright & Wilkinson, 2001).

Coda repertoires are unlikely to result from adaptations to local ecological conditions. Acoustic signals may be adapted to certain medium characteristics (Slabbekoorn & Smith, 2002) and this constrains the range of parameters that can be varied to encode signals. For example white-throated dippers (*Cinclus cinclus*) avoid the masking effect caused by the constant noise of running water in their riverine habitat by calling at frequencies above the noise's dominant spectrum (Brumm & Slabbekoorn, 2006). This limits the frequency range over which communication can be effective. Sperm whale clicks are short, broadband pulses which consequently do not have much signal parameter space for coding in the frequency domain. The coding scheme of codas seems to be based on the time domain alone through variation of the inter-click intervals (ICIs). Such a scheme is less influenced by propagation effects than other systems based on frequency domain coding, and therefore codas may be more robust to local acoustic conditions. The presence of

sympatric groups with distinct vocal repertoires such as found in the Pacific (Rendell & Whitehead, 2003b) and observations of certain coda types that are found across wide ranges (*e.g.* codas with five equally spaced clicks in the Azores: Chapter 5, Caribbean: Moore *et al.*, 1993, and the Pacific Ocean: Weilgart & Whitehead, 1993; Weilgart & Whitehead, 1997) also suggests that codas are not the result of adaptation to local conditions.

Whitehead *et al.* (1998) found that groups with similar coda repertoires have similar mitochondrial DNA (mtDNA) variation, and suggested that this pattern was explained by maternal inheritance of the coda dialects. However, sperm whale social units are not strictly matrilineal and often several mtDNA haplotypes are found within units (Mesnick, 2001). Because the vocal output of unit members is shared, the presence of several mtDNA haplotypes within units argues against an important causal role for maternally inherited genes in coda repertoires. Other genetic evidence points to male dispersal, female philopatry and mating outside natal units (Lyrholm *et al.*, 1999; Engelhaupt, 2004) which does not support the inheritance of coda repertoires through the bi-parental genome. The presence of population structuring in the Pacific based on vocal repertoires associated with a weak nuclear DNA genetic differentiation also offers no support for this.

Other less direct genetic effects have been proposed to influence behavioural traits. For example, Brown (2001) suggested that genomic imprinting (the inactivation of a particular allele dependent upon the sex of the parent from which it was inherited) could account for parallel transmission of maternally inherited genome and behavioural traits in a scenario of multiple paternity of social unit members exhibiting similar behaviour. Janik (2001) argued that differences in the effectiveness of mitochondrial proteins would affect the energetic budget of animals and therefore a wide range of behavioural patterns. A scenario in which differences in cellular metabolism could account for the variation in coda ICIs does not, however, seem a parsimonious explanation. I suggest that in the case of the social units where multiple mtDNA haplotypes are present, different individuals would have dissimilar repertoires, which does not seem to be the case because mtDNA haplotypes are shared across vocally dissimilar groups (Rendell & Whitehead, 2003b).

Despite the potential effects of indirect genetic determination, vocal learning where individual whales modify the coda patterns in their repertoires as a result of interaction with other whales remains a parsimonious explanation for the sharing of individual repertoires within social units. However, neither individual nor social learning have been experimentally demonstrated in

sperm whales.

In a comparative review of methods such as telemetry, photographic identification, various types of genetic analysis, contaminants, morphology and others for determining population structure and movements in sperm whales, Whitehead & Mesnick (2003) concluded that analysis of coda repertoires provides information at the temporal level of generations (decades) and was the only characteristic that reliably showed geographical variation in sperm whales at spatial scales of less than an ocean basin (~5,000 km). The knowledge about sperm whale coda repertoire variation is however restricted to the Eastern Pacific and further studies in other locations are required for a better understanding of the global variation of repertoires in sperm whale populations.

1.2 Thesis overview

The characteristic multi-pulsed structure of sperm whale clicks allows the estimation of whale size from measurement of the IPIs (Gordon, 1991; Rhinelander & Dawson, 2004). This provides not only a very useful tool for estimation of the body lengths of individual sperm whale populations, but also, as demonstrated by Schulz (2007) a way of investigating individual vocal repertoire in cases where each animal has a different IPI. In Chapter 2 I describe two new methods of automatic inter-pulse interval estimation, and compare their accuracy and consistency to those of a manual method and other previously described automatic IPI measurement methods.

Earlier studies have not found support for individual specific coda type repertoires (Weilgart & Whitehead 1993; Schulz, 2007), however, these studies have looked only at variation among coda types. I hypothesise that variation within a coda type may carry individual specific information and test this idea in Chapter 3.

The study of how sperm whales associate is important in the understanding of the factors that may drive variation in the coda repertoires. Most of the research on sperm whale social structure has been carried out in the Pacific Ocean (Christal *et al.*, 1998; Coakes & Whitehead, 2004; Jaquet & Gendron, in Press). However, a more recent study has hinted at differences between the Pacific locations and the Atlantic, that may be driven by ecological factors (Jaquet & Gendron, in Press). In chapter 4 I analyse the sperm whale social structure found in the Azores archipelago and compare my findings with those previously reported in the Pacific Ocean.

In order to investigate if the patterns of coda repertoire variation observed in the Pacific Ocean could be generalized to other populations, I investigated the spatial variation of coda repertoires in the North Atlantic and Gulf of Mexico and present my findings in Chapters 5.

In summary, the aim of this study is to complement the studies of sperm whale social structure and coda repertoire variation from the Pacific Ocean, with new analysis from locations in the Atlantic Ocean. In addition to facilitating this study, the improvements in the methodology of IPI measurement presented in Chapter 2 will hopefully be useful in future studies that measure this parameter to estimate body length. I hope that these contributions will improve the understanding of the mechanisms and function of variation in coda repertoires and social structure of this species.

CHAPTER 2

Measuring inter-pulse intervals in Sperm whale clicks: Consistency of automatic estimation methods

2.1. Introduction

2.1.1. Sound production in the sperm whale

One of the first descriptions of sperm whale vocalizations noted the characteristic multi-pulsed structure of individual clicks (Backus & Schevil, 1966). The initial understanding of the mechanism causing this multi-pulsed structure was that sound reverberated between air sacs, acting as sound reflectors, at both ends of the spermaceti organ, resulting in pulses of decaying amplitude and equal spacing determined by the lengthwise two-way travel time through the spermaceti organ (Norris & Harvey, 1972). The inter-pulse interval (IPI), *i.e.* the time delay between consecutive pulses, was therefore proposed as a method for acoustic estimation of the size of the whale (Norris & Harvey, 1972). Møhl *et al.* (2003) elaborated on the Norris & Harvey theory and proposed the "*bent horn*" model of sound production in the sperm whale. According to this model an initial pulse originates when the whale forces air through a lip-like structure of connective tissue (the *museau-de-singe*, or monkey lips) at the anterior end of the right nasal passage. Part of the generated acoustic energy is passed to the water creating an initial pulse, p_0 . A proportion of the acoustic energy produced at the *museau-de-singe* is reflected backwards by an air filled cavity, the distal sac, at the anterior end of the spermaceti organ. This pulse travels through the oil filled spermaceti organ until it is reflected forward by another air filled structure (frontal sac), propagating through the structure called *junk* (Cranford, 1999; Møhl *et al.*, 2003). This structure, located ventrally to the spermaceti organ, acts as an acoustic lens focusing the acoustic energy of the outgoing pulse, p_1 in a

directional beam (Møhl *et al.*, 2003, 2000; Zimmer *et al.*, 2005b). Part of the forward reflected energy from the frontal sac also propagates back through the spermaceti organ to again be reflected by the frontal sac, initiating another cycle of reflections. Each cycle of reflections creates the subsequent pulses which are characteristic of the multi pulsed structure.

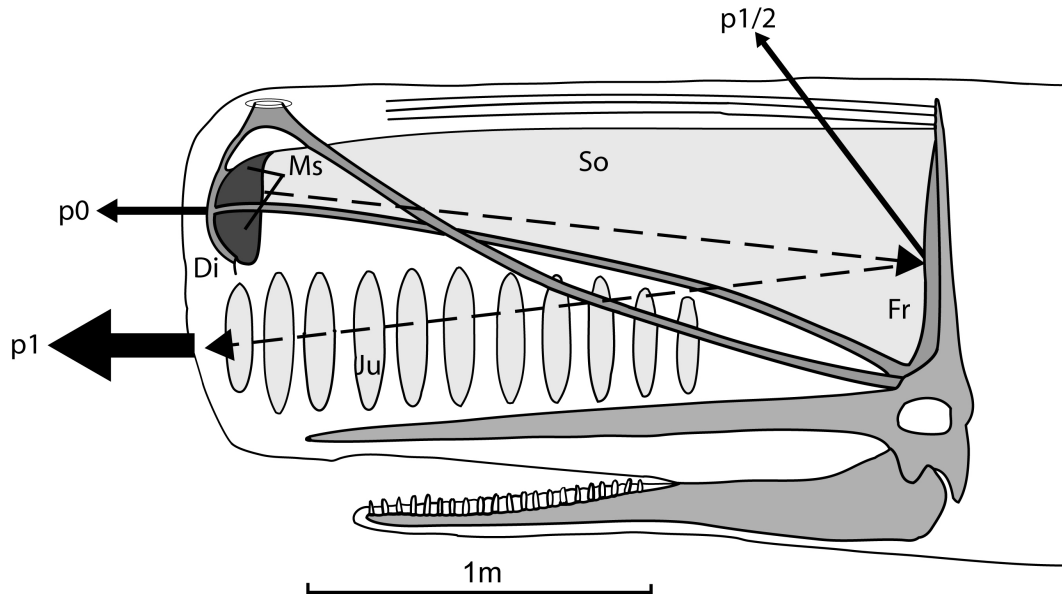


Figure 2.1. Schematic view of the head of a sperm whale depicting the bent-horn model of click sound generation (modified from Figure 1 of Madsen *et al.*, 2002a). The dashed arrows indicate the primary sound path within the nasal complex according to the modified Norris & Harvey (1972) theory. The solid arrows indicate the emission of the weak pulse (p_0) from the phonic lips/*museau de singe* (Ms), the emission of the highly directional sonar pulse (p_1) from the junk (Ju), and the leakage of sound energy as the $p_{1/2}$ pulse from the frontal air sac (Fr). Di, distal air sac; So, spermaceti organ (after Schulz *et al.*, 2008).

The waveforms of sperm whale clicks in typical field recordings are not as clear cut as the classic multi-pulsed structure suggested by the Norris & Harvey model (Figure 2.2). This is especially true for clicks recorded from foraging dives. In the clicks of codas (sequences of clicks produced in stereotyped patterns thought to be used for communication) a much clearer multi-pulsed structure is usually apparent. In most field recordings of foraging sperm whale clicks other pulses can occur within a single click at locations not predicted by the Norris & Harvey (1972) model, which makes measuring IPIs less straightforward than expected. In earlier attempts to estimate IPIs for length measurements, these so-called '*anomalous clicks*' have either been discarded from the analysis or a significant amount of user interpretation was required to measure the '*true*' IPI (e.g. Goold *et al.*, 1996; Rendell & Whitehead, 2004; Rhinelanders & Dawson, 2004).

These '*anomalous clicks*' have subsequently been explained by further developments of the Norris & Harvey theory.

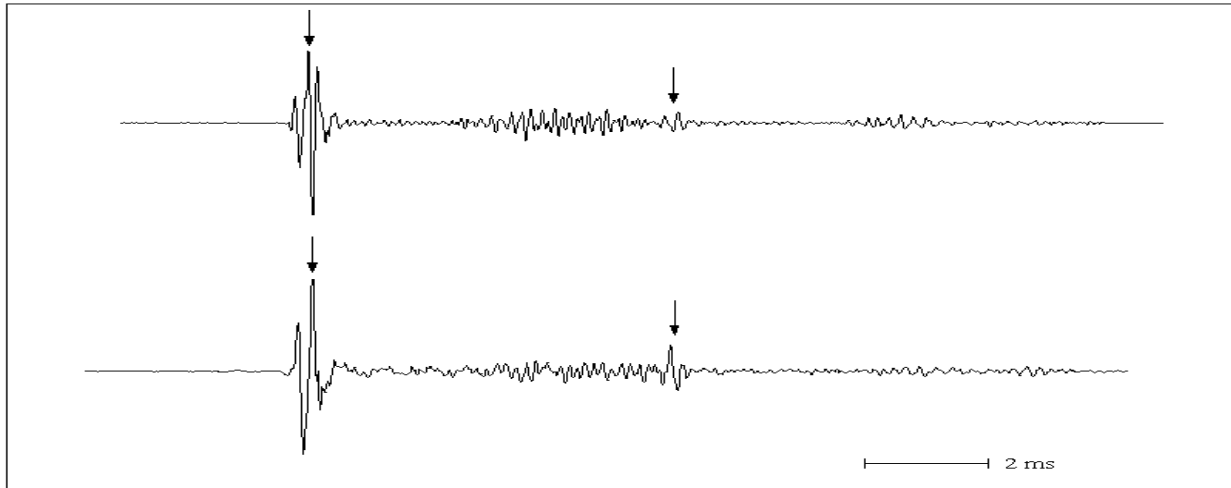


Figure 2.2. Example of typical sperm whale click recorded from a diving whale soon after initiation of the dive '*fluke up*' (60th and 90th clicks from the series depicted in Figures 2.3 to 2.5). Even though it is possible to discriminate two pulses in each click (marked by arrows) the waveform shows other oscillations in between.

Zimmer *et al.* (2005a) proposed a geometric model which explains the variations in the pulsed structure as dependent on the aspect of the whale relative to the receiver. According to this model, intermediate pulses ($p_{1/2}$) occur when the direct path between the reflections at the frontal and distal sacs and the receiver does not propagate lengthwise through the spermaceti or junk, *i.e.* when the receiver is off the axis of the whale (Figure 2.1). This suggests that the estimation of IPIs to measure the size of sperm whales is best performed if recordings are done from either behind or in front of the whale.

A quantitative relationships between IPI and whale length has been derived by relating the IPI to the length of the spermaceti organ, using the speed of sound through the spermaceti oil, and then scaling it to the total whale length using an allometric relationship (Norris & Harvey, 1972; Goold, 1996). Others have derived this relationship empirically by comparing photographic whale size estimation with IPI estimation for individual whales (Gordon, 1991; Rhinelander & Dawson, 2004). Data on the allometric relationship between total length and the size of the spermaceti organ are sparse and have been mostly derived from whales killed during commercial whaling. Sperm whales are no longer a target of commercial exploitation and so the empirical estimation of the relationship between IPI and total length measured in another independent way is the only feasible

way forward.

The ability to estimate size acoustically would be a very useful tool for estimating the size composition of sperm whale populations. In the field, recordings of clicks for size estimation are often made immediately after a whale flukes (*i.e.* initiates a deep foraging dive). '*Fluke-up*' is also the time at which photographic images are collected for identification purposes, allowing the link between identity and IPI to be made. This link is important to avoid considering multiple size estimates from the same whales as different individuals. It may also allow tracking of the increase in size of known individuals over time. Furthermore, automatic methods of IPI estimation have several potential advantages over manual techniques. They are less onerous and more objective, allowing for hundreds or thousands of clicks to be measured in a shorter time period than it would take a human operator. These methods are particularly useful when used in conjunction with automatic click detectors, which automatically select portions of click waveforms that can be used for later analysis.

The linking between whale identity and IPI (and consequently size) may also allow for the identification of vocalisations from particular individuals. This ability was a key step in the study by Schulz (2007) where individual coda repertoires within a sperm whale social unit were investigated for the first time. Schulz (2007) measured IPIs from recordings of identified whales in isolation, providing the calibration of a method for assigning codas to individuals based on IPIs. The breathing periods at the surface between dives are usually when single animals are encountered, and photographic identification images and click recordings made in each encounter provide the calibration data for individual assignment of vocalisations based on IPIs. The recording of foraging clicks made in these encounters have the potential to produce high numbers of clicks, and these clicks usually have a less clear multi-pulsed structure than coda clicks. Automatic or semi-automatic IPI measurement methods may be particularly useful in these cases, potentially reducing the amount of time required to produce an IPI estimate for a series of clicks in comparison with manual measurement.

2.1.2. Approaches to measuring IPIs

IPIs were initially measured from filtered waveforms using an oscilloscope (Alder-Fenchel, 1980; Gordon, 1991). Goold (1996) proposed the use of waveform autocorrelation and cepstral analysis for estimating the IPIs from single clicks. Autocorrelation measures the similarity between a waveform and a time delayed version of itself as a function of the time delay. It can be used to

estimate IPIs, because the time lag between pulses will correspond to the maximum value of the autocorrelation. Cepstral analysis is a non-linear signal analysis tool, firstly described by Bogert *et al.* (1963). The power cepstrum was defined as the power spectrum of the logarithm of the power spectrum of a signal and was proposed as an heuristic technique for finding echo arrival times in a signal (Bogert *et al.*, 1963; Childers *et al.*, 1977). This ability for detecting delayed versions of a signal wavelet makes this technique useful for estimation of IPIs considering that multiple pulses are time delayed versions of the main pulse. The processing of the complex cepstrum, in addition to the arrival time, can be used to determine the waveform of the delayed pulse (Childers *et al.*, 1977). The resulting independent variable in cepstral analysis is in units of time, but to avoid confusion, Bogert *et al.* (1963) proposed quefrency as the term to be used for this, as well as the term gamnitude for the values of the dependent variable. These methods however are not immune to the problems of off-axis estimation. Intermediate pulses confound both automatic and manual estimation of IPIs from recordings of individual clicks. Also, occasionally during manual measurement and visual inspection of waveforms, it is not always clear where the relevant pulses for measurement are located.

Because the intermediate pulses are aspect dependent (Zimmer *et al.*, 2005b) their location between the main pulses varies as a whale moves during a dive, whereas the main pulses corresponding to the lengthwise reflections should be invariant. The time invariant pulses may be discriminated from time variant pulses by averaging click measures over a series of clicks from the same individual whale. For example, Teloni (2008) demonstrated that, by averaging the individual clicks cepstra from a series of regular clicks, it is possible to obtain IPI estimates from whales recorded from an unknown aspect.

Waveform averaging is another method that may increase the consistency of IPI estimates compared to estimates from individual clicks. By aligning the main pulses and averaging the waveforms of several clicks from the same whale the invariant pulses coinciding in time should reinforce each other and contribute more to the resulting waveform than the intermediate pulses. The averaging of the autocorrelation functions may also allow the discrimination of time invariant pulses from series of clicks from the same whale. In this case coinciding peaks in the autocorrelation functions should stand out when averaged across a click series. This method does not depend on temporal alignment as does waveform averaging. Neither waveform nor autocorrelation averaging have been tested so far.

Here I present a comparison of six automatic IPI estimation methods that integrate information from series of clicks from individual sperm whales, including waveform and autocorrelation averaging for the first time. I compare these automated measurements of IPI with those made manually by an experienced operator and evaluate the consistency of each method by comparing multiple recordings of the same whale and produce some recommendations for IPI estimation.

2.2. Methods

2.2.1. Field methods

Single or groups of sperm whales were tracked using visual and acoustic methods (Whitehead & Gordon, 1986) in the Gulf of Mexico and around the Balearic Islands. The focal whales were approached when breathing at the surface between foraging dives. Photographic identification images were taken when whales fluked to initiate deep dives. The vessel was hove to in or close to the dive location (marked by an area of slick water on the surface) and recordings were initiated for acoustic length estimation. The recordings were made using a towed hydrophone array (2x Benthos AQ-4 elements connected to 30dB Magrec pre-amplifiers with 100Hz high-pass filter, inside an oil filled tube at the end of 100m of cable) and either a Creative Labs XTG or a Creative Labs Audigy 2 ZS sound card, sampling at 48 or 96 kHz (temporal resolution of 0.02 and 0.01 ms respectively). The sound files were first analysed using an automatic click detector program (Rainbow Click; Gillespie & Leaper, 1996) in order to identify the series of first clicks. Typically in the Gulf of Mexico, and occasionally in the Balearic recordings, several click series could be heard. The clicks of the focal whale could be distinguished, recognized, tracked and labelled through the early part of the recording based on their loudness, relative bearing and spectral characteristics. Recordings in which the focal whale's first clicks could not be distinguished unambiguously from other clicking animals were not used in the analysis. All clicks from the focal animal were labelled using Rainbow Click and manual IPI measurements were made within Rainbow Click. The waveforms of these clicks were then extracted for further analysis by a custom written Matlab (Mathworks, Natick, Massachusetts) program. The Matlab program took the individual click waveform vectors x_i (*i.e.* a series of sampled amplitude values) from a sequence of clicks assigned to an individual whale as input from which IPI estimates were calculated using several methods.

2.2.1. Manual measurement

I manually measured IPIs using a cross-correlation routine built into the Rainbow Click program. This was done by manually selecting two sections of the waveform containing pulses, which were then cross-correlated. The peak of the cross-correlation was automatically estimated by the program but in some cases it was manually adjusted by the operator when it was considered not to correspond to the best match between waveform sections. The IPI calculated was the sum of the time lag between the start time of each section and the lag measured by the cross-correlation. The peak selection was aided by visualization of each sections waveform, overlaid on each other at the chosen lag in order to evaluate the best match between them. Manual IPI measurement was performed sequentially for each click in a file using Rainbow Clicks built in capability. Only those clicks considered to be suitable for measurement by the operator were measured. Clicks were considered suitable when at least two pulses were clearly identified, with the second having a lower amplitude than the first and, if the cross-correlation produced a clearly distinct peak.

2.2.2. Waveform averaging

Waveform averaging was performed by averaging the amplitude of time aligned individual click waveforms across a series of clicks from the same whale. Waveforms were aligned by their envelope maxima, and zero padded to ensure equal length for all vectors. Envelopes were calculated as the magnitude (complex modulus) of the Hilbert transformed waveform vector.

The IPI estimate (IPI_{waveI}) was then calculated from the average waveform using the autocorrelation method described below.

2.2.3. Click autocorrelation

In this method IPI was estimated by automatically locating the peaks of the positive lags autocorrelation function calculated as:

$$r_{\Delta t} = \frac{\sum_{t=1}^n x_t^2}{\sqrt{(\sum_{t=1}^n x_t^2 \sum_{t=1}^n x_{t+\Delta t}^2)}} \quad (2.1)$$

where n is the number of samples in the waveform, x_t is the amplitude value of the waveform sample at time t , and $x_{t+\Delta t}$ is the amplitude value of the waveform sample at time lag Δt .

For each click series three IPI estimates were derived. The first estimate (IPI_{xcorr}) was the mode of a distribution of the highest autocorrelation peak of all clicks in a series. A second estimate (IPI_{xcorr3}) was calculated as the mode of a distribution of values of the highest autocorrelation peak plus the two highest peaks adjacent to it. This approach followed from the empirical observation that the autocorrelation delay that seemed to correspond to the best match between waveforms was often not the highest, but one of the adjacent positive peaks which took the second or third highest values. The delays corresponding to these peaks were included in an attempt to automatically incorporate these in the analysis. In both cases only values larger than 2 ms were considered to avoid spurious correlations of p_0 with itself.

A third IPI estimate (IPI_{xcorr1}) was calculated by averaging the positive lag autocorrelation functions of all the clicks in a series assigned to the same whale. The autocorrelation vectors were aligned at zero lag, and zero padded to ensure equal number of elements prior to averaging. The IPI was estimated from the time delay of the peak value of the average cross correlation function beyond a minimum threshold (2 ms).

2.2.4. Click cepstrum

Each individual click's IPI_{ceps} was estimated by locating the quefrency corresponding to the peak gamnitude in their complex cepstra above a threshold minimum IPI (2.00 ms). The complex cepstrum C_i was calculated from the sample vector x_i as:

$$C_i = \Re(FFT^{-1}(\log(\hat{U}(FFT(x_i)))))) \quad (2.2)$$

where FFT denotes the Fast Fourier transform and FFT^{-1} its inverse, \hat{U} denotes a phase unwrapping function, \log denotes the complex logarithm and \Re denotes the real part. A FFT size of 1024 points was used. The click waveforms were not windowed prior to calculation to avoid degrading the second pulse detection and were zero padded to reduce aliasing in the cepstrum domain and phase unwrapping errors (Childers *et al.*, 1977).

Cepstrum averaging was performed by averaging the complex cepstra of all clicks in a series. The IPI estimate (IPI_{ceps1}) from averaged cepstra was estimated in the same way as for the individual clicks. This procedure differed from Teloni *et al.* (2008) only in the use of the complex cepstrum whereas Teloni *et al.* (2008) used power cepstrum. The complex cepstrum retains phase information and allows for recovery of the delayed pulse's waveform and it was used in order to

investigate if this would help in the discrimination of the IPI quefrency by identifying a typical wavelet shape.

2.2.5. Estimating uncertainty and consistency

It may be expected that the uncertainty of IPI measurements in a click series decreases as more clicks are included in the analysis. However, as a whale progressed in its foraging dive the uncertainty about its aspect relative to the hydrophones increases, and so the least uncertainty may be obtained from a number of clicks that balances these two factors. The uncertainty of the IPIs for each click series was evaluated by using a bootstrap procedure with 1000 iterations. Each bootstrap sample was constructed by resampling with replacement from each series of clicks assigned to a whale, and recalculating the IPI estimates for each sample. The coefficient of variation of the IPI estimates across the 1000 iterations was used as a measure of uncertainty. To investigate how the number of clicks used for IPI estimation influences the estimate variability, for each click series the bootstrap procedure was repeated for different numbers of clicks in incremental steps of 20 clicks. At each incremental step clicks were added in the same order in which they were produced. This was done for all of the aforementioned estimation methods, with the exception of manual measurement.

For each click series and for each method's bootstrap, two IPI estimates were produced. One estimate was produced as the mean IPI of all bootstrap iterations, obtained when all clicks were included in the bootstrap (*All*). Another estimate (*Min CV*) was produced as the mean IPI of all bootstrap iterations on the number of clicks included that gave the minimum coefficient of variation.

The consistency of each of the methods was investigated by comparing estimates produced for series of clicks from the same whale that had been recorded on at least two different occasions within the same year. Whales were identified by comparing photographs of their flukes (Arnbom, 1987). The range (maximum minus minimum values) of each individual whale's IPIs was used as a measure of consistency and was calculated for each of the automatic methods.

Assuming the manually measured IPIs to be the closest estimate to the '*true*' IPIs, for each click series I also calculated each automatic IPI estimate's absolute deviation from the mean manual IPI estimate, both for *All* and *Min CV* estimates.

All analyses were implemented as custom written Matlab programs.

2.3. Results

For this analysis 35 first-click recordings from seven individual whales recorded on more than one dive were used. Three of these whales were recorded from the Gulf of Mexico and four from around the Balearic Islands. Each whale was recorded on between 3 and 10 occasions. The mean number of clicks per series was 210 (range 50-382).

2.3.1. Manual measurements

In all but one click series there were clicks in which pulses could be discriminated sufficiently well for manual measurement. The percentage of manually measured clicks from each series varied between 1 and 81% (2 and 149 clicks). Manual measurements had coefficients of variation (CV) between <0.01 and 0.08, but only on three (9%) recordings for which manual measurements were made were these larger than 0.03.

2.3.2. Waveform averaging

In only 26% of the recordings was it possible to distinguish a main pulse followed by another of lesser amplitude in the average waveform (Table 2.1; *e.g.* Figure 2.2). In the cases where pulses were distinguished, other intermediate oscillations that were visible in the individual waveforms contributed less to the overall average waveform.

Measuring the average waveform reliably depended to a great extent on the alignment of individual waveforms. In some cases, where a series of clicks assigned to the same whale contained many in which the highest amplitude did not correspond to the main pulse, the alignment criterion failed to align them. Also, in cases where the main pulses were composed of several cycles, and the one with the highest amplitude was not consistent across clicks in a series, the alignment, and consequently the resulting average waveform, was affected.

The bootstrap CVs obtained for waveform averaging IPIs had ranged between <0.01 and 0.32 both for when all clicks were used and for *Min CV* estimates. In 45% of recordings, lower bootstrap CVs resulted when fewer than the total clicks in the series were used for estimation. In these cases the number of clicks whose bootstrap produced the lowest CV ranged between 20 and 320.

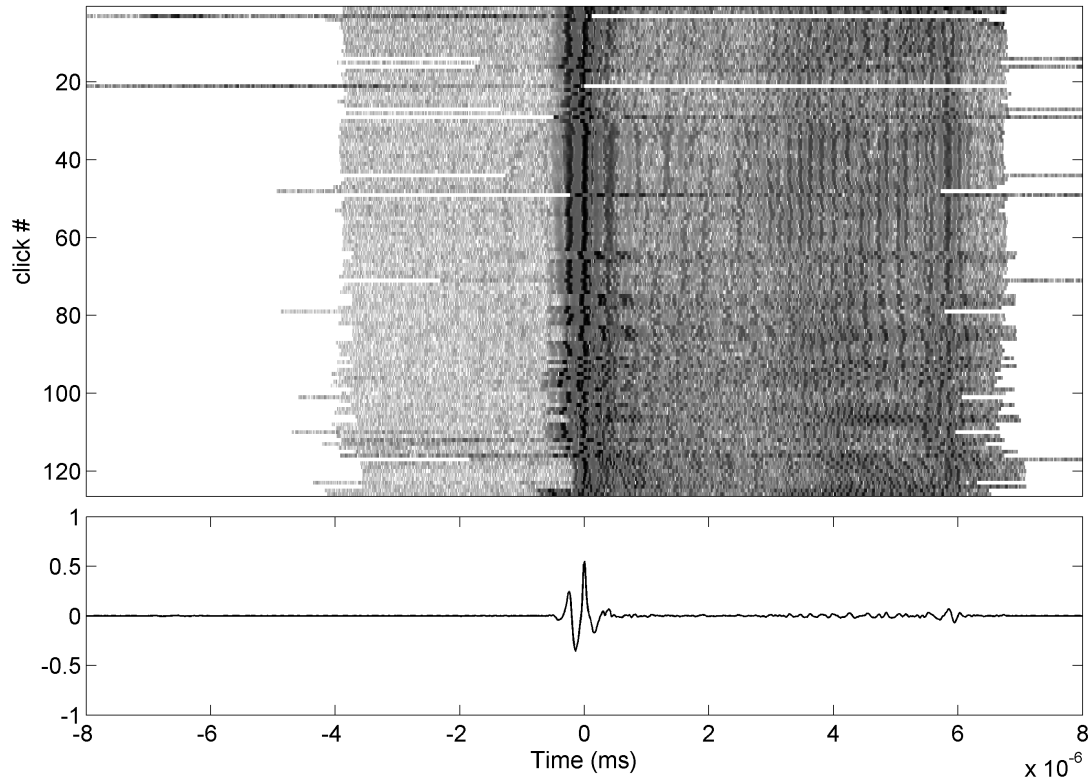


Figure 2.3. Example of waveform averaging for a single whale (#3003) recorded in the Balearics. The top panel represents the waveforms of 126 clicks, in the same order in which they were recorded on the ordinate scale and time in the abscissa. Grey scale represents the logarithm of the waveform envelope. Waveforms were time aligned by their envelope maxima. Bottom panel represents the average of the time aligned waveforms. The time scale origin is set to the average waveform maximum amplitude.

Table 2.1. Number of recordings in which peaks could be discriminated in the waveform, autocorrelation and cepstrum averaging plots. Last row values represent the number of recordings in which peaks could be discriminated for each one of the methods. Last column values represent the number of recording in which peaks could not be discriminated. Row and heading intersections represent the number of recordings in which one method showed a peak and the other did not. The total number of recordings was 35.

	Waveform peak absent	Autocorrelation peak absent	Cepstrum peak absent	
Waveform peak present	-	0	1	9
Autocorrelation peak present	19	-	5	29
Cepstrum peak present	15	0	-	23
	26	6	12	

2.3.3. IPI estimation using autocorrelation

It was possible to identify a peak value by averaging of autocorrelation function plots in which in 83% of the click series (Table 2.1; *e.g.* Figure 2.4). This peak usually coincided with the peak of some of the individual click's autocorrelation functions. Even in the cases where many individual clicks did not show a clear peak in their autocorrelation functions, the averaging of the whole series of clicks resulted in an averaged function that exhibited a clear peak. In the six recordings in which a clear peak was not identified in the average autocorrelation, the other averaging methods (waveform and cepstra) did not exhibit a clear peak either (Table 2.1).

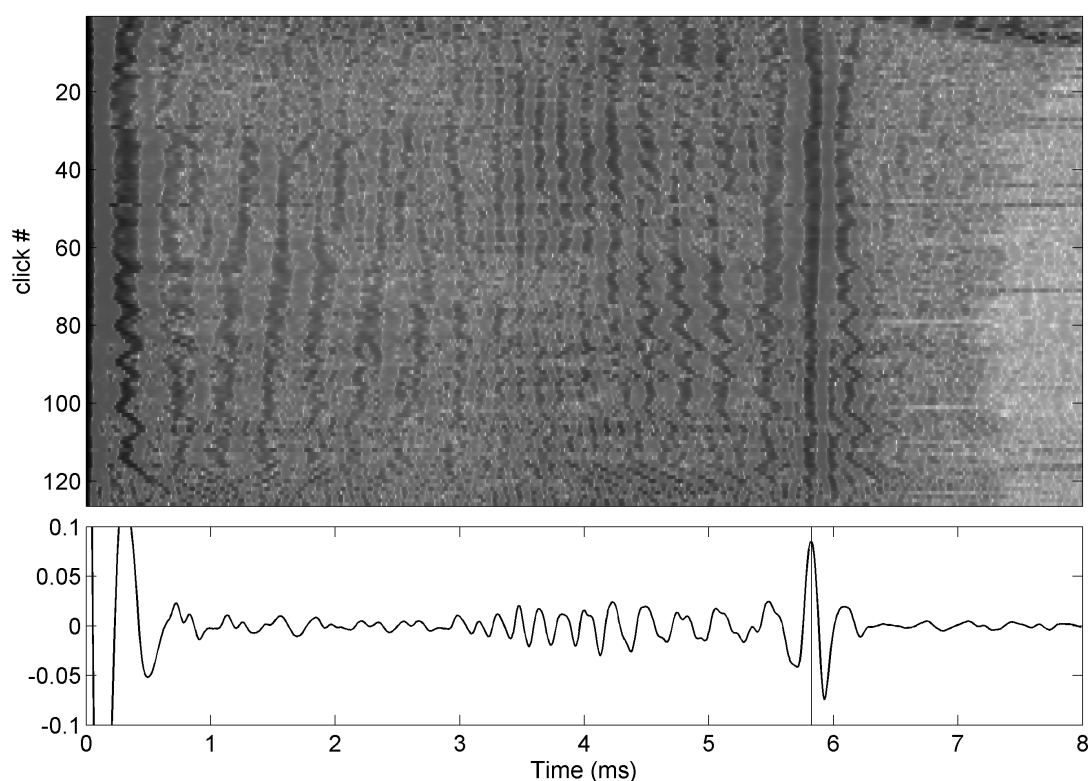


Figure 2.4. Example of autocorrelation averaging for a series of clicks from single whale (#3003) recorded in the Balearics. The top panel represents the positive lag autocorrelation function of 126 clicks, in the same order in which they were recorded on the ordinate scale and time in the abscissa. Grey scale represents the autocorrelation value. Bottom panel represents the averaged autocorrelation function across all clicks in the top panel. Vertical line shows the automatically measured IPI value.

The bootstrap CVs obtained for autocorrelation averaging IPIs ranged between <0.01 and 0.21. Only in six (17%) recordings for *All* clicks estimates, and in only three (9%) for *Min CV* were these values not 0.00. In four click series (11%) the averaging of less than total number of clicks produced a lower estimate. In these cases the number of clicks averaged ranged between 80 and 280.

2.3.4. IPI estimation using cepstra

The bootstrap CVs obtained from individual click cepstra IPIs ranged between <0.01 and 0.64. In 66% of recordings, lower bootstrap CVs (between 0.01 and 0.41) resulted when fewer than the total number clicks in the series were used for estimation. In these cases the number of clicks in which bootstrap produced the lowest CV ranged between 20 and 220.

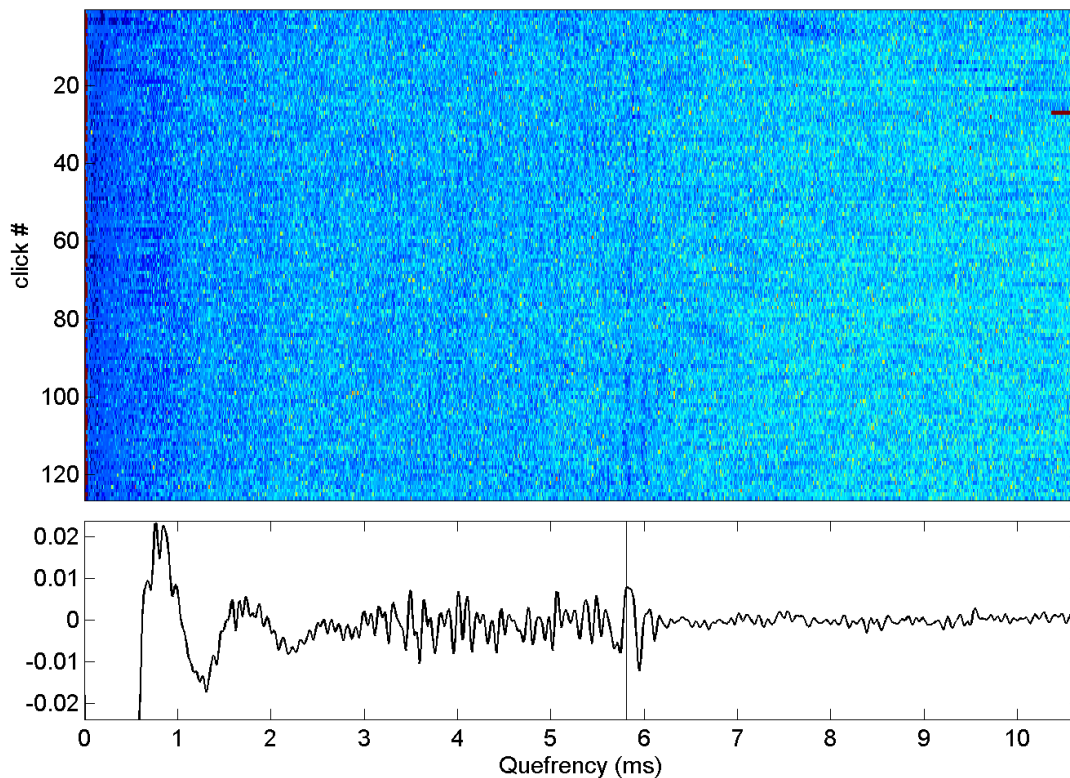


Figure 2.5. Example of cepstra averaging for a single whale (#3003) recorded in the Balearics. The top panel represents the cepstra of 126 clicks, in the same order in which they were recorded on the ordinate scale and time in the abscissa. Color scale represents the logarithm of the magnitude values. Vertical line shows the automatically measured IPI value.

In 66% of recordings the averaging of individual clicks' cepstra produced curves in which it was possible to visually identify a peak value (Table 2.1; *e.g.* Figure 2.5). In all cases where this peak could be distinguished, it was preceded by several oscillations of larger amplitude than the ones following it.

The bootstrap CVs for cepstra averaging ranged between <0.01 and 0.35. In 40% of recordings, lower bootstrap CVs resulted when fewer than the total number of clicks in the series was used for estimation. In these cases where the number of clicks in which bootstrap produced the lowest CV ranged between 20 and 260.

2.3.5. Uncertainty and consistency of IPI measurements

The bootstrapping procedure revealed that, in many cases, as more clicks from a series were included, the mean of IPI estimates remained constant whilst the 95% percentile range either decreased or remained stable (Figure 2.6, panels a,b,d and e). This was considered a convergence and it was observed in 69% of the bootstraps for autocorrelation on individual clicks, both when using autocorrelation maxima or the three highest peaks. In the case when three peaks were used, more clicks were required for convergence than when a single peak was used. Because of this, the three peak method was dropped from subsequent comparisons.

Waveform averaging and individual click cepstra methods only showed convergence in 7% of the recordings, whilst cepstral averaging converged on 58% of the recordings. Convergence occurred more frequently (81%) when using autocorrelation averaging than in any other method. When several estimation methods in a single recording converged, they always did so to a similar value (*e.g.* Figure 2.6).

The manual IPI estimates were consistent across recordings of the same whale made on different occasions (ranges between 0.00 and 0.21ms). From the automatic estimation methods, both individual click and averaging autocorrelation produced the most consistent values across recordings of the same whale (ranges between 0.02 and 2.04 ms, and between 0.01 and 1.91, respectively). The highest ranges of IPIs (between 0.97 and 3.26 ms) were obtained using cepstral estimation from individual clicks. Averaging cepstra from a click series tended to produce more consistent IPI estimates (within whale ranges between 0.02 and 1.92 ms) than estimation from individual click cepstra (within whale ranges between 0.91 and 2.31 ms).

For averaging methods, only those averages for which plots produced distinguishable peaks, autocorrelation provided the estimates closest to the manual measurements (Table 2.2). Only for individual #1018 was autocorrelation not the method that least deviated from the manual measurement (Table 2.2).

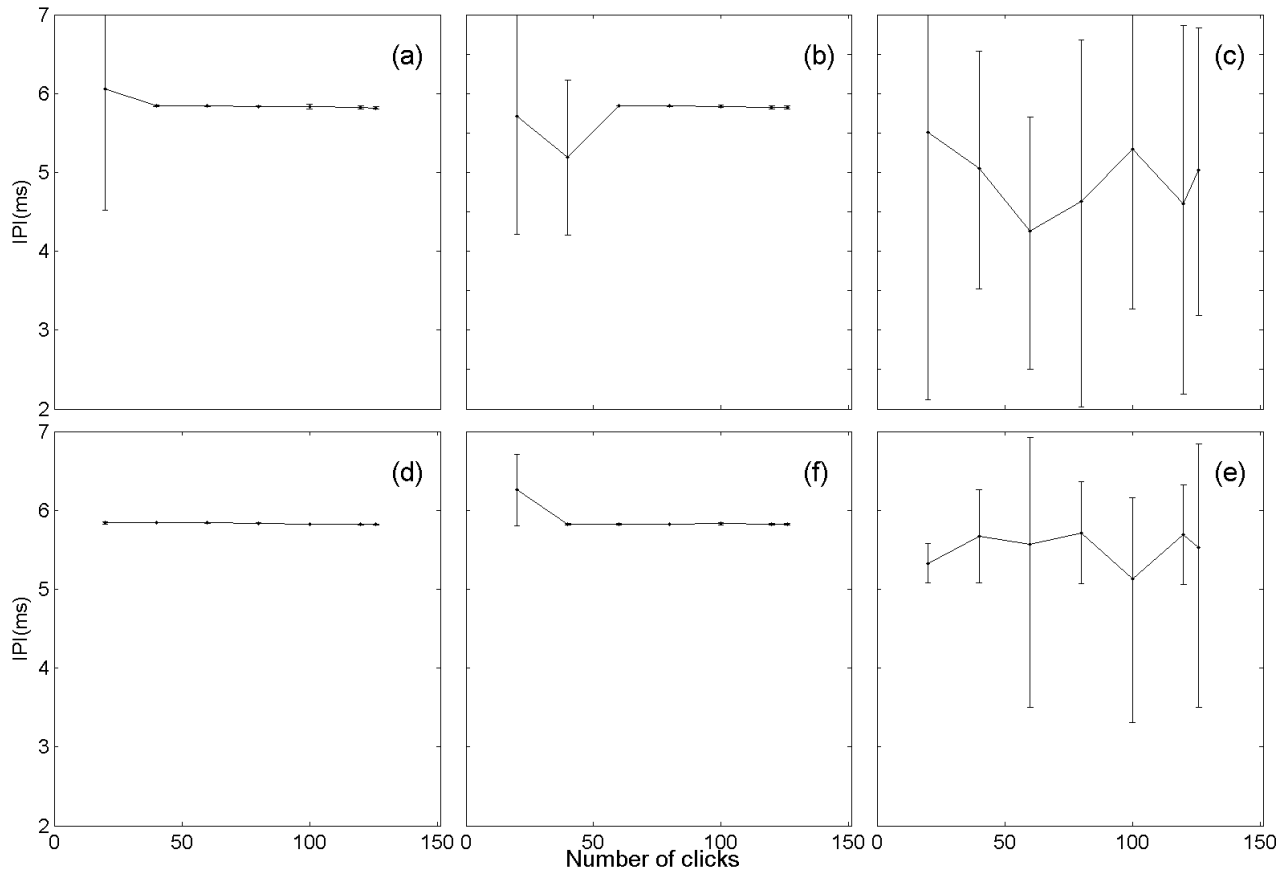


Figure 2.6. IPI estimates for the same click series represented in figures 2.3 to 2.5, obtained using several methods: a) individual click autocorrelation maxima; b) individual click autocorrelation - 3 peaks; c) individual click cepstra; d) average autocorrelation; e) average cepstrum; f) average waveform. Horizontal lines join the mean of 1000 estimates obtained by bootstrapping the first n clicks in a series, with n in the abscissa. Vertical lines represent the 95% percentile range.

Although the general trend was for *Min CV* IPIs to produce more consistent values than using *All* clicks in the series there were a few cases where this did not happen (*e.g.* IPI_{ceps} for #3001; Tables 2.3 and 2.4).

Table 2.2. IPIs measured using manual and automatic methods for three individual whales from the Gulf of Mexico.

ID	Total Number Of clicks	Manually measured clicks	Individual click autocorrelation			Individual click cepstrum			Waveform integration			Cepstrum integration			Autocorrelation integration			
			All	Min CV	clicks	All	Min CV	clicks	All	Min CV	clicks	All	Min CV	clicks	All	Min CV	clicks	
#1007	319	100	3.14(0.01)	2.57(0.18)	2.93(0.01)	300	3.13(0.64)	3.15(0.00)	40	2.34(0.13)	3.14(0.08)	40	3.06(0.11)	3.17(0.00)	260	3.13(0.00)*	3.13(0.00)	260
	156	67	3.16(0.00)	3.11(0.03)	3.11(0.03)	156	5.43(0.17)	5.26(0.10)	80	2.75(0.01)	2.75(0.01)	120	3.03(0.10)	3.17(0.00)	120	3.12(0.01)	2.96(0.00)	20
	250	74	3.15(0.00)	3.03(0.12)	3.03(0.12)	250	3.48(0.47)	2.84(0.34)	80	2.49(0.17)	2.04(0.01)	220	3.02(0.12)	3.17(0.00)	120	2.66(0.21)	3.15(0.00)	100
	57	23	3.22(0.06)	3.09(0.09)	3.21(0.08)	57	3.49(0.29)	3.49(0.29)	57	3.15(0.03)	3.15(0.03)	57	3.26(0.02)	3.28(0.00)	40	3.15(0.00)*	3.15(0.00)	57
#1016	52	34	2.97(0.00)	2.98(0.00)	2.98(0.00)	52	3.17(0.41)	3.17(0.41)	52	2.98(0.00)	2.98(0.00)	52	3.00(0.00)	3.00(0.00)	40	2.97(0.00)*	2.98(0.00)	40
	56	18	2.77(0.08)	2.86(0.02)	2.86(0.02)	56	2.74(0.14)	2.74(0.14)	56	2.71(0.07)	2.71(0.07)	56	2.78(0.08)	3.03(0.03)	20	2.83(0.00)	2.83(0.00)	20
	318	75	2.99(0.01)	2.65(0.13)	2.02(0.02)	120	2.04(0.02)	2.02(0.00)	120	2.49(0.09)	2.24(0.04)	60	2.14(0.14)	2.10(0.02)	100	2.76(0.06)	2.81(0.00)	280
	159	129	5.12(0.03)	5.13(0.00)	5.13(0.00)	159	4.18(0.16)	3.77(0.00)	100	5.13(0.00)*	5.13(0.00)	159	5.19(0.00)*	5.19(0.00)	159	5.15(0.00)*	5.17(0.00)	40
#1018	134	83	5.12(0.03)	5.15(0.00)	5.15(0.00)	134	5.01(0.09)	5.15(0.00)	100	4.52(0.12)	5.14(0.09)	60	5.19(0.00)*	5.19(0.00)	80	5.17(0.00)*	5.17(0.00)	60
	173	114	5.15(0.00)	5.15(0.00)	5.15(0.00)	173	5.15(0.00)	5.15(0.00)	160	5.14(0.00)	5.14(0.00)	173	5.21(0.00)*	5.21(0.00)	140	5.15(0.00)*	5.17(0.00)	60

Table 2.3. IPIs measured using manual and automatic methods for four individual whales from the Balearic Islands.

ID	Total number of clicks	Manually measured clicks	Individual click autocorrelation			Individual click cepstrum			Waveform integration			Cepstrum integration			Autocorrelation integration		
			All	Min CV	IPI (CV)	All	Min CV	IPI (CV)	All	Min CV	IPI (CV)	All	Min CV	IPI (CV)	All	Min CV	IPI (CV)
#3001	221	30	3.91 (0.02)	3.91 (0.02)	221	3.91 (0.33)	4.46 (0.10)	220	5.17 (0.16)	5.17 (0.16)	221	4.69 (0.10)	4.96 (0.00)	120	4.02 (0.05)	5.89 (0.00)	80
	140	47	5.76 (0.12)	5.76 (0.12)	140	3.39 (0.52)	3.48 (0.26)	20	4.75 (0.07)	4.75 (0.05)	100	4.77 (0.35)	4.20 (0.03)	80	5.93 (0.00)*	5.93 (0.00)	140
	160	51	5.94 (0.11)	4.12 (0.07)	60	4.55 (0.46)	2.35 (0.24)	100	5.79 (0.10)*	5.79 (0.10)	160	6.02 (0.02)	5.95 (0.00)	140	5.91 (0.00)*	5.91 (0.00)	160
	155	0	4.05 (0.03)	4.15 (0.03)	120	3.58 (0.31)	3.56 (0.23)	20	4.24 (0.12)	4.24 (0.12)	155	4.10 (0.18)	4.65 (0.16)	120	4.10 (0.03)	4.10 (0.03)	155
#3002	61	10	4.44 (0.32)	5.17 (0.09)	60	3.88 (0.45)	2.72 (0.40)	20	3.18 (0.32)	3.18 (0.32)	61	5.49 (0.21)*	5.49 (0.21)	61	5.57 (0.02)*	5.67 (0.02)	40
	50	8	5.59 (0.00)	5.59 (0.00)	50	5.44 (0.07)	5.44 (0.07)	50	2.61 (0.03)	2.61 (0.03)	50	5.64 (0.00)*	5.64 (0.00)	50	5.60 (0.00)*	5.60 (0.00)	50
	309	149	5.57 (0.00)	5.57 (0.00)	309	5.60 (0.02)	5.57 (0.02)	200	4.71 (0.15)	2.85 (0.14)	20	5.60 (0.00)*	5.61 (0.00)	120	5.56 (0.00)*	5.58 (0.00)	80
	264	17	5.56 (0.03)	4.96 (0.23)	180	5.61 (0.22)	5.47 (0.02)	180	4.97 (0.09)	5.29 (0.02)	260	5.55 (0.00)*	5.55 (0.00)	260	5.53 (0.00)*	5.53 (0.00)	40
#3003	361	18	5.50 (0.02)	5.50 (0.00)	361	2.35 (0.47)	2.05 (0.06)	180	5.01 (0.09)*	5.31 (0.02)	320	5.57 (0.00)*	5.57 (0.00)	361	5.51 (0.00)*	5.52 (0.00)	160
	113	46	5.83 (0.00)	5.83 (0.00)	113	5.83 (0.00)	5.83 (0.00)	60	5.15 (0.10)*	5.86 (0.07)	80	5.87 (0.00)*	5.86 (0.00)	60	5.83 (0.00)*	5.83 (0.00)	80
	330	56	5.83 (0.00)	5.83 (0.00)	330	5.63 (0.10)	5.84 (0.00)	100	5.11 (0.06)	5.82 (0.05)	120	5.17 (0.17)*	5.92 (0.00)	120	5.80 (0.00)*	5.83 (0.00)	100
	125	31	5.83 (0.01)	5.81 (0.00)	125	5.78 (0.00)	5.78 (0.00)	125	5.65 (0.06)	5.80 (0.05)	120	5.65 (0.07)*	5.80 (0.01)	100	5.80 (0.00)*	5.80 (0.00)	120
#3004	218	39	5.81 (0.00)	5.81 (0.00)	218	4.98 (0.18)	5.24 (0.13)	140	5.35 (0.13)	5.35 (0.13)	218	5.86 (0.00)*	6.08 (0.00)	20	5.80 (0.00)*	5.83 (0.00)	60
	180	21	5.81 (0.00)	5.81 (0.00)	180	5.47 (0.19)	5.83 (0.02)	100	5.71 (0.07)	5.55 (0.06)	100	5.85 (0.00)*	5.85 (0.00)	180	5.80 (0.00)*	5.80 (0.00)	180
	382	51	5.83 (0.01)	5.82 (0.00)	382	5.72 (0.01)	5.82 (0.00)	120	4.78 (0.08)	4.72 (0.02)	260	5.82 (0.01)*	5.86 (0.00)	100	5.84 (0.00)*	5.83 (0.00)	300
	286	22	5.81 (0.00)	5.80 (0.00)	286	5.78 (0.00)	5.78 (0.00)	260	5.54 (0.13)	5.81 (0.06)	100	5.84 (0.00)*	5.84 (0.00)	280	5.79 (0.00)*	5.81 (0.00)	120
#3005	207	70	5.81 (0.01)	5.80 (0.00)	207	5.80 (0.00)	5.79 (0.00)	160	5.78 (0.03)	5.78 (0.03)	207	5.84 (0.00)*	5.83 (0.00)	160	5.81 (0.00)*	5.83 (0.00)	80
	126	58	5.83 (0.00)	5.83 (0.00)	126	4.92 (0.20)	4.92 (0.20)	126	5.83 (0.00)*	5.83 (0.00)	126	5.13 (0.22)*	5.80 (0.04)	60	5.82 (0.00)*	5.84 (0.00)	60
	57	21	5.84 (0.00)	5.84 (0.00)	57	4.97 (0.22)	5.06 (0.16)	40	5.73 (0.07)*	5.73 (0.07)	57	4.56 (0.11)	5.41 (0.06)	20	5.85 (0.00)*	5.85 (0.00)	57
	367	27	5.70 (0.01)	5.73 (0.00)	367	5.72 (0.01)	5.28 (0.00)	40	5.73 (0.00)*	5.73 (0.00)	367	5.79 (0.00)*	5.79 (0.00)	300	5.75 (0.00)*	5.75 (0.00)	240
#3006	216	54	5.77 (0.00)	5.76 (0.00)	216	3.88 (0.38)	2.75 (0.28)	100	5.73 (0.02)	5.73 (0.02)	216	5.80 (0.00)*	5.80 (0.00)	200	5.77 (0.00)*	5.77 (0.00)	180
	304	22	5.80 (0.01)	5.74 (0.00)	304	4.12 (0.39)	2.16 (0.04)	140	5.13 (0.16)	4.60 (0.03)	160	5.79 (0.00)*	5.79 (0.00)	300	5.75 (0.00)*	5.75 (0.00)	304
	224	92	5.78 (0.01)	5.77 (0.00)	224	5.19 (0.25)	5.78 (0.00)	200	5.77 (0.00)*	5.77 (0.00)	224	5.84 (0.00)*	5.84 (0.00)	140	5.78 (0.00)*	5.79 (0.00)	120
	244	64	5.76 (0.01)	5.75 (0.00)	244	3.21 (0.49)	3.64 (0.31)	140	4.54 (0.20)*	4.43 (0.11)	40	5.80 (0.00)*	5.80 (0.00)	244	5.76 (0.00)*	5.76 (0.00)	240
381	35		5.64 (0.05)	5.78 (0.04)	140	5.72 (0.00)	5.71 (0.00)	340	5.76 (0.01)	5.76 (0.01)	381	5.76 (0.00)*	5.82 (0.00)	200	5.73 (0.00)*	5.76 (0.00)	260

* Peak present

Table 2.4. Absolute deviations of IPIs measured using averaging methods from the manually measured IPIs using data only for the average curves in which a peak was discriminated. The mean values are shown for each individual's click series and for all individuals. The number of click series in which a peak could be discriminated is shown in parenthesis. Values in boldface represent the minimum value of each row. All deviation values in milliseconds.

ID	Autocorrelation integration		Cesptrum integration		Waveform integration	
	Min CV	All	Min CV	All	Min CV	All
#1007	0.04 (2)	0.04 (2)	-	-	-	-
#1016	0.01 (1)	0.00 (1)	-	-	-	-
#1018	0.04 (3)	0.03 (3)	0.07 (3)	0.07 (3)	0.01 (1)	0.01 (1)
#3001	0.18 (2)	0.18 (2)	-	-	0.30 (1)	0.30 (1)
#3002	0.03 (5)	0.02 (5)	0.06 (5)	0.06 (5)	0.19 (1)	0.49 (1)
#3003	0.01(10)	0.01 (10)	0.06 (9)	0.19 (9)	0.05 (3)	0.26 (3)
#3004	0.03 (6)	0.02 (6)	0.06 (6)	0.05 (6)	0.03 (3)	0.03 (3)
All	0.03 (29)	0.03 (29)	0.06 (23)	0.11 (23)	0.08 (9)	0.19 (9)

2.4. Discussion

Manual IPI measurement provided the most consistent IPI estimates for the same whale on different occasions, indicating that it remains an= useful, if labour intensive, method. Methods that averaged autocorrelation and cepstra values across clicks in a sequence provided more consistent results than those that relied on taking the mean of values from individual clicks. Averaging of autocorrelation data seemed to require fewer clicks than averaging of cepstra to converge on an IPI estimate (*e.g.* Figure 2.6), as well as producing more consistent estimates. This method may therefore be preferable for IPI estimation, although there were a few cases where cepstral averaging converged whilst autocorrelation did not. Apart from applications where IPI is required to be estimated in real-time and the added processing power is a limitation, running both methods simultaneously and comparing results may prove useful to cover situations in which one of the techniques outperforms the other. Amongst the averaging methods, waveform averaging produced the least consistent estimates. The main difficulty in using waveform averaging is the alignment of clicks' waveforms as this is sensitive to the presence of pulses other than p_0 and p_1 (*e.g.* $p_{1/2}$ pulses, or surface reflections), and variation in the relative amplitude of the different cycles in the main pulse between clicks. Cepstral and autocorrelation averaging do not suffer from the problem of alignment as both have a defined reference (zero time-lag in the case of autocorrelation averaging, and zero quefrency in the case of cepstral averaging).

Manual IPI measurement depends on the choice of suitable pulses to be measured and therefore is heavily dependent on the operator's experience. The judgement of the operator measuring each click is unlikely to be independent between clicks when several from the same series are analysed at the same time. In cases where the selection of pulses for measurement is problematic (*e.g.* when $p_{1/2}$ pulses occur) the operator will likely rely on prior information from other clicks to decide how to measure IPI. An important additional disadvantage of manual IPI measurement is that it is time consuming. The automatic estimation methods overcome both these limitations, allowing for a great number of recordings to be analysed in less time and in a more systematic way.

Teloni *et al.* (2008) investigated the use of cepstral averaging to estimate IPIs from clicks recorded from whales of unknown aspect. Their average cepstrum plot showed a plateau that corresponded to aspect-dependent pulses at quefrequencies below the IPI peak. This plateau was not observed in the present study because the complex cepstrum that retains phase information was used here, while Teloni *et al.* (2008) used the power cepstrum (Equation 1 in Teloni *et al.*, 2008). However, the higher oscillations observed before the peak gamnitude in the present study correspond to this plateau. Teloni *et al.* (2008) also noted that only after averaging between 200 to 1000 clicks, did a peak appear in the average cepstrum that could be discriminated. For some of the cases in the present study a peak was obtained with fewer clicks (*e.g.* after 40 clicks in the case of the recording shown in Figures 2.5 and 2.6). This is not interpreted as being due to differences resulting from use of different forms of cepstral analysis, but rather due to differences in recording aspect between both studies. In the present study the clicks were recorded from directly behind the whale and it is therefore likely that relatively more clicks without intermediate pulses were recorded, compared with Teloni *et al.* (2008) whose recordings would have covered a wider range of aspects. As pointed out by Teloni *et al.* (2008) in cases when it is not possible to record in the whales anteroposterior axis, more clicks will be required to ensure a wide coverage of a range of whale aspects.

The consistency of IPI estimation methods was evaluated here using a comparison between recordings of the same individually identified whale on different occasions. This approach does not directly address the question of accuracy of IPI as a method for assessing animal body length because the actual size of the animal was not known. However the consistency of IPI measures is key towards this goal.

Due to the conditions in which the recordings were made it is likely that the true IPI was captured, and its closest estimate is the manually measured IPI. Zimmer *et al.* (2005b) pointed out that sperm whale body length can only be estimated correctly when clicks are recorded close to the body axis. The recordings used in the present study were made in or close to the surface location from where the whale dived, and sperm whales normally dive vertically during the initial part of the dives (Watwood *et al.*, 2006). Thus the recording hydrophones were likely to have been directly behind the focal animal during at least the early part of the recordings.

None of the techniques here compared can extract IPI information from poor quality recordings, although methods that involve averaging should help in this respect. Good signal to noise ratio recordings greatly enhance reliable IPI estimation. Good signal to noise ratio recordings can be made by recording from as close as possible to a whale without disturbing it. In this study using small boats for this purpose proved useful. If possible it is also recommended that the boats' machinery is turned off to avoid contamination of recordings. The use of signal filters for attenuation of low frequency noise is also useful in increasing signal to noise ratio. If the recording hydrophone is placed at a shallow depth, surface reflected clicks may overlap with direct path clicks making the discrimination between pulses difficult, as reported for some cases in Teloni *et al.*, (2008). It is recommended that the recording hydrophone is placed as deeply as possible to avoid this effect. It may also be advantageous to vary the depth of the hydrophone during recording to avoid recording surface reflections with a constant delay. This may have been partially achieved in the recordings used in this study by the gradual sinking of the towed hydrophone array while recording first clicks.

The measures of dispersion obtained from the bootstrap provide a measure of the confidence of the IPI estimates, and this procedure is thus recommended. High dispersion of bootstrap IPI estimates may indicate a weak or absent multi-pulsed structure in the recorded click waveforms. The aforementioned bootstrap procedure where different numbers of clicks are averaged, is also useful in identifying the number of clicks that need to be averaged to produce the IPI estimate with the highest confidence.

Associating whale identification with IPI measurements also allows for individual vocal repertoire to be studied provided the individuals being investigated have distinguishable IPIs. This method was used by Schulz (2007) and is applied in Chapter 3.

In conclusion I have developed and tested two new methods of automatic IPI measurement and compared their accuracy and consistency with other previously used methods. Manual measurement by an experienced operator provided the most self-consistent estimates. The autocorrelation averaging technique had the best overall performance of the automated methods achieving a very similar performance to manual measurement. On some recordings cepstrum averaging methods converged when autocorrelation did not, so running both of these automated methods and choosing the best of the two is recommended.

CHAPTER 3

Individual discrimination in sperm whale codas

3.1. Introduction

3.1.1. Individual recognition

Living in groups provides a number of situations where members can gain advantages by coordinating activities and maintaining cohesion. This may require the exchange of information through some form of communication. In long term social groups, animals may develop behavioural strategies that are based on individualized relationships among members such as dominance hierarchies and roles within groups (Wilson, 2000). In these cases there might be a selective pressure for the development of identity signals and mechanisms that allow discrimination and recognition of particular individual and/or group members, from non-target individuals or groups. In fact, some studies suggest that individual recognition is an important factor in the structure of group hierarchies (Dugatkin & Earley, 2004). Long term associations among animals also provide the prior experience of particular individuals required for the development of individual-level signal recognition, based on learned familiarization (Bradbury & Vehrencamp 1998; Tibbetts & Dale, 2007).

The ability to discriminate among group members can also be advantageous when behavioural responses to signals have different consequences depending on the signaller. For example receivers can optimize the costs of responding to alarm calls given, by varying responses depending on their reliability and spatial relationship of the signaller(s) (Robinson, 1981; Ydenberg & Dill, 1986, Cheney & Seyfarth, 1988, Bachman, 1993, Kildaw, 1995). Animals can also keep track of hierarchical relationships within groups by eavesdropping on signals from interactions of

other individuals (Bergman *et al.*, 2003).

Individual discrimination is possible when individual signal parameters have unique attributes, or when the signal parameters' variability is greater among than within individuals (Beecher, 1982; 1989). For example white-winged vampire bats (*Diaemus youngi*) show individual variation in the structure of social calls, that can be discriminated by the animals (Carter *et al.*, 2008).

3.1.2. Sperm whale vocalizations

The sperm whale (*Physeter macrocephalus*) is a social cetacean species. This is particularly the case for females, calves and immature animals of both sexes who live in long term social units of 12 animals on average (Christal *et al.*, 1998). These generally matrilinear units are distributed throughout subtropical and tropical waters (Rice, 1989) and their composition is largely stable over decades (Whitehead & Weilgart, 2000), albeit with occasional movements among units (Christal *et al.*, 1998). In the Pacific Ocean these units frequently form groups with one or two other units that persist for days (Whitehead & Weilgart, 2000). Sperm whale groups often move in a coordinated fashion, spreading themselves beyond visibility range over hundreds or thousands of meters of ocean (Whitehead, 2003).

Some authors have suggested that post-menopausal females might play a special role within social units by assisting with the care of calves and acting as repositories of information that are advantageous (Gero, 2005; McAuliffe & Whitehead, 2005). Individuals within social units have preferred associates among members (Gero *et al.*, 2008). These observations suggest that individuals might interact differently among unit members. Differential interaction among unit members primes the need for an individual discrimination system.

Sperm whales rely mostly on the emission of pulsed sounds for communication, orientation and finding prey (Jaquet *et al.*, 2001; Whitehead, 2003; Johnson & Tyack, 2003; Madsen *et al.*, 2002a; 2002b; Miller *et al.*, 2004a; 2004b). These clicks are characterized by having a series of usually evenly spaced pulses of decaying amplitude (Backus & Schevill, 1966) whose inter-pulse interval (IPI) has been shown to be correlated with the whales' size (Gordon, 1991; Rhinelander & Dawson, 2004). Series of clicks are produced during foraging dives at rates of 1-2 clicks per second.

Occasionally sperm whales produce stereotyped series of 4 to 40 clicks termed codas which

are assumed to have a communicative function (Watkins & Schevill, 1977; Whitehead & Weilgart, 1991; Schulz, 2007; Schulz *et al.*, 2008). Sperm whale groups in the South Pacific Ocean have distinct coda dialects which are stable for periods of at least six years (Weilgart & Whitehead, 1997; Rendell & Whitehead, 2005a). Whitehead *et al.* (1998) found that in the Pacific coda dialect variation was correlated with mtDNA variation. This was interpreted as an indication of parallel vertical transmission of both mitochondrial haplotypes and vocal repertoires within the mostly matrilinear units. Rendell & Whitehead (2003b) also found that sperm whale units and groups in the Pacific Ocean could be aggregated into vocal clans based on their coda repertoires. Because vocal clans were often sympatric and shared most nuclear DNA haplotypes they suggested that vocal clans are the result of culturally transmitted behaviour.

The function initially proposed for codas was one of individual signatures (Watkins & Schevill, 1977; Watkins *et al.*, 1985). Later studies which classified codas into distinct types showed evidence of coda type sharing among individuals, challenging the initial hypothesis (Whitehead & Weilgart, 1991; Rendell & Whitehead, 2004). Schulz (2007) found that most adult animals within a social unit shared the most common coda type, with the exception of the mother-calf pair whose repertoires were different from those of other unit members. Apart from the mother-calf differences, the repertoire similarities of other members did not support the idea of individually distinctiveness coda type repertoires, as most individuals share most common coda types, and produced them at similar rates. This sharing of coda repertoires suggests the function of coda repertoires to be group membership recognition, either at the unit or clan levels. This idea is further supported by the fact that social units seem preferentially to form groups with other units of their own clan (Whitehead, 2003).

Codas are not perfectly stereotyped however. Within particular coda types which might be identified statistically there is often considerable variation and it is possible that some of this variability is specific to individuals. Thus, individuals within groups might be recognisable by the way they make particular coda types rather than by the range of coda types they produce. With this in mind I hypothesise that despite similarities in coda types, variations within these could potentially carry information on animals' identity and therefore codas could have both group and individual level information. Here I test the hypothesis that variation within coda types allows statistical discrimination of individual social unit members, potentially allowing for individual identity to be communicated between members in a social unit.

3.2. Methods

3.2.1. Field methods

The study uses the same dataset used and collected by Schulz (2007) consisting of recordings of codas from a single social unit collected on the lee coast of the island of Dominica. This unit termed the “*Group of Seven*” consisted of five adult females (Identification codes #5130, #5563, #5722, #5561, #5560), one juvenile male (#5727), and one male calf (#5703), forming a social unit (see Gero, 2005). This unit was followed for a total of 41 days from January 16 to March 26, 2005. The whales were tracked visually and acoustically using a directional hydrophone (Whitehead & Gordon, 1986). During daylight hours the animals were approached while on the surface, usually between foraging dives, and digital photographs of their flukes were taken for individual identification purposes (Arnbom, 1987) using a Canon D10 digital SLR camera and a Canon EF 300mm lens.

Fifteen coda recordings of this unit were made using a towed hydrophone array (consisting of 2x Benthos AQ-4 elements coupled to Magrec 30dB preamplifiers located 3 metres apart in a oil filled tube, towed on 100m of cable). Recordings were made using a Foxtex VF-160 multi-track recorder sampling at 48kHz. Coda recordings were made opportunistically, usually when there were whales visible at the surface. Additionally recordings of regular clicks were made whenever solitary individuals fluked at the beginning of a foraging dive.

The recordings were analysed by Tyler Schulz using Rainbow Click, an automatic click detection program (Gillespie, 1997) which was used to mark the clicks belonging to the same coda, as well as the series of regular clicks from solitary whales. Typically a series of regular clicks from a diving whale could be distinguished when it first started vocalizing. These could be recognized, tracked and labelled through the early part of the recording based on their loudness, relative bearing and spectral characteristics.

3.2.2. Assignment of codas to individuals and types

The waveforms of the selected clicks were exported and analysed using a custom written Matlab (Mathworks Inc., Natick MA, USA) program used to estimate the IPI modal class of each coda, and each regular click series (Schultz, 2007). The clicks of each of the “*Group of Seven*”

whales had sufficiently distinct IPI among themselves to allow for individual discrimination based on it. Codas were assigned to individuals based on the clicks' IPIs by Tyler Schulz as described in Schulz (2007). I classified codas having between 4 and 10 clicks into types based on the number and temporal patterns of their clicks using k-means classification of inter-click intervals vectors (ICIs) standardized by coda duration, as described in Rendell & Whitehead (2003a; 2003b), using a custom written computer program in Matlab. The coda types obtained were named following the nomenclature used by Weilgart & Whitehead (1993).

3.2.3. Individual discrimination

The coda types represented by the arbitrary quantity of at least five codas from each individual, were selected for subsequent analysis. Individual discrimination was tested by calculating linear discriminant functions using four sets of variables: standardized ICIs (RelICI), absolute ICIs (AbsICI), the envelope amplitude of each coda click relative to the loudest in the codas (Amp), and a combination of the latter two (AbsICI+Amp). RelICI was calculated by standardizing the AbsICI values by their sum i.e., the total duration of the coda. Because the sum of RelICI equals unity, one of the values is redundant, and so for this dataset the last standardised ICI was not included in the analysis. The peak amplitude was calculated as the ratio between the maximum value of the waveform envelope of each click in a coda, and the maximum of those values, therefore taking values between 0 and 1.

To test if individuals could be discriminated by their codas I performed a linear discriminant analysis for each coda type. For each discriminant analysis the classification error rates were calculated as the proportion of incorrect classifications across all individuals. I also calculated the incorrect classification rate for each individual being compared. For each comparison, a random classification was performed by sampling from the initial set of individuals being compared and randomly assigning test codas to individuals, thus keeping the proportion of codas for each individual. The proportion of codas incorrectly classified in this way was taken as the random assignment error rate. The random assignment procedure described above was repeated 10,000 times for each comparison. The proportion of random assignment iterations whose error rates were lower than the discriminant function error, is a measure of the probability that the calculated classification error rate could have been obtained by chance. The discriminant analysis and error rate calculations were performed using custom written Matlab code which used the “Discriminant Analysis Toolbox” by Michael Kieft (1999) after the methods in Ripley (1996).

3.2.3. Partial Mantel tests

Because differences observed among individuals could have also been due to differences in the whales' vocal output among days, I evaluated the combined effects of day of recording and individual using a partial Mantel test (Smouse *et al.*, 1986). This was performed for each coda type. The test was performed using a matrix of pairwise coda similarities (Rendell & Whitehead, 2003a; basal similarity = 0.001, Euclidean norm) as a response matrix. Two binary pairwise matrices of the same size as the response matrix were used as explanatory variables. The first matrix was built with elements equal to unity for the cases when the pairs of codas were from the *same individual*, and zero otherwise. A second matrix was similarly built with unity for pairs of codas recorded on the *same day*. The partial correlation between the response matrix and '*same individual*' taking '*same day*' into account was then calculated. The obtained value was compared to a distribution of the same parameter calculated by randomizing the binary matrices, for 1,000 iterations.

3.3. Results

3.3.1. The *Group of Seven* coda repertoire

The analysis of the coda recordings from the “*Group of Seven*” resulted in a total of 315 codas, assigned to 15 types using k-means clustering (Table 3.1). From these only coda types 1+3 (16% of the total group repertoire) with four clicks, and 1+1+3 (33%) and 5Reg (26%) with five clicks (Figure 3.1) had at least two individuals represented by at least five codas and could therefore be used for discriminant analysis (Table 3.1).

The calf (individual #5703) was left out of the analysis altogether either due to its low representation for some coda types, or because it was the only whale to make a certain coda type.

Most of the individual whale repertoires used for discriminant analysis included codas recorded on at least two different days for each coda type, with the exception of individual #5727 with only one recording day for both coda types represented, and individual #5563 for coda type 1+1+3 (Table. 3.2).

Table 3.1. Coda type repertoire of the *Group of Seven* social unit, classified using k-means clustering. Column headings indicate whale identification numbers and row heading indicate coda type. Numbers in the classification table correspond to frequency with which individual produced each coda type. Bold frequencies correspond to the the codas used in the analysis.

	#5130	#5560	#5561	#5563	#5703	#5722	#5727	Σ
4R	2	3	3	0	1	1	0	10
1+3	11	0	3	1	0	34	0	49
2+1+1+1	0	3	0	6	4	0	0	13
1+1+3	21	36	22	18	0	0	7	104
5R	0	38	33	4	0	0	8	83
5+1	0	0	0	0	12	0	0	12
6R	1	0	0	0	1	1	1	4
7R	1	6	0	0	0	0	0	7
6+1	0	0	0	1	5	0	0	6
6+1+1	0	1	0	0	1	0	0	2
1+1+6	0	3	1	0	0	0	0	4
8R	0	6	0	1	1	0	0	8
1+1+7	0	1	0	0	0	0	0	1
9R	0	5	0	1	3	0	0	9
9+1	0	1	0	0	2	0	0	3
Σ	36	103	62	32	30	36	16	315

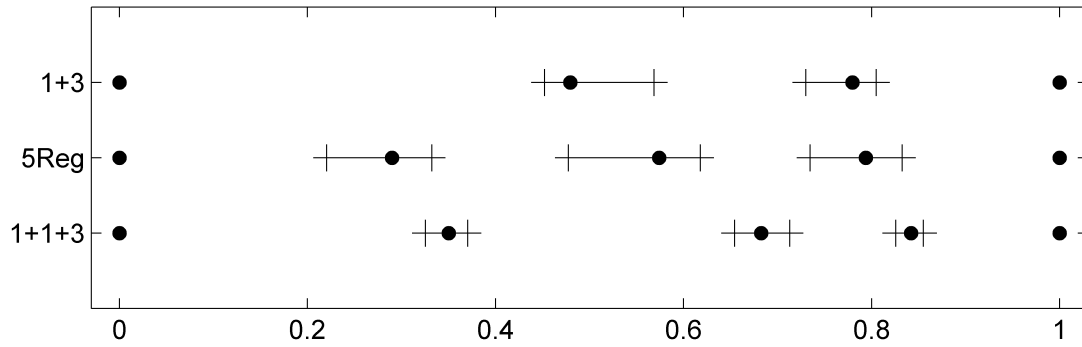


Figure 3.1. Relative time patterns for the three coda types used in discriminant analysis. Error bars represent 95 % percentiles across all codas for all individuals.

3.3.2. Discriminant analysis

For all but one of the coda types and variable sets included in the analysis, all discriminant function analyses resulted in a number of canonical discriminant functions equal to the number of individual whales being compared. This permits the discrimination among all individuals being

compared. In the case of the variable set RelICIs for coda type 1+1+3, it was only possible to calculate three canonical discriminant functions, the same as the number of variables in the analysis.

Only two individuals (#5130 and #5722) were represented with more than five codas of type 1+3 therefore only allowing for discrimination between them (Table. 3.1). The classification error rates for this coda type were always lower than the random classification error for variable sets Amplitudes and AbsICIs+Amplitudes indicating that the classification of codas to individual whales performed better than random assignment of codas to individuals (Table 3.3). Variable sets AbsICIs and RelICIs presented error rates with a higher probability of being obtained by random classification, but still fairly low. The observed classification error rates were lowest for variable set AbsoluteICIs+Amplitudes. In all variable sets the individual error rates were always higher for individual #5722 than individual #5130.

The distribution of canonical discriminant values for individual #5130 completely overlapped those for #5722 in all datasets (Figure 3.2).

Coda type 1+1+3 was represented with enough codas per individual to allow discriminant analysis for five adult whales (#5130, #5560, #5561, #5563 and #5727).

Mean classification error rate values were lowest for variable set AbsICI+Amp, while individual error rates were either lowest or similar to AbsICI (Table 3.3).

Table 3.2. Distribution of codas assigned to individuals by date of recording in 2005. First column indicates coda type classified using k-means and second column correspond to individual whale identification codes. Column headings corresponds to recording dates.

		23 th Jan	26 th Jan	1 st Feb	2 nd Feb	3 rd Feb	7 th Feb	15 th Feb	17 th Feb	27 th Feb	2 nd Mar	9 th Mar
1+3	#5130	-	-	3	-	-	7	1	-	-	-	-
	#5722	-	-	2	-	-	-	7	-	7	-	18
1+1+3	#5130	-	-	16	5	-	-	-	-	-	-	-
	#5560	8	-	17	-	9	-	-	-	-	-	-
	#5561	9	-	-	2	11	-	-	-	-	-	-
	#5563	18	-	-	-	-	-	-	-	-	-	-
	#5727	6	-	-	-	1	-	-	-	-	-	-
5Reg	#5560	10	-	1	-	7	-	-	8	-	4	-
	#5561	12	-	-	-	8	-	-	7	-	-	6
	#5727	-	8	-	-	-	-	-	-	-	-	-

With the exception of two variable set and coda type combinations (AbsICI, 1+3: $p=0.014$; RelICI, 1+3: $p=0.034$), discriminations for all datasets exhibited low probabilities of having been obtained by random assignment (0.001 or less). However, canonical discriminant function values for all individuals exhibited considerable overlap, and a clear separation pattern was not found for any variable set (Figure 3.3). This indicates that separation of individuals using linear discriminants is not possible.

Only individuals #5160, #5561 and #5727 were represented with more than five codas of type 5Reg. Mean classification error rates for each variable set in type 5Reg were lower in variable set AbsICI+Ampl. Individual error rates for this dataset were either the lowest of all datasets or similar to AbsICI (Table 3.3).

Table 3.3. Overall and individual whale classification error rates for coda types 1+3, 1+1+3 and 5Reg, and for variable sets Absolute ICIs, Relative ICIs, Amplitude and Absolute ICIs + Amplitude. Individual specific error rates are in the same order as in line labels. Last column contains the probability of obtaining a better classification error rate than by random assignment of identification to individuals.

AbsICI		mean error		ID error				p
1+3	5130+5722	0.22	0.46	0.15				0.014
1+1+3	5130+5560+5561+5563+5727	0.58	0.62	0.42	0.50	0.89	0.71	<0.001
5Reg	5560+5561+5727	0.13	0.11	0.06	0.50			<0.001
RelICI		mean error		ID error				p
1+3	5130+5722	0.24	0.64	0.12				0.034
1+1+3	5130+5560+5561+5563+5727	0.58	0.62	0.36	0.46	0.94	1.00	<0.001
5Reg	5560+5561+5727	0.25	0.21	0.12	1.00			<0.001
Ampl		mean error		ID error				p
1+3	5130+5722	0.16	0.46	0.06				<0.001
1+1+3	5130+5560+5561+5563+5727	0.63	0.95	0.19	0.68	0.94	0.86	0.001
5Reg	5560+5561+5727	0.39	0.16	0.52	1.00			<0.001
Abs ICI + Ampl		mean error		ID error				p
1+3	5130+5722	0.09	0.18	0.06				<0.001
1+1+3	5130+5560+5561+5563+5727	0.47	0.62	0.25	0.46	0.67	0.71	<0.001
5Reg	5560+5561+5727	0.08	0.11	0.00	0.25			<0.001

In the majority of cases the standardized canonical discriminant coefficients corresponding to click amplitudes were one order of magnitude lower than the variables corresponding to the Absolute ICIs. This indicates that the subset of variables that correspond to the ICIs has a stronger

effect on the discrimination, than click amplitudes.

In two of the four variable sets (RelICI and Amp) the canonical discriminant function values for coda type 5Reg did not show a clear separation among the different individuals (Figure 3.4). However, the same values for the datasets including absolute ICIs (AbsICI and AbsICI+Amp) showed an obvious separation of individuals using linear discriminants.

The comparisons within coda types 1+1+3 and 5 Reg had individuals in common (#5560, #5561 and #5727; Table 3.1). This allowed for the comparison of the relative ability to discriminate among individuals across coda types, by comparing their individual classification error rates. Individual error rates for individuals #5560 and #5561 were always lower for coda type 5Reg than for 1+1+3. Individual #5727 only exhibited lower error rates for coda type 5Reg, in variable sets AbsICI and AbsICI+Amp.

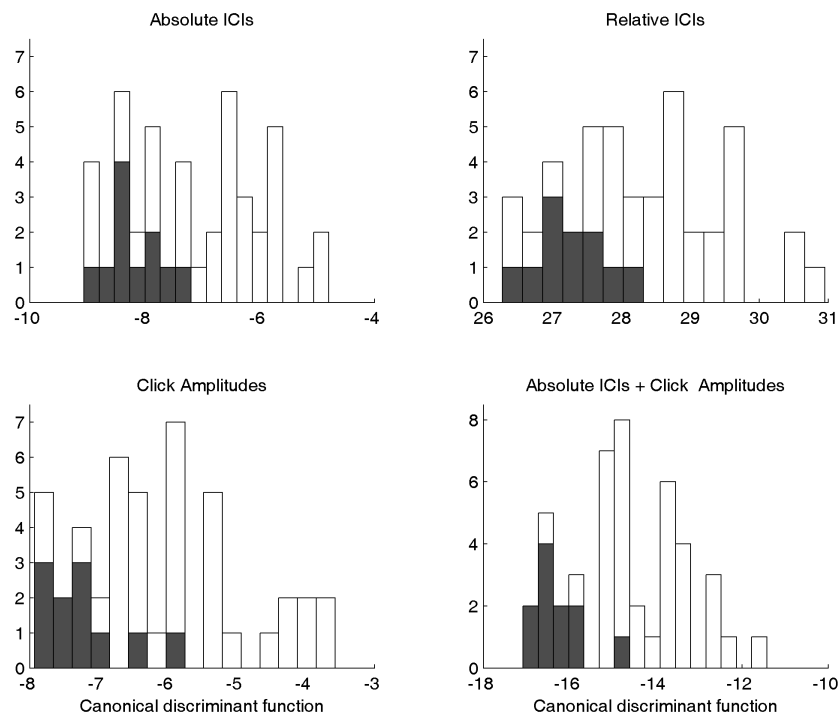


Figure 3.2. Histograms of canonical discriminant function values for comparisons between individuals #5130 (dark bars) and #5722 (white bars) for coda type 1+3 and variable sets AbsoluteICIs, RelativeICIs, Amplitudes and AbsoluteICIs+Amplitudes.

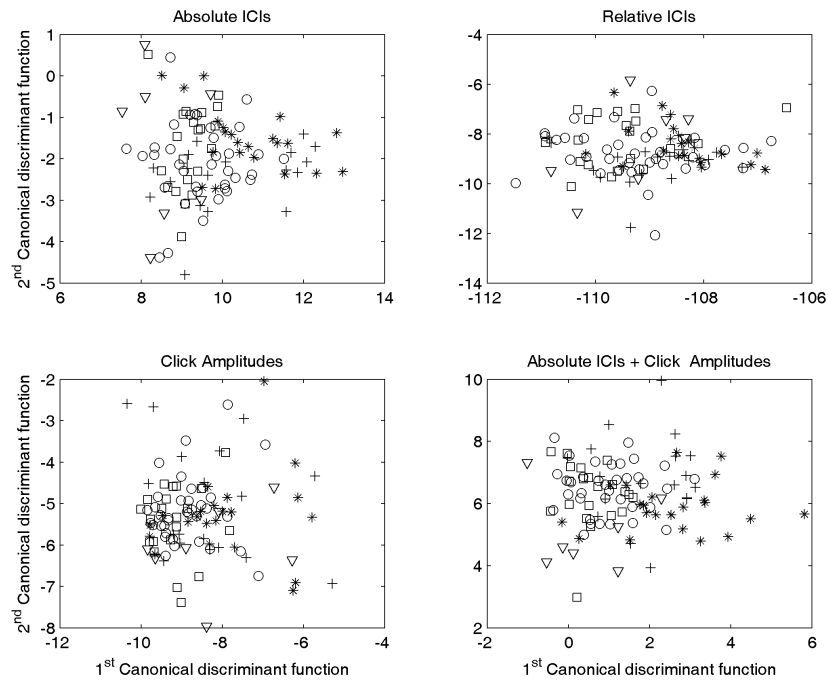


Figure 3.3. First two canonical discriminant functions for comparison among individuals #5130(\square), #5560(\circ), #5561($*$), #5563($+$) and #5727(∇) for coda type 1+1+3 and variable sets AbsoluteICIs, RelativeICIs, Amplitudes and AbsoluteICIs+Amplitudes.

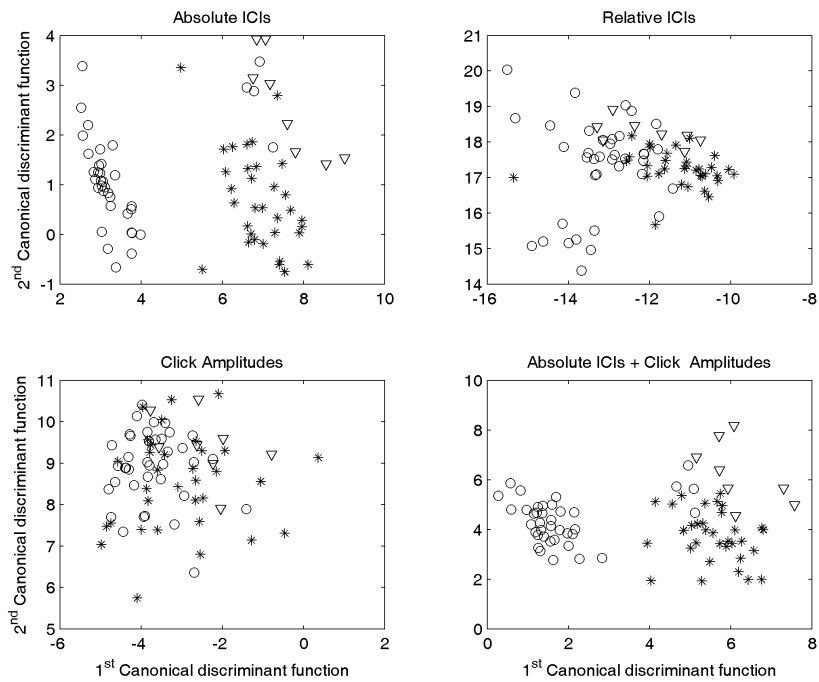


Figure 3.4. First two canonical discriminant functions for comparison among individuals #5560(\circ), #5561($*$) and #5727(∇) for coda type 5Reg and variable sets AbsoluteICIs, RelativeICIs, Amplitudes and AbsoluteICIs+Amplitudes.

The pairwise similarity for 5Reg codas showed higher values for comparisons within *same individual* than between individuals, both within and between days. The same pattern was not apparent for coda types 1+3 and 1+1+3, where similarities were identical regardless of individual identity and day of recording (Figure 3.5).

3.3.3. Partial Mantel tests

The partial Mantel tests resulted in significant correlation coefficients of 0.37 ($p < 0.001$), 0.11 ($p < 0.001$) and 0.55 ($p < 0.001$) for coda types 1+3, 1+1+3 and 5Reg respectively. The low correlation value for coda type 1+1+3 indicates a relatively weak effect of individual in the similarity of codas. The highest value for coda type 5Reg indicates that the effect of individual identity is strong even taking into account variation among days. Coda type 1+3 exhibited an intermediate correlation value.

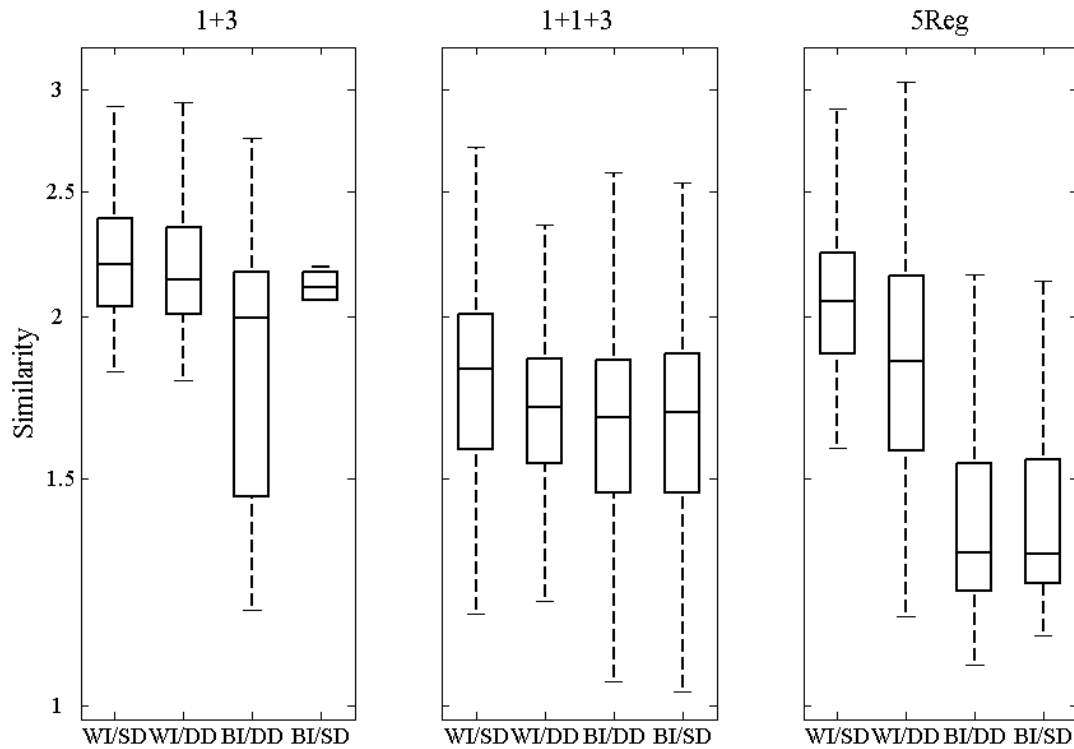


Figure 3.5. Boxplots of coda similarity values within individuals on same day (WI/SD); within individuals on different days (WI/DD); between individuals on different days (BI/DD); and between individuals on different days (BI/SD) for coda types 1+3, 1+1+3 and 5Reg.

3.4. Discussion

For some coda types the classifiers could discriminate among individual sperm whales better than random assignment, indicating that individual variation does exist within coda types.

Relative click amplitudes have not previously been tested as a potential variant in sperm whale coda communication, but it proved not to be a useful carrier of identity information. Relative ICIs did not perform better than Absolute ICIs in discriminating among individual whales for all coda types analysed. Generally the classification with AbsoluteICIs + Amplitudes performed better than using AbsoluteICIs alone. However the differences were probably due to slight differences in the randomization distributions and I do not interpret these as a considerable improvement in discrimination.

Despite the fact that the performance of the best variable sets for each coda type was better than random assignment, only for coda type 5Reg did the discrimination appear robust enough to allow a reliable assignment of codas to individuals. It was also clear that this discrimination relied heavily on absolute, rather than relative, inter-click intervals, suggesting that the common practice of standardising intervals in these kinds of analyses (*e.g.* Moore *et al.*, Weilgart & Whitehead, 1997; Rendell & Whitehead, 2003a) might actually be throwing away important information. These results raise the possibility that differences in discrimination ability between coda types suggests different functionality of those types. In the case of the social unit studied here, coda type 5Reg seems to carry more information with respect to individual identity than the other types. This coda type is noteworthy because it is ubiquitous across geographical areas in which sperm whale coda repertoire have been studied (Caribbean: Moore *et al.*, 1993; Pacific Ocean: Weilgart & Whitehead, 1993; Weilgart & Whitehead, 1997). It has also been highlighted as being more likely to occur at the start of coda exchanges than other coda types (Weilgart & Whitehead 1993). The results raise the possibility that this particular coda type may be preferably used for encoding individual identity in the species, which would also help explain both its ubiquity and its frequent occurrence at the start of exchanges.

One strategy by which individual identity can be encoded is through variation in signal type repertoires. Individual type repertoire variation seems not to be present in sperm whales as individual whales share the majority of coda types (Schulz, 2007). Unique individual voice characteristics can also be used to transmit the vocalizer's identity such as for the *grunt* calls of wild

chacma baboon (*Papio cynocephalus ursinus*) (Owren *et al.*, 1997). This has not been demonstrated in sperm whales so far. Sperm whale clicks are short broadband pulses and likely do not have enough parameter space in the frequency domain to allow for signal coding. One feature particular to sperm whales clicks is the multi-pulsed structure. Some authors have hypothesised that the whales can discriminate IPIs (Whitehead, 2003) and because this parameter is correlated with the whale size (Gordon, 1991; Rhinelander & Dawson, 2004) it could potentially be used to discriminate among individuals of different sizes. This ability still remains to be demonstrated, and individual discrimination of all unit members by IPI would only be possible for cases where each individual is of a different size. This was the case for the small social unit studied here but it is unlikely that this criterion is satisfied sufficiently generally to allow for the development of an individual recognition system based on IPIs alone. Also, IPIs will change during a whale's life with the growth of the spermaceti organ. IPI discrimination is further complicated by off-axis effects which change the clicks' multi-pulsed structures depending on the vocalizing whales aspect in relation to the receiver (Zimmer *et al.*, 2005b).

The fact that the within coda type individual variation can be used to distinguish individuals suggests hierarchical mapping as the individuality coding scheme in codas. Hierarchical mapping is typical in bird song, where a mean pattern of vocalizations indicates species identity, and deviations from this indicate individual identity (Becker, 1982; Falls, 1982). Hierarchical mapping has also been found to code for individual and gender in electrical fish (Crawford, 1992; Friedman & Hopkins, 1996). In codas, individual information seems to be encoded in variations in timing around the coda type's stereotyped rhythm. For the social unit studied here, the 5Reg type, defined by five (fairly) equally spaced clicks, provides the mean pattern from which idiosyncratic variations depart. Such a coding scheme would be constrained by the amount of within type variability possible that would still allow the coda to be recognised as a 5Reg type.

Signal coding in species that rely on frequency coding allow for the time domain to code for motivation and arousal state cueing while retaining signal functionality. In dolphins for example, the frequency contour shape of signature whistles is conserved within each individual, while frequency, duration, and intensity varied with behavioural context (Caldwell & Caldwell, 1965). Another example is the variation of call structure in elephant rumbles which reflects both identity and emotional state (Soltis *et al.*, 2005). Variation in parameters such as formant, minimum and maximum frequencies can be used to discriminate between individual elephants, whereas

coefficients which reflect tonality (periodicity of the pitch period) and jitter (temporal stability of the pitch period) seemed to vary depending on the relative dominance rank of other individuals present. If sperm whale codas coding rules rely on changes in the time domain alone, there may be limitations in the amount of variability that can be introduced by motivational and emotional cueing without changing the signal's functionality. Variation due to motivation and emotional states could also potentially complicate individual discrimination, if the variation occurs in the same coding parameter. I found a positive correlation between coda similarity and individual identity, when controlling for differences between recording days. This indicates that individual discrimination is robust to the range of arousal and motivational contexts sampled across recordings. Also for the cases of individuals #5560 and #5561 there is almost no overlap in the discriminant space even though the animals were simultaneously recorded on three different days. However I cannot rule out that similar contextual and motivational conditions were present in the various recording events. Motivational cueing could still be transmitted in the click amplitudes. These showed less consistency in the ability to discriminate among individuals.

The ability of the clustering used in the analysis to group codas into functional categories is a potential limiting factor in my conclusions. K-means clustering has been previously used in studies that showed that the technique can pick out naturally occurring groupings in sperm whale coda datasets (Rendell & Whitehead, 2003a). The method has also previously been used to support the grouping of sperm whale social units into clans (Rendell & Whitehead, 2003b) which in turn showed differences in biological relevant aspects such as reproductive and foraging success (Marcoux *et al.*, 2007a, Marcoux *et al.*, 2007b, Whitehead & Rendell, 2004). This suggests that the method captures biological meaningful differences. Furthermore, since I have studied only a single social unit here is analysed, and from this only a subset of individuals, any generalization of these conclusions should be taken with caution.

These results suggest that there is a selection pressure for the development of mechanisms that allow the discrimination and recognition between individuals within social units. This idea remains to be tested and doing so is a major challenge. The ability for discrimination and recognition among social unit members could be tested with coda playback experiments, if differences in behavioural reactions among social unit members could be evaluated. These would require a priori knowledge of individual repertoires from the specific social units being tested. Were individual recognition to be demonstrated in sperm whales, it would help clarify whether the

observed individual differences are the result of non-functional individual biases in the learning and/or production of codas, or the consequences of pressure for the transmission of individuality. In the former case the observed differences in discrimination suggest that individual biases vary between coda types.

Most of the research on individual recognition has focused on territoriality, aggressive competition and parental care (Tibbetts & Dale, 2007). Recognition of parent and offspring is particularly important in species that breed in large, high-density colonies, such as bats, seals and seabirds, and is likely to be common in animals that live in herds (Tibbetts & Dale, 2007). It is also an advantage for mother-calf sperm whale pairs to be able to recognize each other among other unit members. Differences between the mother and calf, and the remainder of the social unit were the only differences in coda type repertoires found in the "*Group of Seven*" (Schulz, 2007). This was interpreted as a response to the increased necessity to locate each other and ensure the efficient transfer of milk, providing a mutual recognition system. This suggests the presence of two individual recognition schemes; one for mother-calf pairs based on coda type repertoire; and another based of within type variations for other unit members. A possible explanation that accommodates both observations is a scenario where identifying individuals from within type variation requires that whales interact and learn socially over long periods of time. Since the calf has not experienced such a learning period, a less subtle coding scheme based on different coda types is used.

Individual recognition is thought to have an important role in the evolution of cooperation (Crowley *et al.*, 1996) and on the stabilization of linear dominance hierarchies (Dugatkin & Earley, 2004). Sperm whales are thought to live in non-hierarchical societies (Whitehead, 2003) although little evidence of this has been put forward. Intraspecific competition within social units should be low since in the pelagic realm few, if any resources of interest are defensible. Therefore one would not expect agonistic encounters and territoriality to drive the development of individual recognition within social units. On the other hand, some studies have suggested several forms of individualized relationships within sperm whale units, which would require individual recognition. For instance, Gero *et al.* (2008) found that sperm whales form preferred associations and avoidances with particular unit members. Others (Weilgart *et al.*, 1996; Whitehead, 2003; McAuliffe & Whitehead, 2005) have suggested that similarly to elephants (McComb *et al.*, 2001) menopausal female sperm whales act as repositories of knowledge, and as cohesive agents, which would benefit social units as

a whole. The long lives and the stability of social units allow familiarization to take place providing the context for individual recognition.

The present study calls for further work on the contextual use of codas. If indeed coda types have different functionalities, these could be reflected in contextual use. Longer term study of the individual repertoires of the “*Group of Seven*” would increase the sample size allowing for a greater control of context and motivational variables and more precise conclusions on the presence of individuality information and its variation between coda types. Also, further research targeting the individual repertoires of other social units from the same and other geographical areas with different coda type repertoires, will allow the verification of the hypothesis of differential functionality of coda types in transmitting individuality.

In conclusion I have demonstrated that it is possible to discriminate between individual sperm whales based on absolute ICI variability. This supports the initial hypothesis that variation within coda types allows distinction among group members. However the discrimination performance was not the same for all coda types which suggests differential functionality between coda types. The present study also suggests that codas are hierarchically coded signals in which individuality information is encoded in finer variations in timing around the stereotyped rhythm of a given coda type.

CHAPTER 4

Ecology-driven variation in sperm whale social structure?

4.1. Introduction

4.1.1. Animal groups

Variations in animal group sizes and their social structure represent compromises accommodating associative and dissociative factors (Wrangham *et al.*, 1993). Protection from predators through dilution and early detection (Hamilton, 1971; van Schaik *et al.*, 1983), resource defence (Garber, 1988; Peres, 1989) and communal offspring care (Taborsky, 1984; Packer *et al.*, 1992; Whitehead, 1996; Koenig & Dickinson, 2004) are all advantages of group living which work as associative factors bringing animals together. On the other hand competition for resources such as food, mates, and shelter work as dissociative factors which limit group sizes (Terborgh & Janson 1986; Wilson, 2000). The ability to vary group size allows for flexibility in response to ecological conditions depending of the balance of cost/benefits of group living. For example in fission-fusion societies, primates balance the costs of increased competition in large groups with the benefits of group living by adjusting group sizes (Dunbar, 1992; Takahata *et al.*, 1994; Kummer, 1995; van Schaik, 1999). Spinner dolphins (*Stenella longirostris*) in the Pacific Ocean also show differences in social structure that depend on ecological conditions (Karczmarski *et al.*, 2005). Around Midway Atoll, spinner dolphins live in a stable society of long-term associates while off the large Hawaiian Islands they live in a fission–fusion society with great day-to-day variability in group size and membership. Karczmarski *et al.* (2005) suggest that in Midway Atoll due to the reduced availability of sheltered shallow-water locations in which to rest in daytime, and easy access to deep water foraging locations, it is less costly not to disperse and stable societies are favoured. On the other

hand, the larger islands offer a more heterogeneous environment with several locations capable of holding a proportion of the foraging groups, favouring a more variable society.

The group sizes and social structure that result from balancing the pros and cons of group living affect other aspects of an animal's biology such as gene flow (Whitehead, 1998); habitat use (Baird & Dill, 1996; Ersts & Rosenbaum, 2003), the spread of diseases (Lee, 1994; Guimarães *et al.*, 2007) and the manner in which information is retained and transmitted among individuals (McComb *et al.*, 2001; Wittemyer *et al.*, 2005).

4.1.2. Sperm whale social structure

The sperm whale (*Physeter macrocephalus*, L., 1758) is one of the most wide ranging marine mammals, and is found in all oceanic deep waters (Rice, 1989). Attempts to correlate oceanographic features with sperm whale distribution are not agreed upon, and different studies have proposed different factors that determine sperm whale abundance (Whitehead, 2003). In an attempt to resolve the discrepancies between studies, Jaquet (1996) argued that the correlation between sperm whale distribution and oceanography is scale dependent. At spatial scales of a few hundred kilometres and a temporal scale of months sperm whale abundance is correlated with areas of high primary productivity (Jaquet & Whitehead, 1996). At smaller spatial and temporal scales whales seem to be correlated with the presence of oceanographic features such as the continental shelf break, oceanic fronts where water masses meet, cyclonic eddies, and warm-core rings (Waring *et al.*, 1993; André, 1997; Griffin, 1999; Biggs *et al.*, 2000; Gregr & Trites, 2001; Waring *et al.*, 2001; Whitehead, 2003).

The sperm whale's long life span (Rice, 1989) allows for the formation of long-term social bonds between individuals, which is a characteristic of the social structure seen in females (Christal *et al.*, 1998). Most of the information we have on sperm whale societies comes from research in the Pacific Ocean (Christal *et al.*, 1998; Coakes & Whitehead, 2004; Jaquet & Gendron, in Press). These studies have shown that females and their offspring form stable units of between 10 to 12 individuals, with only occasional movements of individuals between units (Christal *et al.*, 1998). Temporal analyses of association rates have shown that social units tend to form short term groupings which persist for periods of days, with other units that share cultural traits (Whitehead, 2003). This pattern of social structure appears to be typical within the Pacific (Galapagos Islands: Christal *et al.*, 1998; Chile: Coakes & Whitehead, 2004; Gulf of California: Jaquet & Gendron, in

Press).

Jaquet & Gendron (in Press) compared the social structure patterns they found in the Gulf of California with those reported for the Pacific and the Gulf of Mexico, Dominica and the Sargasso Sea. They found larger mean typical group sizes in the Pacific than in the Atlantic. Based on this comparison they suggested that differences in site-specific ecological factors such as predation pressure and/or food resources are likely to influence sperm whale social organization. This comparison however relied on limited datasets for the Atlantic, which could not adequately parameterise the social structure models for comparison. The present study uses a dataset from the Azores of a similar size to those described from the Pacific to allow a more detailed comparison. The sperm whale social structure for this archipelago located in the Atlantic Ocean has not been previously analysed. The analysis follows the methodological standards used in the Pacific studies to allow a direct comparison and provide a better understanding of how ecological factors may influence social structure, and which selective forces drive sperm whale social structure.

4.2. Methods

4.2.1. Field methods

Identification photographs of sperm whales were collected in the central and eastern island group of the Azores archipelago (Figure 4.1) between 1989 and 2007, with the exception of 1992 and 1994. Most photographs were of adult female and immature sperm whales of both sexes although a few adult males were also encountered.

Data were collected from the International Fund for Animal Welfare research vessel *Song of the Whale*, a 14m auxiliary powered ketch (between 1987 and 1995), from *Whale Watch Azores* vessel *Colomban* a 18m schooner (between 1993 and 2002) and *Physeter*, a 12m motor catamaran (2003 onwards).

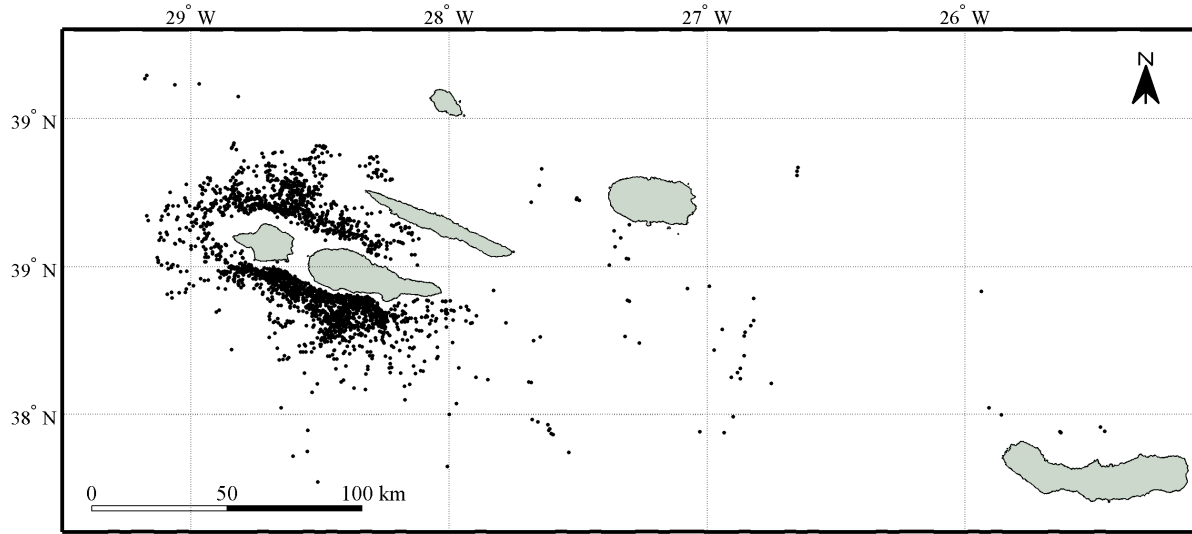


Figure 4.1. Study area including the Azorean Central Group of islands (Faial, Pico, São Jorge, Graciosa, Terceira from West to East) and São Miguel in the Eastern Group. The locations where the photo-identifications used in the study were made are shown as points.

Sperm whales were located and tracked visually and acoustically using either a directional or towed hydrophone (Whitehead & Gordon, 1986). In later years detections were also made in conjunction with a network of land based lookouts. Whales were approached while on the surface, between foraging dives. By carefully manoeuvring the vessel directly behind the whale, photographs of their flukes were taken for individual identification purposes when the animals fluked. Photographic equipment used varied through the study period; a Canon T90 35mm film SLR camera with a 300mm lens (between 1987 and 1995), a Canon EOS 600 film camera with a Sigma 70-300mm zoom lens (between 1993 and 2003) and a Canon EOS 10D digital camera with a Tamron 28-300mm zoom lens (between 2004 and 2006) were used. Fluke photographs were assigned a quality rating value Q , between 1 (worst quality) and 5 (best quality) following the scheme described by Arnborn (1987), organized into a catalogue and matched within the catalogue by Lisa Steiner. All analysis in this chapter used only photographs classified with $Q \geq 3$.

4.2.2. Group sizes

The sizes of groups encountered at sea were estimated using a mark recapture technique with a Petersen estimator and Chapman correction for small samples (Seber, 1982; Whitehead, 2003; Coakes & Whitehead, 2004). Following Coakes & Whitehead (2004) the period between the

first and last identifications of each day was divided into two sections of equal duration ($S1$ and $S2$), and the number of individuals identified in the first section (n_{S1}), the number of individuals identified in the second section (n_{S2}) and the number of individuals in common to both (n_{S12}) were used to calculate the group size estimate N_g :

$$N_g = \frac{(n_{S1} + 1) \cdot (n_{S2} + 1)}{n_{S12}} - 1 \quad (4.1)$$

and its coefficient of variation calculated as:

$$CV_g = \frac{\sqrt{\frac{(n_{S1} + 1) \cdot (n_{S2} + 1) \cdot (n_{S1} - n_{S12}) \cdot (n_{S2} - n_{S12})}{(n_{S12} + 1)^2 \cdot (n_{S12} + 2)}}}{N_g} \quad (4.2)$$

Following the rationale from previous work (Whitehead, 2003) group size estimates were divided into those with $CVs \leq 0.25$ and a more inclusive set with $0.25 < CVs \leq 0.40$. The former provides a more accurate measure, but is biased towards smaller groups, while the latter, though less precise, takes into account larger groups (Whitehead, 2003; Coakes & Whitehead, 2004).

The group sizes calculated using equation 4.1 are as observed by an observer from outside of the group, such as a predator or a researcher. *Typical group size* corresponds to the size of the group experience by a member of the population (Jarman, 1974). The mean typical group size N_{tg} was calculated as:

$$N_{tg} = \frac{\sum_{i=1}^M N_g(i)^2}{\sum_{i=1}^M N_g(i)} \quad (4.3)$$

where $N_g(i)$ is the group size for group i (from equation 4.1) and M is the number of groups (Whitehead, 2008).

4.2.3. Temporal patterns of association

Temporal association patterns were investigated by calculating the Standardized Lagged Association Rate (SLAR), as the probability of two animals being associated τ time lags after a previous association (Whitehead, 1995; Whitehead, 2008). Day was used as the sampling period, τ . The SLAR was calculated using program SOCPROG (v2.3, written by H. Whitehead and available

from <http://myweb.dal.ca/hwhitehe/social.htm>). The program also calculates approximate standard errors using a temporal jackknife process in which sampling periods are omitted from the analysis in turn (Whitehead, 1995; Whitehead, 2007). The Standardized Null Association Rate (SNAR) was also calculated as the association rate expected under random association (Whitehead, 2008).

Program SOCPROG was also used to fit four models (of the exponential family using a maximum likelihood procedure) of how association rate changes with time lag (Table 4.1). In these models the SLAR is fitted to a combination of processes of either constant or exponential decay whose effects are equally likely to occur at any time (Whitehead, 1995; Whitehead, 2008).

4.2.4. Identification of key individuals

To identify the sets of individuals that were likely to be long term companions, 'Key individuals' were identified as animals that had been associated with each other at least three times, each separated from all others by at least 30 days (Christal *et al.*, 1998).

Table 4.1. Models of the exponential family fitted by program SOCPROG to lagged association data (Whitehead, 2008)

	Model	Description
Model 1	$h(\tau)=a$	Level of association between individuals a , invariant with time
Model 2	$h(\tau)=a \cdot e^{-b\tau}$	Short term level of association a , followed by disassociation at rate $1/b$
Model 3	$h(\tau)=a+c \cdot e^{-b\tau}$	Short term level of association $(a+c)$ falling off at disassociation rate $1/b$, and leveling off at association level a
Model 4	$h(\tau)=a \cdot e^{-b\tau}+c \cdot e^{-d\tau}$	Combination of two processes with two levels of association $(a+c)$ and disassociation rates $(1/b \text{ and } 1/d)$

4.2.5. Estimation of numbers of constant companions

Christal *et al.*, (1998) compared several temporal association criteria to investigate which allows for the most accurate estimation of individuals' true numbers of constant companions. They found that considering animals to be associates if identified within 12 hour periods, best estimates the true number of constant companions. This essentially corresponds to individuals being

identified in the same day and this was the criterion used in the Azores dataset.

The number of constant companions for each 'key individual' was estimated using a mark-recapture procedure (Christal *et al.*, 1998), that considered animals identified in the same day as associates. If we assume that individual whales that associated with each other on at least three days, t_1 , t_2 and t_3 , each separated from the others by at least 30 days, are constant companions, the number of constant companions for each individual is estimated as:

$$N_{cc} = \frac{(n_{12}+1) \cdot (n_{13}+1) \cdot (n_{23}+1)}{(n_{123}+1)^2} - 1 \quad (4.4)$$

where n_{12} , n_{13} and n_{23} are respectively the number of individuals commonly identified in t_1 and t_2 , in t_1 and t_3 and in t_2 and t_3 , and n_{123} the number of associates common to the three. For key individuals with four or more identification periods, the number of constant companions was calculated as the median of all sets of three identification periods. Each key individual's unit size is then estimated as the number of constant companions plus one.

4.2.6. Unit delineation

The results of the SLAR analysis (see Results) indicated that the temporal threshold of 30 days, previously used in the Pacific (Whitehead, 1991; Christal *et al.*, 1998) for identifying constant companions and units was also applicable to the Azores data. Two whales that remained associated for longer than this threshold were considered to be constant companions, and therefore the threshold has to be larger than any temporary association period. As no short term groups seem to form in the Azores (see Results) the same rules may also be applied, therefore making the results comparable across locations. Social units were delineated following the rules previously applied for the Pacific: key individuals that were associated with at least two others during at least two identification periods, were considered to be members of the same unit. In the cases where a unit was represented by a single key individual, all animals associated with it on at least two identification periods were considered member of its unit (Christal *et al.*, 1998; Coakes & Whitehead, 2004; Jaquet & Gendron, in Press).

The mean number of unit members for each delineated unit was calculated as the mean of the estimated unit size of all the key individuals that make up the unit.

4.3. Results

4.3.1. Identifications

The initial photographic identification dataset comprised a total of 3121 photographs (Table 4.2). When restricted to photographic quality $Q \geq 3$, the data were limited to a total of 2,217 identifications from 988 individuals, on 433 days (mean identifications per sampling period: 5.12, mean individuals identified per day sampling period: 3.65).

4.3.2. Group size estimation

The number of identifications per sampling period was low. In many cases this meant that once sampling periods had been divided into two periods there were often no identifications in common to both. It was therefore only possible to estimate group sizes for a total of 44 sampling periods. Estimates ranged from 7.0 to 15.5 for estimates with $0.25 < CV \leq 0.40$ and 11.0 and 16.14 for estimates with $CV \leq 0.25$.

Table 4.2. Distribution of number of photographic identifications by year and photographic quality index (Q). Columns Σ and $\Sigma_{Q \geq 3}$ represent respectively, the total of identifications with photographic quality indexes three or greater and overall total.

	Q = 1	Q = 2	Q = 3	Q = 4	Q = 5	$\Sigma_{Q \geq 3}$	Σ
1987	-	4	8	6	-	14	18
1988	-	3	6	15	1	22	25
1989	-	4	10	9	-	19	23
1990	-	1	6	7	-	13	14
1991	-	2	7	7	-	14	16
1993	-	12	23	8	-	31	43
1995	-	35	69	26	1	96	131
1996	3	5	3	-	-	3	11
1997	-	2	4	-	-	4	6
1998	6	39	15	2	-	17	62
1999	2	91	36	3	-	39	132
2000	5	51	16	1	-	17	73
2001	-	29	26	2	-	28	57
2002	4	116	31	1	-	32	152
2003	3	101	96	5	-	101	205
2004	1	42	212	188	5	405	448
2005	8	138	228	151	9	388	534
2006	2	73	195	210	21	426	501
2007	1	121	337	206	5	548	670
Σ	35	869	1328	847	42	2217	3121

Table 4.3. Estimates of mean group size (N_g) and mean typical group size (N_{tg}) for all days which produced estimates with coefficients of variation within the ranges of 0 to 0.25 and 0.25 to 0.40. Also included are group size estimates for the same ranges when the dataset is restricted to days where the first and last identification photographs were taken at least five hours apart.

	n	CV \leq 0.25		n	0.25 \leq CV \leq 0.40	
		N_g (SD)	N_{tg}		N_g (SD)	N_{tg}
all days	18	11.42 (2.30)	11.56	26	8.98 (2.18)	9.36
at least 5 hours between first and last identifications	3	11.50 (0.98)	12.22	4	12.29 (1.20)	12.69

In addition, because the time span between the first and last identification photograph was often short, I also produced group size estimates restricted to days where this period was at least five hours (Table 4.3).

4.3.3. Identification of key individuals

68 "*key individual*" whales were identified using the criteria described above. The maximum number of sampling periods separated by at least 30 days from each other used to identify key individuals was nine, and the maximum time lag between sampling periods was 6926 days (more than 18 years).

4.3.4. Unit size estimation

The estimated unit sizes for all key individuals ranged from 2 to 20 (mean 6.52 SD 4.43) (Figure 4.2).

4.3.5. Temporal association patterns

The calculated SLAR showed that the level of association was fairly stable for periods of about 100 days (which roughly corresponds to the length of a field season), after which it decayed more rapidly although it never reached the level of null association during the range of temporal lags considered (Figure 4.3).

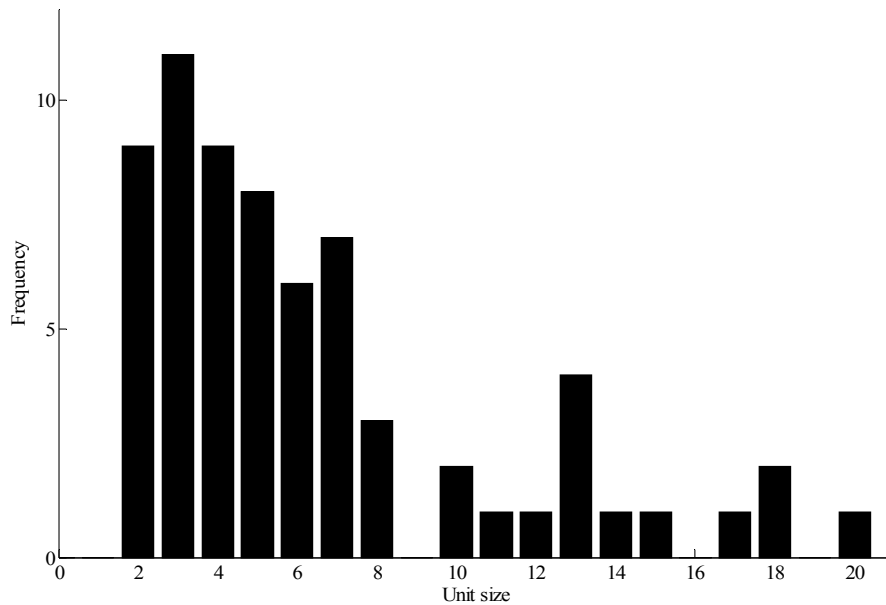


Figure 4.2. Frequency distribution of estimated unit sizes for 68 key individuals.

While fitting of model 3 gave the lowest QAIC value suggesting it as the best explanatory model, the QAIC for model 2 was very similar indicating a similar level of support and that these models could not be distinguished using the available data (Table 4.4). The negative value of parameter a for model 3 does not have a realistic meaning since it allows for a negative SLAR with time lags beyond 3,613 days, which calls into the question the suitability of this model for these data.

Even though model 3 usually allows for a high level of short term associations plus a second level of stable associations ('*Constant companions + casual acquaintances*', Whitehead *et al.*, 1991; Whitehead, 2008), it can be seen from visual inspection of this model's fit that it is essentially identical to model 2 (Figure 4.3). This is also true for model 4. The data do not support the existence of any higher level of association at shorter time lags. For this reason it appears that the simpler model 2, which also has good support, and consistent and realistic parameters is a better description of the temporal patterning of associations. Model 2 is labelled as '*Casual acquaintances*' in Whitehead (2008) as its exponential decay function without a baseline level of persistent associations, can be used to describe patterns of temporary short term associations, followed by rapid disassociation. I refrain from using that terminology here because the associations persist for

longer than 100 days so the nomenclature can be misleading because over these timescales demographic processes such as mortality, births and migration can all have important effects along with social dynamics.

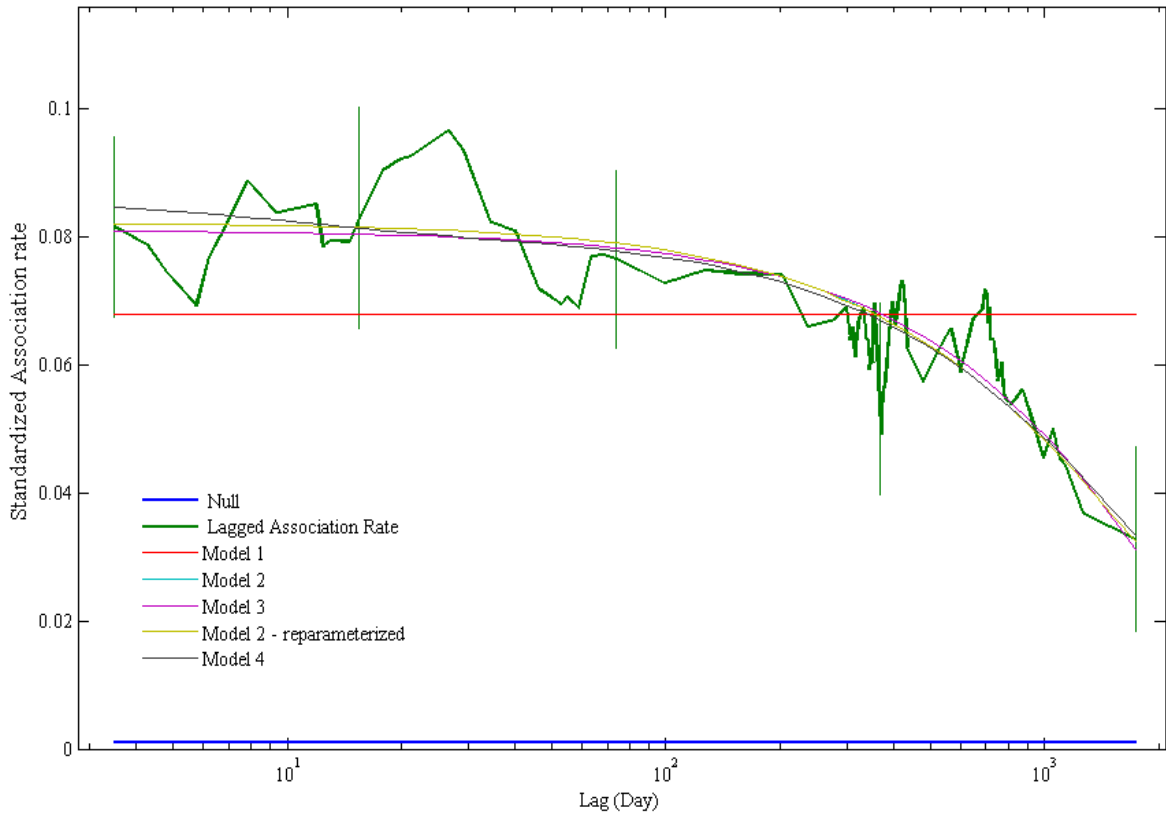


Figure 4.3. Standardized null and lagged association (SLAR) rates and fitted models (Table 4.4). Error bars represent temporal jackknife standard errors. The SLAR curve was smoothed with a 4,000 associations moving average, but model fitting was performed on the unsmoothed data.

Model 2 can be reparameterized to aid in its interpretation to provide value for measures of social structure and their associated standard errors directly:

$$h(\tau) = \frac{1}{m} \cdot e^{-\frac{r}{365.25} \cdot \tau} \quad (4.5)$$

where $h(t)$ is the standardized lagged association rate, m corresponds to the mean number of associated individuals, and r to the annual disassociation rate (Whitehead, 2008). This model's fit estimates a gregariousness of 12.16 individuals (SE 1.38), with a disassociation rate of 0.195/year (SE 0.06) (Table 4.4).

Table 4.4. Parameters and goodness of fit values of the models of variation of Standardized Lagged Association Rates ($h(\tau)$) with association time lag (τ). QAIC is the quasiliikelihood Akaike Information Criterion, and Δ QAIC indicates the difference between QAIC and that of the lowest from all models. Figures in parenthesis denote standard errors of the estimated parameters.

Model		Estimated parameters				QAIC	Δ QAIC
		a ($\times 10^{-3}$)	b ($\times 10^{-3}$)	c ($\times 10^{-3}$)	d ($\times 10^{-3}$)		
Model 1	$h(\tau)=a$	67.91 (6.88)				12800.93	80.38
Model 2	$h(\tau)=a \cdot e^{-b\tau}$	82.22 (9.02)	0.54 (0.16)			12720.86	0.31
Model 3	$h(\tau)=a+c \cdot e^{-b\tau}$	-39.66 (17.18)	120.69 (13.09)	0.31 (17.21)		12720.55	0
Model 4	$h(\tau)=a \cdot e^{-b\tau}+c \cdot e^{-d\tau}$	5.79 (77.84)	144.76 (17.21)	81.09 (80.85)	0.515 (2.07)	12724.52	3.97
		r	m				
Model 2 Reparameterized	$h(\tau)=\frac{1}{m} \cdot e^{-\left(\frac{r}{365.25}\right)\tau}$	0.19 (0.06)	12.16 (1.38)			12720.86	0.31

4.3.6. Unit delineation

The application of the unit delineation rule to the dataset resulted in the assignment of 104 individuals to 19 units (Table 4.5). Of the 68 key individuals, two were not assigned to a unit because no associations that met the unit delineation criteria were found.

Unit sizes ranged between two and 17 individuals. For most units, the mean estimated unit size was similar to the number of whales that had been assigned to it. However for some units (Az4, Az8) the number of assigned individuals was more than double that of the mean estimated unit size.

Whales were identified on 433 days. Pairs of whales that had been assigned to different units were seen on only five of these; (units Az4 and Az8 on 8 July 2004, units Az4 and Az17 on 27 June 2005, units Az2 and Az8 on 18 August 2006 and 27 September 2006, units Az6 and Az17 on the 17 June 2007).

Table 4.5. Summary information for delineated social units. Unit labels are shown in the first column. Other columns correspond to (from left to right): the number of individuals assigned to each unit; the mean of the unit size is estimated from all 'key individuals' in the unit; the total number of days in which at least two unit member were associated; the longest time interval between the first recorded association among unit members; and the years in which at least two unit member were observed as associates.

Unit	Individuals	Mean estimated unit size (CV)	N days	Longest lag (days)	Years observed
Az 1	16	14.59 (0.56)	389	1211	2004, 2006, 2007
Az 2	7	3.25 (0.29)	25	6968	1988, 1989, 2005, 2006, 2007
Az 3	3	4.00 (0.00)	6	403	2006, 2007
Az 4	17	6.26 (0.39)	351	1520	2003 – 2007
Az 5	4	4.33 (0.27)	15	2947	1998, 2002, 2003, 2006
Az 6	5	6.00 (0.00)	42	773	2005, 2007
Az 7	3	3.00 (0.00)	10	431	2005, 2006
Az 8	11	4.87 (0.40)	258	1465	2002 – 2006
Az 9	4	3.83 (0.20)	11	2179	2001, 2005, 2007
Az 10	4	7.00 (0.00)	10	621	2004 – 2006
Az 11	3	3.75 (0.09)	10	1574	2003, 2004, 2007
Az 12	7	8.67 (0.44)	42	735	2005 – 2007
Az 13	3	*	6	678	2005, 2007
Az 14	3	*	6	236	2006, 2007
Az 15	2	2.50 (0.00)	2	342	1988, 1989
Az 16	4	2.00 (0.00)	15	9	2007
Az 17	4	2.75 (0.00)	15	1138	2004, 2005, 2007
Az 18	2	2.50 (0.00)	2	319	2003 – 2004
Az 19	2	3.00 (0.00)	3	367	2005 – 2006

* No key individuals identified in unit

4.4. Discussion

The analysis of temporal patterns of associations of sperm whales in the Azores revealed a pattern unlike those previously reported for studies in the Pacific Ocean. The temporal patterns of association found in Gulf of California (Jaquet & Gendron, in Press), Chile (Coakes & Whitehead, 2004) and the Galapagos Islands (Whitehead, 2003 and Coakes & Whitehead, 2004), are generally characterized by short term associations of more than one long term stable social unit over periods of a few weeks, which then disassociate into their constituent units. In these cases the models that best described the variation of SLAR are similar to model 3, the so-called 'Constant companions and casual acquaintances' model, which accommodates two levels of association of different durations (Whitehead, 2008). This pattern is also observable in the differences between group and unit size estimates for these areas (Table 4.6), with the former being about twice the latter since, groups observed at sea are typically aggregations of more than a single social unit.

Table 4.6. Estimated unit size, typical group size and disassociation rates for sperm whales in the Gulf of California, Galápagos, Chile, Northern Gulf of Mexico (from Jaquet & Gendron, in Press, Whitehead, 2003 and Coakes & Whitehead, 2004, Coakes & Whitehead, 2004 and Richter *et al.*, in Press, respectively), and the Azores (current study). Standard errors shown in parenthesis.

	Gulf of California	Galápagos	Chile	Northern Gulf of Mexico	Azores
Identification photographs	1782	4475	1971	714	2217
Identified individuals	612	1548	898	285	988
Estimated unit size	12.5 (4.51)	11.5 (6.3)	11.0 (18.0)	5.2 (3.48)	12.16 (1.38)
Estimated typical group size	28.4 (6.42)	27.7 (8.1)	31.3 (18.7)	7.4 (4.03)	11.50 (0.98)
Disassociation rate (days ⁻¹)	0.0126 (0.0297)	0.053 (0.065)	0.134 (0.185)	0.016 (0.021)	0.082 (0.009)

The observed temporal patterns of association do not lend themselves to the same interpretation. The SLAR variation in the Azores does not suggest the formation of temporary groups. It is characterized by a persistent level of association of 12.16 (SE 1.38) individuals on average; lasting for periods of about 100 days (essentially about a single sampling season), after which the level of association drops. This suggests that social units in the Azores, although of similar sizes to other locations, do not form short term groups. After the initial level of association, the longer term trend in association, shows a decrease until the highest time lag considered (6968 days). Although it remains above the null association rate, there is no evidence of the rate stabilizing at a second level. Some cases of associations lasting for at least 19 (Az2), 8 (Az5) and 6 (Az9) years were found, indicating that Azorean sperm whales can remain associated for very long periods. The largest of these is the longest association period recorded to date for sperm whales. The frequent sighting of these social units in the Azores spanning more than a decade suggests long term philopatry. Apparent disassociation over periods greater than 100 days could easily be due to demographic factors such as dispersal, mortality or movements of individuals between units (Christal *et al.*, 1998 estimated this rate at around 0.1 per unit per year, which is not highly dissimilar to the disassociation rate reported here), or sampling factors such as changes in the ability to identify marked individuals (*e.g.* changes in distinct marks). An alternative explanation for the temporal pattern observed is that long term units form groups that last for a season, and then dissociate between years. This, however, is at odds with the result that the estimated unit sizes are similar to the estimated group sizes (about 12 individuals).

Only on five out of 433 occasions were members from more than one unit identified on a single day, suggesting that occurrence of different units in the same location occurs only very rarely.

These observations indicate that the groups of whales encountered at sea typically correspond to single social units.

The few data available for the Gulf of Mexico (Jaquet *et al.*, 2005; Richter *et al.*, in Press) and other locations in the Atlantic Ocean (Sargasso Sea; Dominica: Gero, 2005) support the idea of differences between the Pacific and other locations. Sperm whale typical group sizes in the Sargasso Sea are similar in size to those found in the Azores (around 12 individuals), that corresponds to the estimated mean unit size in the latter location. In Dominica and in the Northern Gulf of Mexico group size estimates are approximately half of these values. The differences in social structure between locations potentially correspond to underlying differences in the balance of benefits and costs of group living. The social unit sizes are similar in the Pacific and in the Azores suggesting that the determinants for this level of association are similar in both locations but are different for group level associations.

The advantage gained in defence against predators is a frequent factor attributed to group living. Animals in groups experience a reduced chance of being predated upon due to a dilution effect, communal defence and increased vigilance (Hamilton, 1971; van Schaik *et al.*, 1983). Predator defence has been suggested as one of the factors driving sperm whale group living (Pitman *et al.*, 2001; Whitehead, 2003). As a consequence of their large size sperm whales do not have many predators. Despite reports of harassment by false-killer whales (*Pseudorca crassidens*) and pilot-whales (*Globicephala sp.*) the killer whale (*Orcinus orca*) is the only species whose attacks have been reported to cause mortality (Jeferson *et al.*, 1991; Pitman *et al.*, 2001; Whitehead, 2003). Some of the reported attacks elicited defensive formations in which whales remain at the surface and adopt a radial distribution, either with their heads or their flukes towards the centre. This ability to bunch together for defence may be one of the advantages of group formation in sperm whales. Early predator detection and increased vigilance are also other possible advantages that would increase with the number of animals in a group.

Most reports of killer whale attacks come from the Eastern Pacific Ocean (Whitehead, 2003), and there are no reports so far for the Atlantic. In the Azores despite more than 20 years of whale watching activities focused on sperm whales, not a single attack or harassment event has been reported (Lisa Steiner, personal communication; Serge Viallele, personal communication). Killer whale sightings are rare in the Azores (Pereira, 2008, Lisa Steiner, unpublished data) and in the Gulf of Mexico (O'Sullivan & Mullin 1997, Mullin & Hoggard 2000, Fulling *et al.*, 2003).

These differences may reflect differences in killer whale abundance between locations. Also killer whales have been shown to have different foraging specializations and food preference (Lopez & Lopez 1985; Bigg *et al.*, 1990; Similä & Ugarte, 1993; Baird & Dill, 1995; Ford *et al.*, 1998; Ford & Ellis, 1999; Pitman & Ensor 2003). Even in the Pacific where reports of attacks exist, mortality by killer whales is not likely to be a major cause of death for adult sperm whales. Several instances where both species were seen together with no apparent interaction have been reported, as well as cases where sperm whales displaced killer whales (Whitehead, 2003). Mature male sperm whales are solitary and are usually found at high latitudes where killer whale abundance is higher (Corkeron & Connor, 1999; Forney & Wade, 2006). Defence against predators does not appear to necessitate group living in adult males, although they are larger than females making them more difficult to prey upon. However, calves are highly vulnerable. With their smaller sizes and inability to dive deep they are a more likely target of killer whale attacks, and their protection is highly likely to be an important factor in the evolution of group living and long-term social bonds in females sperm whales (Whitehead, 2003).

A particular form of cooperation which has been put forward as one of the main functions of sperm whale units is allomaternal care of calves (Whitehead, 1996a; Gero, 2005). Sperm whale calves are often escorted at the surface by social unit members other than their mothers (Gero, 2005). Allomaternal care might allow increased foraging time at depth for the mothers, while leaving their calves at the surface under the care of others. This is specially advantageous for sperm whales where the high investment in a single offspring is threatened by the lack of protection from predators in an open environment.

Some authors have speculated that because sperm whales are long lived, they can benefit from the knowledge acquired by older social unit members. Cooperation in the form of communal knowledge is another possible driver of group formation (Whitehead, 1996a; Whitehead, 2003). This has also been proposed for African savannah elephants (*Loxodonta africana*; McComb *et al.*, 2001), whose social structure is very similar to sperm whales (Weilgart, *et al.*, 1996). Nonetheless, it appears likely that defence against predation is a major associative factor promoting the evolution of social bonds in sperm whales. When it comes to defence from predators, bigger groups are better (Wilson, 2000)

The need for refuge should not be an important source of intraspecific competition for sperm whales, as none is to be found in their pelagic environment. Competition for reproductive partners

is also likely not to be important for female sperm whales, as they do not form long term mated pairs, and one male can probably inseminate several of the oestrous females when accompanying a group/unit (Whitehead, 2003). However, intraspecific scramble competition for food could well be the main disadvantage of group living in sperm whales, and the major dissociative factor in the formation of social groups. Thus prey density is expected to limit maximum group sizes.

Savannah elephants show many similarities to sperm whales in their life histories and social structure (Best, 1979; Weilgart *et al.*, 1996). Both species are long lived, and are among the largest in their habitats. Females and their offspring live in long term stable matrilinear groups of about a dozen animals, which move through their habitats in a coordinated fashion. Males of both species disperse from the maternal groups when they mature and then rove between cooperative groups of related females in search of oestrous females. Despite the disparity of their terrestrial and aquatic habitats, these and other life history similarities suggest convergences driven by similar evolutionary pressures.

Wittemeyer *et al.* (2005) showed quantitatively that savannah elephants possess a multitiered society with an increasing level of cohesion from upper to lower tiers. One can find equivalence in the levels of association between the two species. Sperm whale social units consisting of groups of long term associated females and their calves are equivalent to second tier, or family groups described by Wittemeyer *et al.* (2005). The fusion of second tier groups into third tier bond groups in elephants, is equivalent to the formation of sperm whale groups by sperm whale social units. Wittemeyer *et al.* (2005) observed that the cohesion of second tier units was little altered with different ecological conditions, whereas the formation of third and forth tier units was significantly reduced in conditions of increased intraspecific competition. These parallels support the idea that multi-unit group formation in sperm whales can also be dependent on ecological conditions, as suggested for savannah elephants.

Sperm whale prey density is virtually impossible to measure directly. However, although primary productivity at the surface should not have immediate and direct consequences on the sperm whales mesopelagic prey, it has been shown to correlate positively with sperm whale distribution at large temporal and spatial scales (Jaquet & Whitehead, 1996). Export production (the amount of organic matter produced by primary production that is not remineralised before being transferred to below the euphotic zone) is the main source of organic carbon for mesopelagic and bathypelagic habitats (Honjo *et al.*, 2008). Lampit & Antia (1997) found that outside the polar

regions, there is a positive correlation between surface primary production and vertical particle carbon flux normalized to depth of 2000m (the mesopelagic/bathypelagic boundary). In the mesopelagic zone at depths of up to 1500 m, the vertical migrations of zooplankton also play an important role in the way by which primary production is vertically transferred in the water column (Steinberg *et al.*, 2000; Honjo *et al.*, 2008). By engaging in diel vertical migrations to feed in the euphotic zone during the night and sinking back to depth during the day, organisms transfer primary production to the mesopelagic zone. Increased organic carbon input in the mesopelagic environment under high primary production areas potentially contributes to increase sperm whales prey density, by increasing the available food source at the bottom of the mesopelagic food chain. This appears to be the case for all the areas where sperm whales have been studied in the Pacific. The primary production in the Gulf of California has been reported to reach levels at least two to three fold higher than in open ocean areas of the Atlantic and Pacific at the same latitudes (Zeitzschel, 1969). Production is usually high in the winter when strong Southerly winds induce upwelling of nutrient rich waters on the east side of the Gulf (Alvarez-Borrego & Lara-Lara, 1991), reaching on occasions one of the highest surface nutrient concentrations in any of the oceans in the world (Alvarez-Borrego *et al.*, 1978). The Eastern Tropical Pacific (ETP), an area defined between the coast of Central and South America to 140° W, and between the Tropics of Cancer and Capricorn, is characterized by enhanced nutrient supply to the euphotic zone caused by wind driven currents. Nutrient input causes primary production levels in this region to be higher than the adjacent sub-tropical gyres (Pennington *et al.*, 2006). Its unique oceanographic conditions have a strong impact on the species-habitat interactions of the animals that inhabit it. For instance even though yellow fin tuna (*Thunnus albacares*), spotted (*Stenella attenuata*) and spinner dolphins are common across the tropical oceans, only in the ETP do these species commonly associate in feeding assemblages (Ballance *et al.*, 2006). Also it is the only region where four booby species (*Sula* spp.) of seabird are found, one endemic and the other three represented by the largest known breeding colonies (Ballance *et al.*, 2006).

Around the Galapagos Islands the phytoplankton biomass is at least twice that of open-ocean and equatorial upwelling regions of the ETP. This increased productivity is supported by abundant nutrients from iron fertilization from land and mixing and upwelling caused by the collision of equatorial upwelling current with the islands (Martin *et al.*, 1994; Pennington *et al.*, 2006). Finally, the Humboldt Current is a predominant northward flow of surface waters of subantarctic origin

along the West coast of South America, from Southern Chile to Ecuador and the Galapagos Islands. The strong upwelling of cool nutrient-rich subsurface waters makes its zone of influence one of the most productive marine ecosystems on earth, supporting strong fisheries off Peru and Chile (Alheit & Bernal, 1993; Kudela *et al.*, 2005; Thiel *et al.*, 2007).

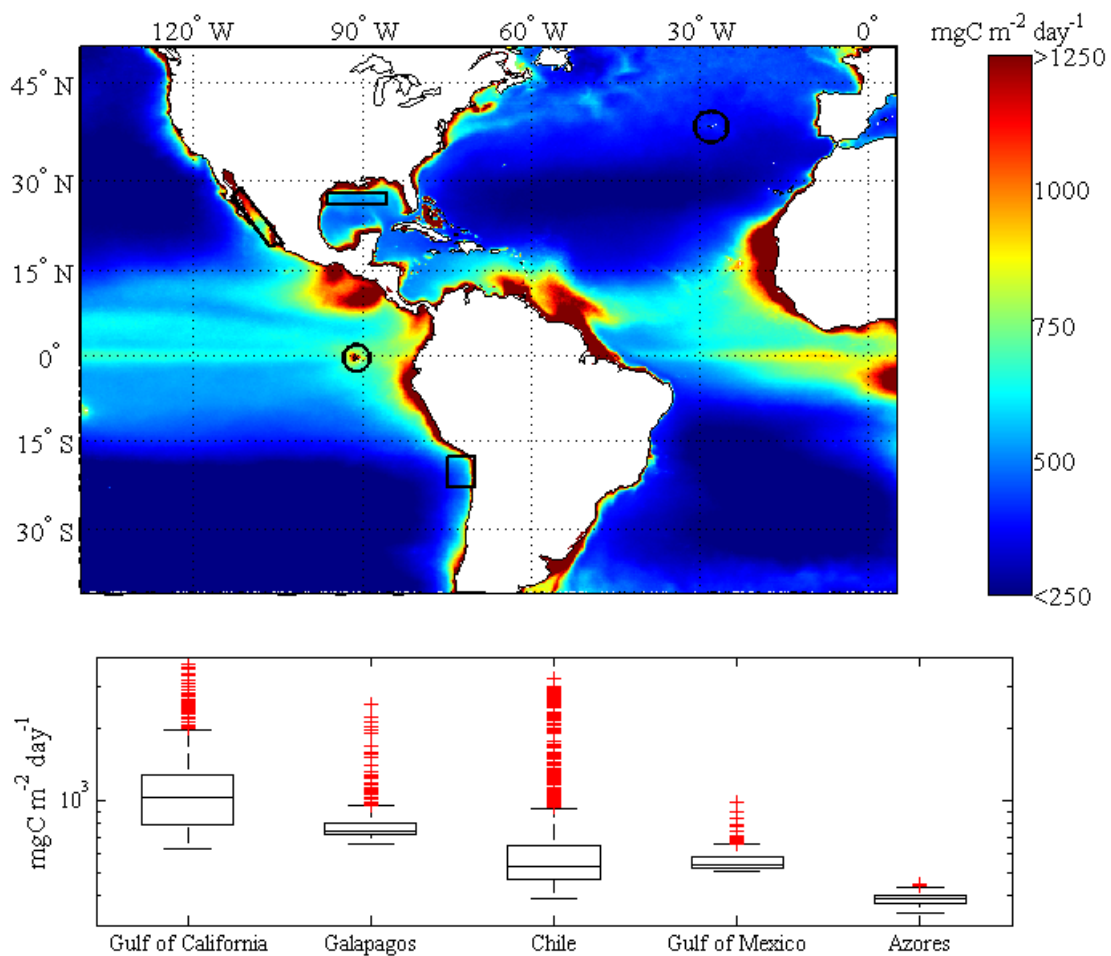


Figure 4.4. Mean primary productivity rate for months between September 1997 and August 2007 calculated from SeaWiFS remote sensing data calculated using the Vertically Generalized Production Model (Behrenfeld & Falkowski, 1997), downloaded from <http://www.science.oregonstate.edu/ocean.productivity/custom.php>. Five zones centred at the locations of the studies by Christal *et al.* (1998), Coakes & Whitehead (2004), Jaquet & Gendron (in Press) and the present study, are shown. The radii for the Azores and Galapagos circular areas are about 250km; the spatial scale of concentrations of sperm whale according to Whitehead (2003). Lower panel shows boxplots of the primary production rate values for the cells in each of the five areas shown on the top plot.

The locations from where comprehensive sperm whale social structure has been published, Galapagos, Chile and Gulf of California (Christal *et al.* 1998; Coakes & Whitehead, 2004; Jaquet & Gendron, in Press) are all very productive under the influence of ocean Eastern boundary, coastal and equatorial effects. In contrast, as can be seen in Figure 4.4, the Azores is a much less productive environment, situated in the North Atlantic subtropical anticyclonic gyre, characterized by oligotrophic conditions and low productivity (Frazel & Berberian, 1990; Longhurst *et al.*, 1995). If these differences in primary production are reflected in the amount of available prey for sperm whales, intraspecific competition for food is expected to be greater in the Azores where resources are fewer.

Little is known about the bathypelagic and mesopelagic Cephalopoda that make up most of the sperm whales' diet, and little inference about their distribution can be made. However sperm whales show variation in the relative proportion of different cephalopod families in their diets between locations. Whales in the Azores seem to feed mostly on squid of the Octopoteuthidae and Histiotheuthidae families, whilst Ommastrephidae and Ancistrocheiridae are additional diet components in Chile and the Galapagos respectively (Whitehead, 2003). Differences in the abundance, population dynamics and distribution of prey between the Azores and the Eastern Pacific locations, are potentially reflected in sperm whale intraspecific competition and consequently social structure, with group formation in the Pacific being supported by larger aggregations of prey.

The previous studies from the Pacific provided until now a well established image of the social structure of sperm whales, mostly due to the mutual support of the findings from several locations within that ocean. The finding of the absence of multi-unit group formation in the Azores indicates that this level of association is not an omnipresent feature of the species social organization. I hypothesise that the relative advantages of multi-unit group formation in sperm whales, such as a larger number of conspecifics for communal defence, are reduced in ecological conditions where intraspecific scramble competition is increased (by low prey concentration). Under such conditions the benefits of forming social units, for example the cooperative care of calves, remain, but the disadvantages of forming larger groups are higher.

Considering the wide ranging distribution of female sperm whales, the ability to alter group size in response to varying ecological conditions would provide an advantageous adaptive flexibility. The studies so far published present an overall description of sperm whale social structure across several years. No analysis of sperm whale social structure in varying ecological

conditions at a single location has been published. Such an analysis would help to clarify if variations in social structure due to ecological conditions were the result of fixed adaptations to local prevalent conditions or, similar to savannah elephants, if sperm whale units vary group formation depending on the experienced conditions.

The conclusions drawn here are limited by the scarce information available on sperm whale ecology, particularly its prey. This precludes accurate conclusions about potential effects in social structure. Another limiting factor is the lack of social structure data from other locations for comparison. Future studies using similar methods are needed to understand better the variation in sperm whale social structure across ecological variation.

In conclusion, this study provides new data on the social structure of sperm whale populations in the North Atlantic Ocean, which supports a previous suggestion of differences between the Atlantic and Pacific Oceans. Results show that female and immature sperm whales in the Azores form long term social units but do not form temporary groups as found in the Pacific. Therefore, I suggest that, similar to what has been found for other mammalian species, differences in ecological conditions, mainly primary production and predation, cause the differences found in sperm whale social structure.

CHAPTER 5

Variation in sperm whale coda repertoires within the North Atlantic Ocean

5.1. Introduction

5.1.1. Variation in sperm whale codas

The study of variation in communication signals is important to inform understanding of how they are influenced by selective pressures they are subject to. When temporal changes in culturally transmitted signals is low, this variation may reliably reflect ancestry (Barrett-Lennard 2000; Deecke *et al.*, 2000). Because cultural variation is faster than genetic variation, it has the potential to reflect more recent changes in population structure than genetic analysis. A species where the study of communication signals is particularly useful in revealing population structure is the sperm whale (*Physeter macrocephalus*) where signal variation was the only characteristic that was a reliably structured trait at spatial scales of less than an ocean basin (Whitehead & Mesnick, 2003).

The sperm whale is a social cetacean species. This is particularly the case for females, calves and immature animals of both sexes which live in social units of 11-12 animals on average (Christal *et al.*, 1998). Social units are defined as groups of whales that remain associated for periods of years. These generally matrilinear units occur in subtropical and tropical waters (Rice, 1989) and their composition is stable over decades (Whitehead & Weilgart, 2000) albeit with occasional movements of individuals among units (Christal *et al.*, 1998). These units frequently form larger groups with one or two other units that persist for days (Whitehead & Weilgart, 2000). Members of groups move in a coordinated fashion, often spreading over hundreds or thousands of meters of ocean (Whitehead, 2003). Males disperse from their natal units at a mean age of about 6 years, and gradually move to cold-water feeding grounds. In their late 20s they begin to make migrations to

the tropics to mate (Whitehead & Weilgart 2000). According to genetic evidence mating generally occurs outside the natal group (Lyrholm *et al.*, 1999; Engelhaupt, 2004).

Occasionally sperm whales produce stereotyped series of 2 to 40 clicks called codas which are assumed to have a communicative function (Watkins & Schevill, 1977; Whitehead & Weilgart, 1991; Schulz, 2007). Within the Pacific Ocean, Weilgart & Whitehead (1997) found evidence of both group specific dialects and geographical variation in coda repertoires. Sperm whale social units in the Pacific Ocean that share their coda repertoire can be considered to be members of larger groupings called clans which also share mtDNA haplotypes and cannot be distinguished genetically (Rendell & Whitehead, 2003b). Because clans are often sympatric and because of the evidence of gene flow among them, their differing acoustic repertoires are best explained by cultural transmission (Rendell & Whitehead 2003b). Within these clans Rendell & Whitehead (2005a) found reduced similarity at geographic scales which approximately correspond to that of sperm whale home ranges (200 - 1000km). Sperm whale social units preferentially associate and form groups with other units of the same clan despite the fact that units from different clans are often sympatric (Whitehead, 2003).

Additional research in the Pacific has discovered differences in diet, habitat use, foraging and reproductive success among sympatric sperm whale clans (Whitehead, 2003; Marcoux *et al.*, 2007a; 2007b). For example two of the clans found in the Galapagos Islands seem to respond differentially to the El Niño/Southern Oscillation (ENSO) oceanic climate phenomenon. The “Regular” clan shows better feeding success than clan “+1” in normal cool years, a scenario that is reversed in warmer ENSO conditions (Whitehead & Rendell, 2004). These observations suggest that clan membership has consequences in terms of individual fitness.

It appears that sperm whale populations in the Pacific are structured such that culturally discrete populations often share the same habitat (Rendell & Whitehead, 2003b). The analysis of variation in coda repertoires is the most readily available way to evaluate cultural variation in sperm whale populations. Until now the study of sperm whale population structure inferred by coda repertoire analysis was restricted to the Pacific Ocean. Here I present new data on spatial variation of coda repertoires in the North Atlantic Ocean.

5.2. Methods

5.2.1. Field methods

The basis of the analysis presented here is a collection of sperm whale coda recordings collected between 1988 and 2006 from several research campaigns targeting sperm whales, in several locations in the North Atlantic Ocean, Gulf of Mexico and Caribbean Sea (Table 5.1; Figure 5.1). I collected the Gulf of Mexico coda recordings in 2002 - 2005 as well as the 2006 recordings in the Azores and Sargasso Sea. The 1990s recordings from the Azores and Dominica were collected by the International Fund for Animal Welfare (IFAW) *Song of the Whale* team, and were kindly made available to this study by Jonathan Gordon. The 2004 coda recordings from Iceland were also made by IFAW's *Song of the Whale* team, and kindly made available by Douglas Gillespie. Tyler Schulz and Hal Whitehead from Dalhousie University made available the 2005 recordings from Dominica and Sargasso Sea, and the 1992 recordings from Panama. Sperm whales were tracked using a combination of visual and acoustic methods and recordings of codas were made using a variety of equipment (Table 5.1). Photographic identifications of individual whales were also collected during the same encounters, and individual photographs were quality rated with Q values between 1 (worst quality) and 5 (best quality) (Arnbom, 1987).

5.2.2. Coda repertoires

Codas from recordings made on the same day were grouped into daily repertoires assuming that in each day a single group of whales was tracked. Information on photographically identified individuals was used to amalgamate daily repertoires further into group repertoires. If n_A and n_B are the number of individual whales identified from good quality photographs ($Q \geq 3$) on days A and B respectively and n_{AB} the number of individuals common to both days, then I grouped the daily repertoires if (Weilgart & Whitehead, 1997):

$$n_{AB} \geq 0.25 \times \text{Minimum}\{n_A, n_B\}.$$

Only repertoires containing more than 30 codas with 3 to 12 clicks (99% of the total) were used in the analysis. Coda vocalizations were identified aurally and marked for analysis using Rainbow Click, an automatic click detector program (Gillespie, 1997), which allows the measurement of inter-click intervals (ICIs). The ICIs were exported for further analysis using

custom written programs in Matlab (Mathworks, Inc., Natick MA, USA).

Table 5.1. Location, years and recording equipment for the recordings used in the study.

Region	Years	Organization/project - Vessel	Recording equipment
Azores	1991, 1993, 1995	IFAW - <i>Song of the Whale</i> - 14m auxiliary sailboat	100m towed array; 2x Benthos AQ-4 hydrophone elements; Sony TCD-D1 DAT recorder @ 48kHz
	2006	Whale Watch Azores - <i>Physeter</i>	100m towed array; 2x Benthos AQ-4 hydrophone elements; Minidisc recorder
Dominica	1995, 1996	IFAW - <i>Song of the Whale</i> - 14m auxiliary sailboat	100m towed array; 2x Benthos AQ-4 hydrophone elements; Sony TCD-D1 DAT recorder @ 48kHz
	2005	Dalhousie University - <i>Balaena</i>	100m towed array; 2x Benthos AQ-4 hydrophone elements; Foxtex VF-160 multi-track recorder @ 48kHz
Iceland	2004	IFAW - <i>Song of the Whale II</i> - 21.5m sailboat	100m towed array; 2x Benthos AQ-4 hydrophone elements,
Gulf of Mexico	2001-2005	TAMUG/SWSS - <i>Gyre</i> - 55m research ship	100m or 200m towed array; 2x Benthos AQ-4 hydrophone elements; Creative Labs XTG sound card @ 96kHz or 2x HTI-96-MIN hydrophones; Creative Nomad recorder @ 48kHz
		SWSS - <i>Summer Breeze</i> - 14m auxiliary sailboat	
Panama	1992	Dalhousie University - <i>Balaena</i> - 12m auxiliary sailboat	30m long towed Benthos AQ-21B hydrophone; Nagra IV-SJ reel-to-reel tape recorder (19 cm/s); Ithaco 453 preamplifier.
Sargasso Sea	2005, 2006	Dalhousie University - <i>Balaena</i> - 12m auxiliary sailboat	100m long towed array; 2x Benthos AQ-4 hydrophone elements

5.2.3. Coda repertoire similarities

Repertoires were compared using a multivariate similarity metric (Rendell & Whitehead, 2003a):

$$S_{AB} = \frac{\sum_{i=1}^{n_A} \sum_{\substack{j=1 \\ l_j=l_i}}^{n_B} \frac{0.001}{0.001 + d_{ij}}}{n_A \cdot n_B},$$

where S_{AB} denotes the similarity between repertoires A and B consisting of n_A and n_B codas respectively, l_i the number of clicks of coda i in repertoire A , l_j the number of clicks of coda j in repertoire B and d_{ij} the distance between ICI vectors. The latter parameter was calculated in two different ways using Euclidean and Infinity norms. This similarity measure was calculated using the absolute ICIs as well as using ICIs standardized by the total duration of the coda (*i.e.* the sum of the ICIs). In the latter case because the sum of standardized ICIs always equals unity, one of the values is redundant, and so the last ICI was not included in the analysis.

The similarity metrics were used to construct four average linkage dendrograms corresponding to the combination of either absolute ICIs (AbsICI) or standardized by duration (RelICI), and either Infinity or Euclidean norms. The dendrograms' ability to represent the original pairwise distances between repertoires was measured by calculating the cophenetic correlation coefficients (Sokal & Rohlf, 1962). For each dendrogram the clustering reliability was evaluated using a bootstrap procedure as used by Rendell & Whitehead (2003b). At each bootstrap iteration the codas from each repertoire were randomly sampled with replacement prior to calculating the pairwise repertoires similarities and building the hierarchical clustering linkages. The reliability for each dendrogram branch was measured as the proportion of bootstrap iterations in which it was recreated.

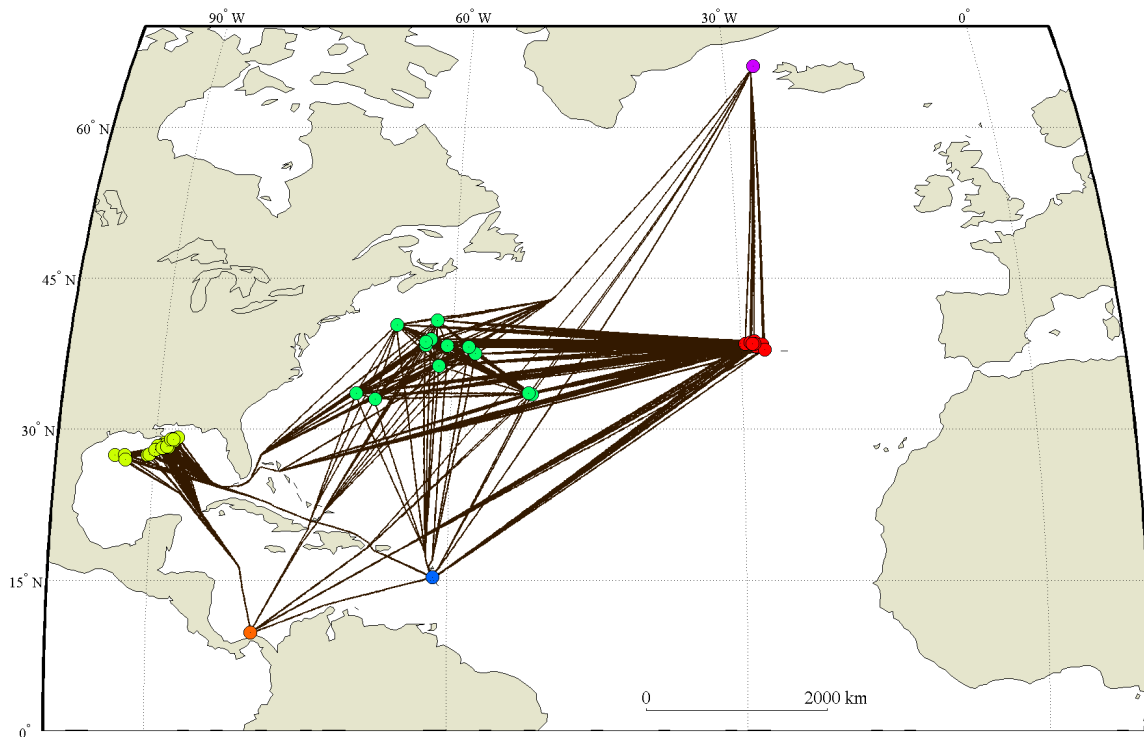


Figure 5.1. Map of coda recording locations colour coded by region: ● Azores; ● Sargasso Sea; ● Iceland; ● Dominica; ● Panama; ● Gulf of Mexico. Also shown are the shortest distance lines over waters deeper than 200m between each pair of repertoires.

The dendrograms were compared to identify common patterns across distance measures and ICI standardization. The variation in coda patterns driving the clustering was investigated by plotting the first against the second ICIs for three click codas, and the first two principal components of a principal component analysis for four click codas when using absolute ICIs. For ICIs standardized by duration (RelICIs) a histogram of the first relative ICI for three click codas was plotted, and the first interval was plotted against the second for four click codas. For the remainder of coda lengths the first two principal components were plotted against each other.

5.2.4. Spatial variation of coda repertoires

The spatial variation of coda repertoires was investigated using Mantel matrix correlation tests which allow correlations between non-independent data matrices from pairwise comparisons to be tested (Mantel, 1967; Schnell *et al.*, 1985). Under the assumption that relative location (*i.e.* how repertoires are arranged in space with respect to each other) is more meaningful than the absolute geographic location, the tests were performed on a square repertoire similarity matrix (Euclidean norm, Absolute ICIs) and a matrix of the same size of pairwise spatial distances between repertoires. The spatial distances were calculated as the lengths of the shortest path between repertoires over waters deeper than 200m. This depth was chosen as the average limit of the continental shelf, inshore of which sperm whales are rarely found (Whitehead, 2003). The shortest path was calculated by the Fast-Marching algorithm (Sethian, 1996, Deschamps & Cohen, 2001) implemented by Gabriel Peyre in the Fast Marching Toolbox for Matlab (downloaded from <http://www.mathworks.com/matlabcentral/fileexchange/loadFile.do?objectId=6110&objectType=FILE>). The Fast Marching algorithm finds the shortest path on a surface using a gradient descent of the distance function. A global gradient grid was created from the General Bathymetric Chart of the Oceans (GEBCO) one minute grid (IOC *et al.*, 2003) by assigning a value of 2^{-32} to all cells with depths over 200m, and one to all other cells. A two-dimensional version of the Fast Marching algorithm was used on this grid to find the shortest path between the mean locations of repertoires for each pairwise comparison (Figure 5.1). The geographical distance along the path obtained in this way was calculated by summing the great circle distances between the central geographical coordinates of the grid cells making up the path. This last measure corresponds to the actual physical separation between the recording locations that the whales would have to swim through typical habitat.

5.3. Results

5.3.1. Coda repertoires

A total of 15,246 codas having between 3 and 12 clicks, distributed by 56 group repertoires were used in the analysis (Table 5.2).

Table 5.2. Number of codas and repertoires recorded for each region sampled

Region	Number of repertoires	Number of codas
Azores [Azo]	11	3238
Gulf of Mexico [GoM]	28	8051
Sargasso Sea [SaS]	13	3012
Caribbean [Car]	2	524
Iceland [Ice]	1	123
Panama [Pan]	1	298
Σ	56	15246

5.3.2. Coda repertoire similarities

The calculated average linkage dendrograms had cophenetic correlation coefficients (CCC) between 0.932 (RelICI, infinity norm) and 0.944 (AbsICI, Euclidean norm) indicating a good representation of the original pairwise distances between repertoires (Figure 5.2).

The variance explained by first two principal components used for identification of the ICI patterns driving clustering ranged from 83% for 12 click codas to 100% for four click codas when using AbsICIs (Figures 5.3 to 5.5) and from 69% for 12 click codas to 85% for five click codas for RelICIs.

Generally all the dendrograms for both absolute and relative ICIs, and Euclidean and infinity norm metrics exhibited three major groupings of repertoires. A first branching consistently separated a group of two repertoires - PaN_10058, and GoM_238520 – from the remainder with a bootstrap support between 0.36 (AbsICI, Infinity norm) and 0.70 (AbsICI, Euclidean norm)(e.g. Figure 5.2). The first of these is the single repertoire from Panama recorded in 1992 and the latter corresponds to a group of whales identified as a '*bachelor group*' of immature males in the Gulf of Mexico in 2005. Three other repertoires (SaS_30010, Azo_1007, Azo_1014) clustered in this

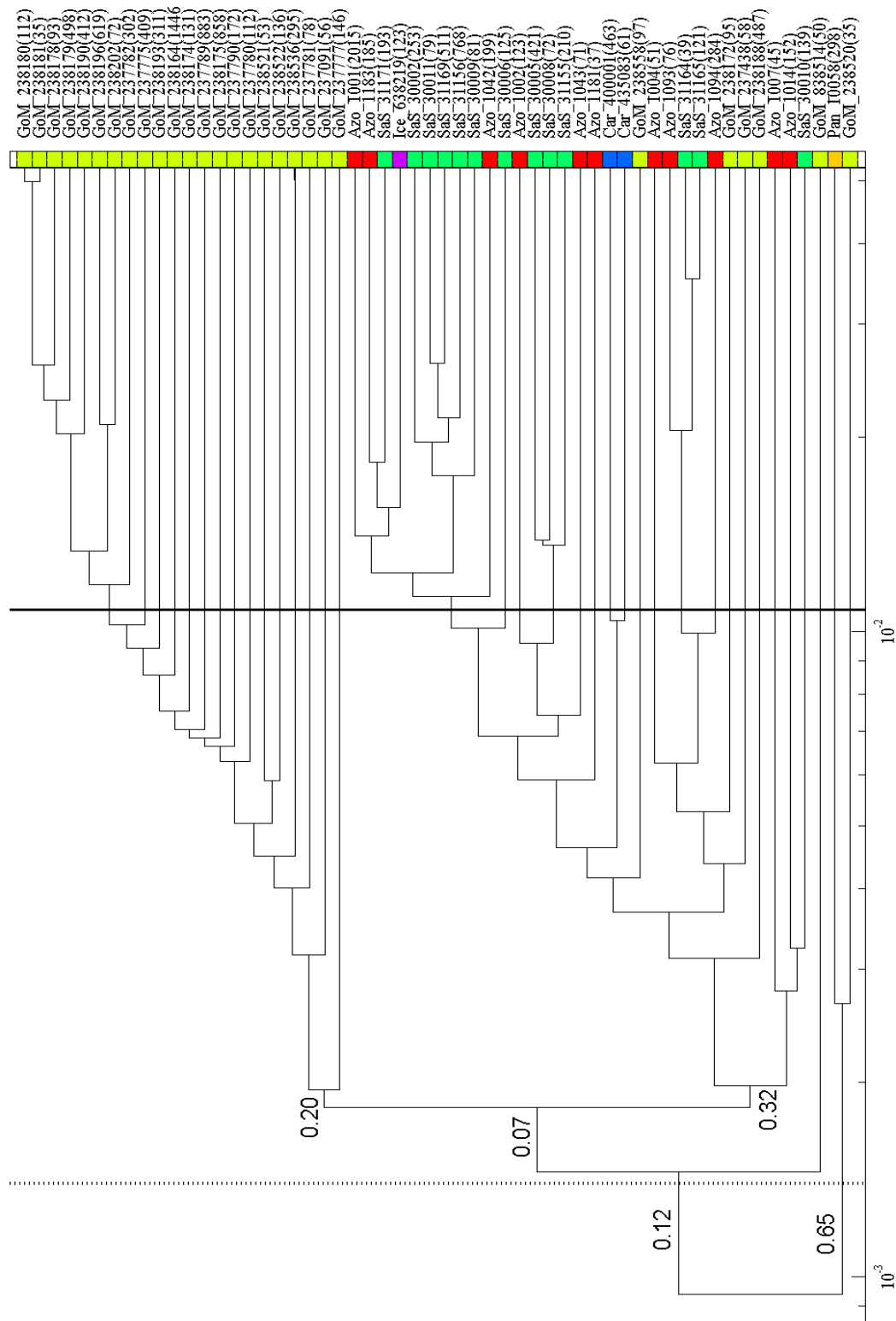


Figure 5.2. Average linkage dendrogram (CCC=0.932) of code repertoires (n=56) from pair-wise code similarities (Rendell & Whitehead, 2003) using standardized ICIs and infinity norm. Bootstrap values are represented for the major branching nodes. Values in parenthesis next to repertoire names correspond to the number of codas in the repertoire. Colors indicate sampling region using the same colour code as figures 5.1, and 5.3 to 5.5. Vertical lines indicate the mean between (dotted line) and within (solid line) clade similarity values for the Pacific from Rendell & Whitehead (2003)

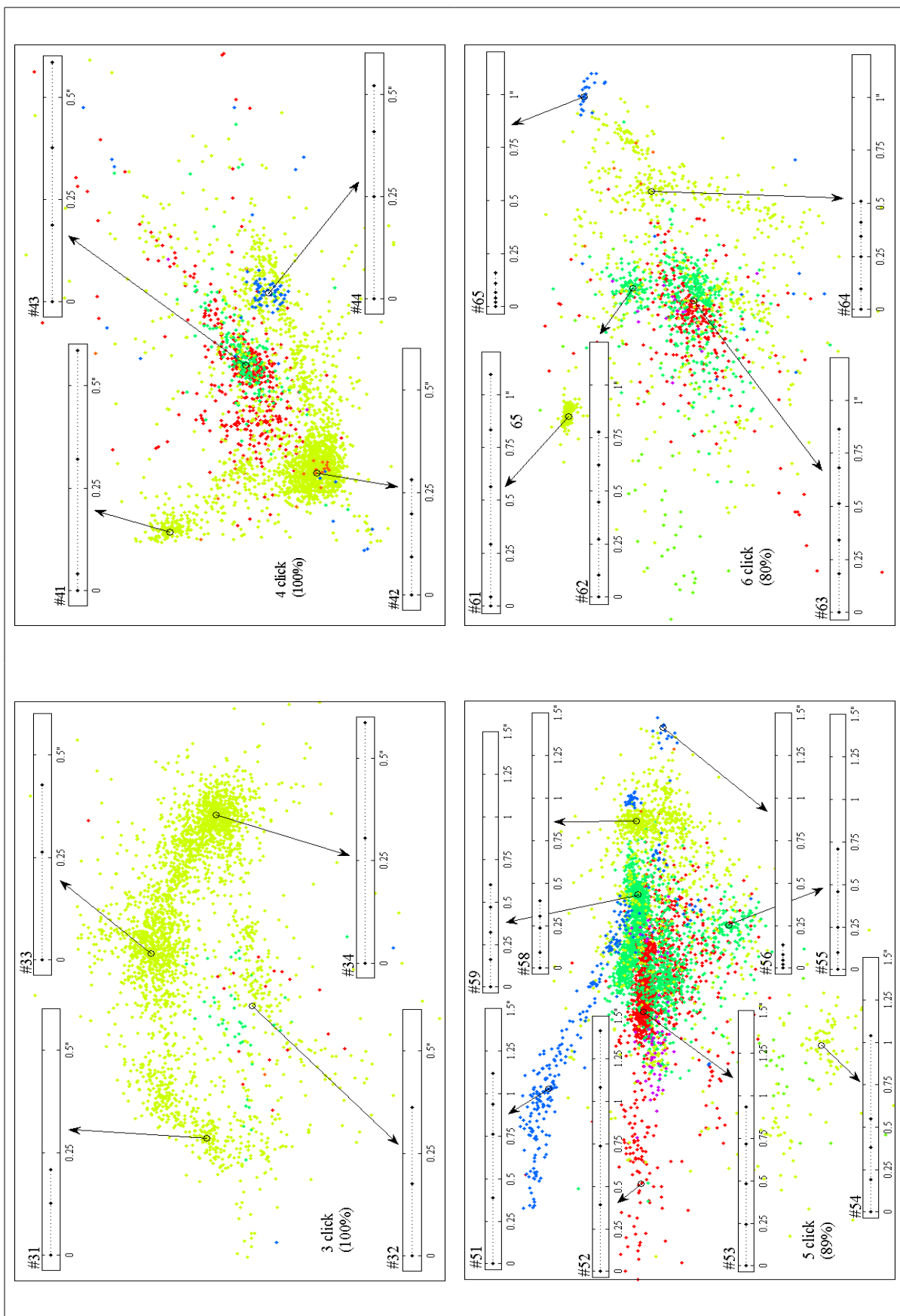


Figure 5.3. Plots of first against second ICI (3 click codas) and first two principal components (4 to 6 click codas) plots. Points are colour coded by recording region using the same code as other figures. Percentage in parenthesis represent the variance explained. Insets show example coda patterns.

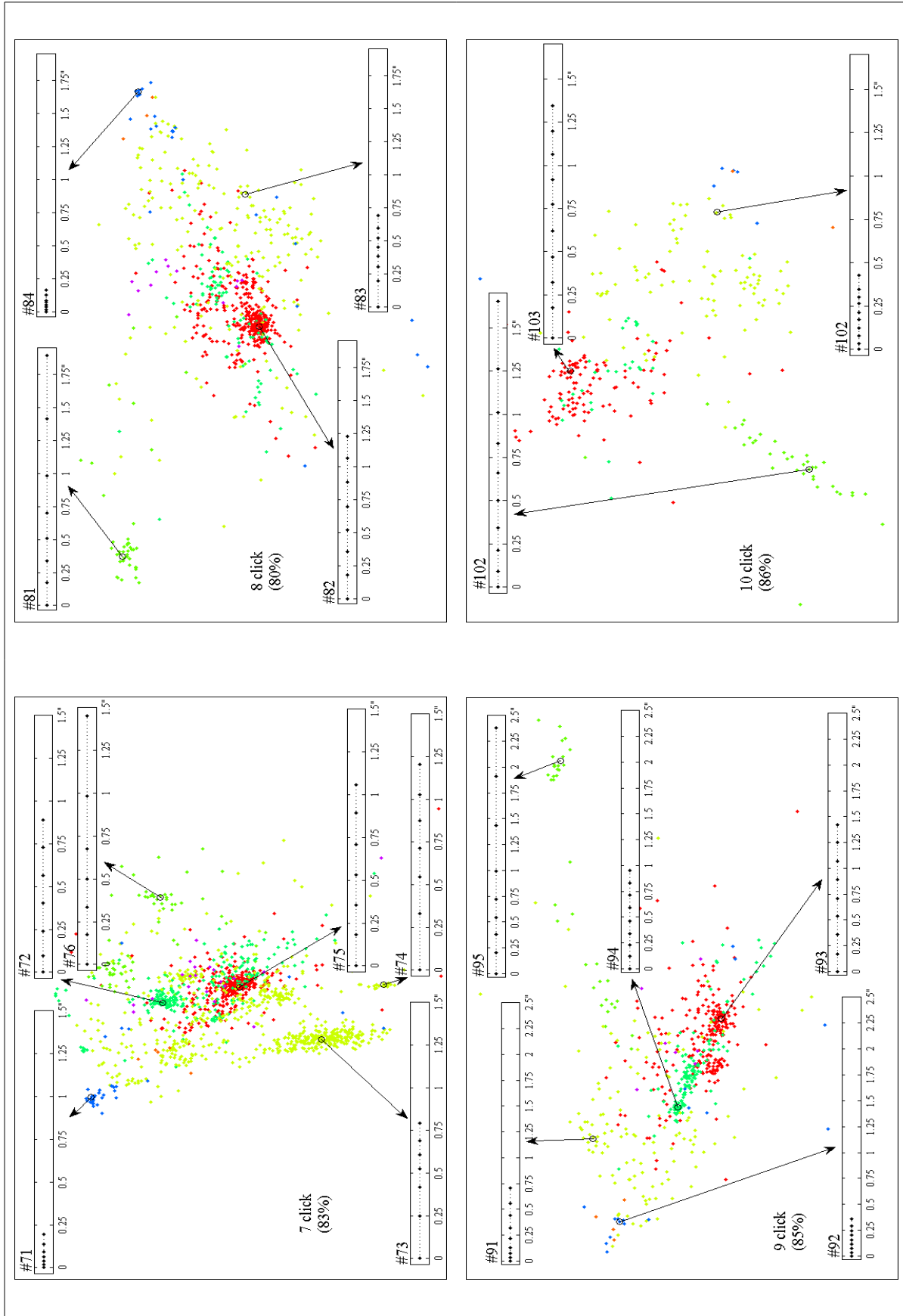


Figure 5.4. Plots of first two principal components for 7 to 10 click codas. Points are colour coded by recording region using the same code as other figures. The percentage in parenthesis represents the variance explained. Insets show example coda patterns.

branch on a few occasions. These repertoires are characterized by having high variation in ICIs and depending on which codas were randomly selected during bootstrap they clustered with repertoires from all regions. By removing these three repertoires from the analysis, bootstrap support for the separation of Pan_10058 and GoM_238520 from other repertoires increased to values between 0.871 and 0.989.

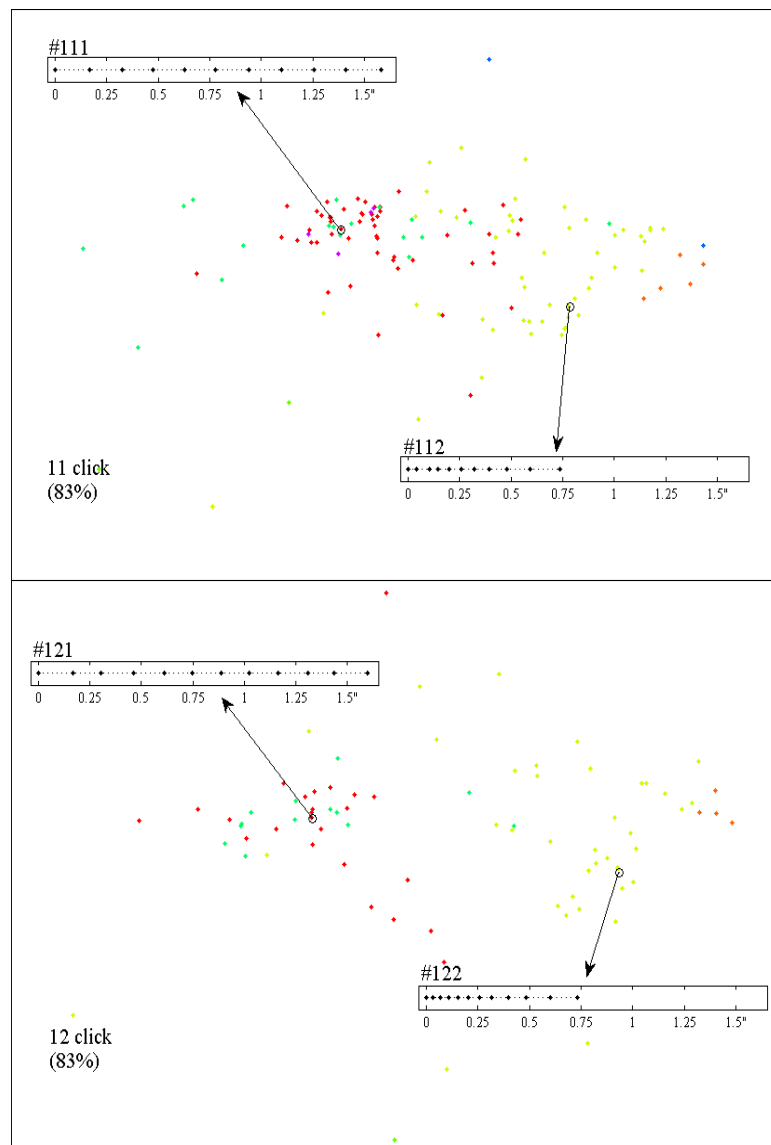


Figure 5.5. Plots of first two principal components for 11 and 12 click codas. Points are colour coded by recording region using the same code as other figures. The percentage in parenthesis represents the variance explained. Insets show example coda patterns.

The separation of repertoires Pan_10058 and GoM_238520 was in part driven by differences in the number of clicks. 98% of codas from these repertoires have between six and 11 clicks. The codas from these repertoires are characterized by regularly spaced clicks lasting for over one second, which tended to be the longest within groups of codas with the same number of clicks in the dataset.

A second major branching, also consistent across analyses, grouped the majority of the repertoires from the Azores and Sargasso Sea (*e.g.* Figure 5.2). More than 93% of the codas from the Azores and Sargasso Sea repertoires had between four and 10 clicks with the exception of repertoires Azo_1002, Azo_10014 and Azo_1007, in which cases codas with 3, 11 and 12 clicks had a representation of more than 10%.

Bootstrap values ranged between 0.108 (AbsICI, Infinity norm) and 0.436 (AbsICI, Euclidean norm) when including all repertoires but increased to between 0.476 (AbsICI, Infinity norm) and 0.851 (RelICI, Euclidean norm) when removing repertoires SaS_31164, Sas_31165, Azo_1093, Azo_1094, SaS_30010, Azo_1007, Azo_1014, and GoM_237777 which showed a tendency to cluster inconsistently across all branches.

Codas from the Azores and the Sargasso Sea tended to be '*regular*' *i.e.* all clicks were approximately equally spaced (*e.g.* Types #43 and #63; Figure 5.3). However there was a tendency for separation between codas of this type from different regions. This can be seen in the principal components plots (*e.g.* Sargasso: types #53, #72, #94, #102; Azores: types #59, #75, #93, #103; Figures 5.3 and 5.4) and these patterns tended not to overlap with those found in the Gulf of Mexico.

The majority of the codas from Dominica had between four and six clicks and had temporal patterns that were distinct from those of other regions (*e.g.* types #51, #56 and #65 in Figure 5.3; type #71 in Figure 5.4). Despite these differences both the repertoires from Dominica always clustered within the branch encompassing the Sargasso Sea and Azorean repertoires, but they were more similar to themselves than to others in the Atlantic Basin (bootstrap support >0.876) in the majority of the dendrograms.

The single repertoire from Iceland also clustered with the Atlantic basin branch in the majority of dendrograms. No coda patterns typical of the Icelandic repertoire were found, and most Icelandic codas were within the typical variation found for the Sargasso Sea and Azores.

When the Iceland and Dominica repertoires did not cluster within the Atlantic basin branch, bootstrap support for the branch encompassing both these repertoires was much lower than when they did. Also, the Gulf of Mexico repertoires GoM_237777, GoM_238188 and GoM_238558, tended to group with the Atlantic basin repertoires, the latter in all dendrograms and the first two only when using relative ICIs.

All dendrograms exhibited a consistent third major grouping of most of the Gulf of Mexico repertoires that separated from most of the Atlantic basin repertoires (*e.g.* Figure 5.2). Although this separation was consistent, its composition was variable and the branch was supported by low bootstrap values ranging from 0.108 (AbsICI, Infinity norm) to 0.436 (AbsICI, Euclidean norm). The Gulf of Mexico repertoires were characterized by having mostly three to five click codas with patterns that did not overlap with those from other regions in most cases (*e.g.* types #31, #33, #34, #41, #42, #58, #61, in Figure 5.3).

Within the Gulf of Mexico, some coda types seemed restricted to a few repertoires. Repertoire GoM_238188 contained coda type #61 (Figure 5.3) that was not shared with others. Coda type #74 (Figure 5.4) occurred mostly in repertoires GoM_237790 and GoM_238164.

A group of two repertoires from the Sargasso Sea and two from the Azores (SaS_31165, SaS_31164, Azo_1093 and Azo_1094) tended to be grouped together consistently with high bootstrap values. These four repertoires were often grouped in the major branch containing the GoM repertoires. Apart from these, no other Atlantic basin repertoires clustered within the Gulf of Mexico branch. When these Atlantic repertoires clustered within the Gulf of Mexico branch repertoires GoM_237438 and GoM_238172 were the two most similar to them. These two GoM repertoires were also the closest repertoires to SaS_31165, SaS_31164, Azo_1093 and Azo_1094 when they occurred in the main Atlantic Basin branch. The two SaS repertoires correspond to recordings made on consecutive days. These may have been recordings of the same group of whales encountered on consecutive days which the photographic identification criterion failed to join in a single group repertoire, which would explain their high similarity and consistent clustering. The two Azorean repertoires were recorded 11 days apart in 1995, and there were no identified whales common to those days suggesting that these were not part of the same group.

Overall, the repertoire similarity values were higher than the mean values found between clans but lower than those found within clans in the Pacific using the same metrics (Rendell &

Whitehead, 2003a; 2003b). Bootstrap support values for the major dendrogram groupings were lower in the Atlantic than for the branches representing the different Pacific clans.

5.3.3. Spatial variation

With the exception of the repertoires within the Azores, there is a significant negative correlation between repertoire similarity and spatial distance (Table 5.3). The correlations were smaller when regions from within the North Atlantic basin were combined than when combinations contained the Gulf of Mexico region, and smaller than the correlation using all sampled regions.

Table 5.3. Correlation between coda repertoire similarity and distance matrices (r), and Monte Carlo Mantel significance (p) obtained from 10,000 permutations. Values are shown for single regions represented by more than two repertoires and for combinations of regions spanning different parts of the area sampled. Also given are the range of values of the respective similarity and distance matrices.

	r (p)	similarity range ($\times 10^{-3}$)	distance range (km)
Azores	0.0715 (0.59358)	0.499 - 5.515	5 - 235
Sargasso Sea	-0.3343 (0.02001)	0.085 - 19.216	33 - 1,990
Gulf of Mexico	-0.3677 (0.00189)	0.022 - 18.425	3 - 805
Azores + Sargasso Sea	-0.1260 (0.03498)	0.085 - 19.216	5 - 4,291
Azores + Sargasso Sea + Iceland	-0.1277 (0.06500)	0.085 - 19.216	5 - 6,722
Azores + Sargasso Sea + Dominica	-0.2235 (0.00356)	0.085 - 19.216	4 - 5,767
Gulf of Mexico + Dominica	-0.3696 (0.00142)	0.022 - 18.425	4 - 4,611
Gulf of Mexico + Panama	-0.3681 (0.00023)	0.022 - 18.425	3 - 3,365
Gulf of Mexico + Panama + Dominica	-0.4282 (0.00011)	0.022 - 18.425	4 - 4,611
All regions	-0.4603 (<0.00001)	0.022 - 19.216	3 - 10,527

5.4. Discussion

The analysis of the spatial variation in sperm whale coda repertoires in the North Atlantic revealed a picture unlike that previously found in the Pacific. Rendell & Whitehead (2003b) were able to allocate sperm whale groups in the Pacific Ocean to clear, often sympatric vocal clans. These clans exhibited differences in habitat use, feeding habits, foraging and reproductive success (Whitehead, 2003, Marcoux *et al.*, 2007a; 2007b), which indicates that the methods were effective

at distinguishing biological meaningful classes. Using similar metrics to the ones used by Rendell & Whitehead (2003) to analyse codas from the North Atlantic and Gulf of Mexico, I have not found any evidence of sympatric but vocally distinct clans. This result persisted even when using non standardized ICIs, which show higher variability in general.

The differences in variation of coda repertoires found between the North Atlantic and Pacific ocean basins are unlikely to be due to differences in the acoustic data collection methods. The differences found in coda timing patterns were compared within ocean basins where recording methods were identical. Within the Pacific, groups of sperm whales recorded in the same way, showed higher coda repertoire differentiation among themselves than that found among North Atlantic groups, which were also collected using consistent methods within themselves.

The significant negative correlation between repertoire similarities and geographic distance in the North Atlantic, and the finding of coda patterns unique to certain regions indicates that the variation of coda repertoires in the North Atlantic is mostly geographically structured. This contrasts with the Pacific, where only after removing the variance in coda output attributed to clans is there a correlation between repertoire similarity and spatial distance, indicating that at the spatial scales analysed the clan effect is stronger than geography (Rendell & Whitehead, 2005a). The lack of significant correlation between repertoire similarity and distance within the Azores suggests that there is no geographic structuring at the scale of a few hundred kilometres, suggested as the spatial scale for concentrations of sperm whales and the scale of movements over periods of weeks to months (Whitehead, 2003). The lack of geographic structure may be due to movements of social units with similar repertoires at these scales.

The bootstrap support values for the two main dendrogram divisions (North Atlantic basin, Gulf of Mexico) were lower than the ones found between vocal clans in the Pacific (Rendell & Whitehead, 2003b). In addition, only the separation of the repertoires from Panama and the bachelor group from the remainder exhibited a similarity value lower than the mean between Pacific clans. This indicates that overall, the coda repertoire variation is lower in the North Atlantic Ocean.

The high similarity between the single repertoire from Panama and that from a Gulf of Mexico male '*bachelor group*' suggests a link between these areas, possibly explained by male dispersal. Male sperm whales are known to disperse from their philopatric natal units to form loose

aggregations called '*bachelor groups*' (Gaskin, 1970; Best, 1979; Whitehead, 2003). These move considerably longer distances than females (Whitehead, 2003). The '*bachelor groups*' recorded in the Gulf of Mexico may have originated in the Western Caribbean Sea and moved 2000km NNW through the Yucatan strait into the Gulf of Mexico, carrying with it a coda repertoire typical of its area of origin. However, the temporal stability of these male groups and the functionality of codas within them is unknown. This may also indicate qualitative differences in the codas produced by bachelor groups which may obscure or replace geographical variation for this component of the population

The two repertoires from Dominica were more similar to each other than to any other repertoire, and more similar to the repertoires of the North Atlantic basin than to the Gulf of Mexico. The most common coda pattern found in this region (Type #51, Figure 5.3), had been recognized as the most common in the area as long ago as the early 80s (Moore *et al.*, 2003), suggesting temporal stability of vocal repertoires within this region.

Codas are most commonly recorded from social groups of females and so the recording of codas in Icelandic waters, at a latitude where usually only males are found, is noteworthy. At the time of recordings no calves were seen, and it was not clear if the group recorded was composed of females.

The differences in coda repertoire variation between the Eastern Tropical Pacific and the North Atlantic are paralleled by the differences I have found in social structure between the two areas (Chapter 4). The apparent lack of temporary multi-unit group formation found in the Azores may remove the need to identify social units as potential group partners. This could account for the absence of vocally distinct clans in the wider North Atlantic and Gulf of Mexico, assuming of course that the social structure that I have shown in the Azores is similar to that in the wider oceanic basin, or at least for the regions sampled. As argued in Chapter 4, the absence of multi-unit group formation in the Azores may be due to reduced predation pressure and to increased costs of forming larger groups because of reduced food availability compared to high productivity areas in the Eastern Tropical Pacific.

The idea that vocal differences between Pacific vocal clans function primarily as the means by which social units identify others with which to associate, assumes that there are advantages in associating with certain units over others. This is consistent with preferred group formation among

units with similar vocal repertoires in the Pacific (Rendell & Whitehead, 2003b; Whitehead, 2003).

Using stable isotope analysis Marcoux *et al.* (2007b) found differences in diet between clans in the same area and proposed that these are due to different foraging behaviours, with some groups using more inshore resources and others depending more on pelagic food sources. Similar ecological niche preferences and requirements for coordinated group movement within multi-unit groups with a particular foraging behaviour may favour the grouping of units possessing that same behaviour. The fact that groups from different clans seem to move through habitat and synchronize diving in different ways suggests that this is the case (Whitehead, 2003). Whales could benefit from associating with others with similar movement patterns and foraging strategies, because they would be more likely to use the same space in similar ways. This benefit may be a selective pressure for the development of signals that are specific to groups having similar foraging specializations in the Pacific. The lack of multi-unit group formation may remove the pressure for vocal differentiation between units resulting in the apparent absence of sympatric vocal dialect groups in the North Atlantic, or units may not have specialised in their feeding strategies.

Some studies of the geographical variation in bird song between closely related species have noticed cases where differences in song type are larger in sympatry than in allopatry (Brown & Lemon, 1979; Wallin, 1986). This has been explained as a form of character displacement where the presence of the other species leads to divergence of song characteristics to maximize differences between them. Similarly, the acoustic structure of chimpanzee (*Pan troglodytes*) pant hoots has also been shown to be more distinct between neighbouring groups than between distant communities. This variation is not explained by genetic differences and suggests vocal convergence within groups and vocal divergence between neighbouring groups (Crockford *et al.*, 2004). In the Pacific character displacement might account for the divergence of coda repertoires between social units with different foraging specializations, leading to the evolution of vocal clans. If vocal clans are the result of a pressure for differentiation of units possessing different foraging strategies, and foraging specializations are not present in the North Atlantic, this could explain why the level of differentiation among sympatric vocal clans found in the Pacific is greater than that found among groups within and among regions in the North Atlantic.

Without any selection process for differentiation between sympatric groups, the observed geographic variation across the North Atlantic may be explained by cultural drift among philopatric social units. Using samples collected in the Azores and Gulf of Mexico, Lyrholm *et al.*, (1999) and Engelhaupt (2004) found support for breeding outside maternal groups and transfer of genetic

material over long ranges, which does not suggest bi-parental inheritance of coda repertoires. Findings of low diversity but significant differentiation between regions and two mtDNA haplotypes unique to the Gulf of Mexico support social philopatry of females (Engelhaupt, 2004). Long term photographic identification data also support long term philopatry, at least in the Azores where several social units have been re-identified over periods of up to 19 years (Chapter 4). In the Northern Gulf of Mexico, sperm whales have been identified in the same group on occasions separated by periods of up to two years (Jochens *et al.*, 2008). No long term identification data exist for Sargasso Sea and Iceland for comparison.

The sympatric occurrence of vocally distinct groups in the Pacific was used to argue against codas constituting local adaptations. The lack of such observation in the Atlantic precludes the same interpretation. However, it is unlikely that codas constitute optimal adaptations to local conditions. Sperm whale clicks are short broadband pulses which do not have much signal parameter space for coding in the frequency domain. The coding scheme of codas seems to be based on the time domain through variation of the ICIs. Such a scheme is less constrained by propagation effects than other signals based on frequency domain coding, and therefore it is not expected to be affected by local conditions.

Despite suggestions of less direct genetic effects that may determine coda repertoires, such as genomic imprinting (Brown, 2001) and differences in the effectiveness of mitochondrial proteins affecting the energetic budget of animals (Janik, 2001), social learning remains the most parsimonious explanation for the variation of coda repertoires reported here. The macrogeographic (Mundinger, 1982) differentiation between repertoires of groups that likely never interact (*e.g.* from the Gulf of Mexico and the Azores) may not be functional and only the product of imperfect cultural transmission of repertoires within units/groups, *i.e.* cultural drift.

In conclusion I have found that the variation of sperm whale coda repertoires in the North Atlantic and Gulf of Mexico basins is mostly geographic. It suggests differentiation of the Gulf of Mexico from the North Atlantic basin which in turn shows weak, but detectable, spatial variation in repertoires. This pattern of variation is unlike that found for the Pacific Ocean, where sympatric dialects were found. I suggest that the differences in coda repertoire variation between ocean basins may be related to differences in the social structure between the locations studied in both oceans which in turn reflect ecological differences (Chapter 4). In the Pacific the differences in coda repertoires between clans may result from selection for advantages gained by multi-unit group formation between social units with similar foraging behaviour. The absence of temporary multi-

unit groups in the Atlantic may thus remove the pressure for vocal differentiation between units. The differences in coda repertoires among different geographical locations here may result from cultural drift.

CHAPTER 6

General discussion

6.1. Introduction

The sperm whale has one of the largest geographic ranges of any mammal on Earth. Throughout this range the species inhabits habitats in both high and low latitudes and is subject to a range of various ecological conditions (Rice, 1989; Whitehead, 2003). The evolution of the natural world's most powerful long range bio-sonar, based on pulsed sounds, has undoubtedly given the species a unique advantage for exploiting resources inaccessible to other marine mammals, and contributed significantly to the success of the species as a mesopelagic predator whose range covers all oceans. The selective pressure for the development of both highly specialized organs that allow the production of loud directional pulses, to an extreme unparalleled in other Odontocetes, and of the neural hardware for processing echoes may have constrained the evolution of communication in this species to the use of similar pulsed sounds.

Group living may well constitute another important adaptation in allowing the species to occupy a wide spatial range and exploit deep waters. Protection in numbers, especially for calves, and allomaternal care, may have been advantageous as the species expanded its range into the deep ocean. Sharing the burden of caring for surface-bound calves among social unit members increases the time adult females have available to spend in long and deep foraging dives, compared to the case of a solitary female and her calf. Moreover, it is easier to protect a calf from predators within a group where conspecifics may join forces in defence of calves.

The evolution of such a social system, along with the necessity of coordinated activity among group members, required a communication system. Given the characteristics of the aquatic

medium, where chemical signals disperse in a slow and unpredictable way, and light is greatly attenuated, acoustic communication is the most likely modality for a long range communication system. As mentioned above, sperm whales show extreme adaptations for long range sonar based on the production of powerful click vocalisations. This may have constrained the species' communication system to use similar pulsed sounds resulting in the distinctive and unusual coda vocalisations of sperm whales, a rare example of a rhythm-based communication system.

This interplay between communication signals and social structure has been demonstrated by studies in the Pacific Ocean, where sperm whale social units were found to preferentially group with others who share the same vocal repertoire. Despite these important findings, our knowledge of sperm whale social structure and vocal behaviour is still restricted and comes from studies of populations over a small part of the species' distribution.

In this study I developed and tested two new methods of measuring inter-click intervals from sperm whale clicks. I investigated coda repertoire variation at the individual level within a single social unit to test the hypothesis that variation within coda type could be used for individual identification. I also set out to investigate aspects of sperm whale behaviour in the North Atlantic Ocean to compare with existing findings that were in great part restricted to the Pacific. I studied social structure and coda repertoire variation in the North Atlantic from locations where longitudinal data already existed.

6.2. Automatic inter-pulse interval measurement

Sperm whale clicks have a characteristic multi-pulse structure that allows for the estimation of the whale's size from the measurement of the inter-pulse interval (IPI) (Backus & Schevil, 1966; Norris & Harvey, 1972). This potentially allows for passive acoustic estimation of the size distribution of sperm whale populations (Adler-Fenchel, 1980), and has also been successfully used to investigate individual whale vocal repertoires (Schulz, 2007). However the measurement of IPI is not straightforward, and is in many cases complicated by clicks which do not conform to the expected multi-pulse structure (Zimmer *et al.*, 2005b). In Chapter 2 I developed two new IPI measurement methods that automatically integrate information from several clicks with the objective of providing a fast, accurate, and objective automated means of estimating IPIs from series of clicks made by diving whales, that is also robust to clicks that do not show a clear multi-

pulse structure. These two automatic methods were compared with one manual and three automatic measurement methods in terms of consistency and uncertainty. One of the newly developed methods, that averages the autocorrelation functions of several clicks in a series, provided the most consistent and least uncertain estimates off all the automated methods.

These methods are of considerable applied value for surveys of sperm whale populations. They should also prove to be an important tool in future studies of individual coda repertoires through the use of IPIs, especially for analyses of foraging dive clicks where the multi-pulsed structure is usually not as obvious as coda clicks. When whales within a group have individually distinct IPIs, codas can be assigned to individuals by comparing IPIs from coda clicks to foraging clicks recorded from a single animal (Schulz, 2007). Automatic IPI measurement methods is useful not only in the initial identification of IPIs unique to each individual, but also at later stages if individual repertoires are to be tracked over periods of years where individual IPIs may change due to growth.

6.3. Individual discrimination in sperm whale codas

The identification of preferred associations and avoidances within sperm whale units (Gero, 2005; Gero *et al.*, 2008) is one indication that group members may have a means of identifying other individuals. Due to the limitations of other sensory modalities in the aquatic environment, identity is likely to be transmitted over medium to long ranges using acoustic signals.

The initial description of codas suggested that they were indeed individually specific (Watkins & Schevill, 1977). Since then however, the results of other studies have not been consistent with the hypothesis that coda types or repertoires were individually specific (Weilgart & Whitehead, 1993). Recently Schulz (2007), who investigated the individual coda repertoires within a single social unit, showed that it was not possible to distinguish among five of the seven unit members by their coda type repertoires. However, I hypothesised that variation within coda types could be individually specific and I tested this in Chapter 3. I showed that in one of the three coda types tested, the within coda type variation of non-standardized inter-click intervals allowed discrimination between individual whales. The fact that one coda type allowed for individual distinction and others did not, suggests that only a subset of coda types may function in this way.

Coda types with different functions may be subject to different selective forces. For example selection may act to maximize differences between individuals in coda types used for individual identification, whereas social affiliation or group membership signals may be subject to convergence pressures, leading to shared call characteristics. Temporal stability may also be different depending on the function. In coda types that function as identity signals within social units, constant exposure to unit members allows individuals to track changes in the call structure of others, and may be less stable than codas subject to a pressure to conform among individuals which are not in permanent contact (*e.g.* clan-specific coda types which still need to be recognised after potentially long separations between social units). For these reasons, future studies of the variation of coda repertoires may benefit from looking at different coda types separately. Similarly, studies of coda functionality will need to include hypotheses that take into account the possibility that different code types have different functions.

Five of the seven individuals in the social unit studied in Chapter 3 shared the most common coda types (Schulz, 2007). However one adult female and her calf each produced its own distinct coda type. This was interpreted as a response to the importance of these individuals locating each other to ensure effective nursing and calf care, and the need for a mutual recognition system (Schulz, 2007). This suggests the presence of two individual recognition schemes; one for mother-calf pairs based on coda type, and another based on within type variations for other unit members. A possible explanation that reconciles both observations is a scenario where identifying individuals from within type variation requires that whales interact and learn socially over long periods of time. Since the calf has not experienced such a learning period, but has an important requirement for locating its mother, a less subtle coding scheme based on different coda types may be more adaptive.

The indication that coda type '5 *Regular*' may serve to transmit identity within the investigated social unit does not explain the function of other coda types. In addition to individual identification, codas have been suggested to function as means of “maintaining social bonds” among social unit members (Schulz, 2007) and as '*clan signatures*' in mediating seemingly altruistic behaviour among units with similar vocal repertoires (Rendell & Whitehead, 2003b). The two coda types for which individual specific variation was not found may function in these ways. ‘Maintaining social bonds’ is however, still a somewhat vague function and should not be viewed as a complete explanation – we still ultimately need to know exactly how these calls function within

the context of social bonds. Also, it is still not clear why many different codas types are produced in the context of these suggested functions.

6.4. Sperm whale social structure

In Chapter 4 the analysis of the temporal patterns of association (Christal *et al.*, 1998; Coakes & Whitehead, 2004; Jaquet & Gendron, in Press) revealed sperm whales in the Azores form long term stable social units of about 12 individuals which is in line with results from several studies from the Pacific. However, unlike previous findings reported from the Pacific (Christal *et al.*, 1998; Coakes & Whitehead, 2004; Jaquet & Gendron, in Press), Azorean sperm whales do not tend to form temporary groupings of several units, indicating that multi-unit formation is not a general feature of the species' social system. I suggest that this variation is caused by underlying differences in ecological conditions, in particular prey availability and possibly predation pressure.

Results showing a social structure characterized by temporary grouping of social units, all originate from studies in the Eastern Tropical Pacific and coast of Chile (Christal *et al.* 1998; Coakes & Whitehead, 2004; Jaquet & Gendron, in Press). The primary production in the Gulf of California has been reported to reach levels at least two to three times higher than in open ocean areas of the Atlantic and Pacific at the same latitudes, and on occasions reaching one the highest surface nutrient concentrations in any of the oceans in the world (Zeitzschel, 1969; Alvarez-Borrego *et al.*, 1978). The Eastern Tropical Pacific (ETP), is characterized by primary production levels that are higher than the adjacent sub-tropical gyres (Pennington *et al.*, 2006). Around the Galápagos Islands the phytoplankton biomass is at least twice that of open-ocean and equatorial upwelling regions of the ETP (Martin *et al.*, 1994; Pennington *et al.*, 2006). The strong upwelling of cool nutrient-rich subsurface waters off Chile and Ecuador makes its zone of influence one of the most productive marine ecosystems on earth (Alheit & Bernal, 1993; Kudela *et al.*, 2005; Thiel *et al.*, 2007). Also, these areas are affected by the El Niño-Southern Oscillation (ENSO) climate phenomenon, which introduces temporal variability at scales of years to decades. This phenomenon has been shown to affect foraging success of different clans in different ways (Rendell & Whitehead, 2004), possibly by differentially affecting the dynamics of the prey on which different clans have specialized, and/or altering the relative efficiency of the different foraging strategies used by the clans. In comparison, the Azores are much less productive. Situated in the North

Atlantic subtropical anticyclonic gyre, this location is characterized by oligotrophic conditions and low productivity (Frazel & Berberian, 1990; Longhurst *et al.*, 1995). These differences are consistent with reduced intraspecific competition for food in the Pacific where primary production may correlate with higher food availability, compared to the Azores where less abundant prey may increase scramble competition. Lower food availability in the Azores may also indirectly affect social structure through demographic effects, by supporting a smaller population in this area, and therefore decreasing the number of units available to form groups.

Other cetacean species also show variation in social structure depending on location ecological conditions. Around Midway Atoll (Hawaii), spinner dolphins (*Stenella longirostris*) live in a stable society of long-term associates while off the large Hawaiian Islands they live in a fission–fusion society with substantial day-to-day variability in group size and membership (Karczmarski *et al.*, 2005). Karczmarski *et al.* (2005) suggested that around Midway Atoll, where there is easy access to deep water foraging locations and reduced availability of sheltered shallow-water locations in which to rest in daytime, it is less costly not to disperse and stable societies are favoured. Around the larger islands a more variable society is favoured due to a more heterogeneous environment with several locations capable of holding a proportion of the foraging groups. In this case, social structure seems to be affected by predation pressure through the availability of sheltered areas that are thought to be important in protection from shark predation in deep waters (Norris & Dohl, 1980). In comparison, in their oceanic habitat, sperm whales have no access to protection from sheltered areas and possibly rely on their social unit/group members as means of reducing predation pressure.

Killer whales (*Orcinus orca*) are likely to be the main predator of sperm whales (Whitehead, 2003). Stronger predation pressure in the Pacific may favour larger groups for increased protection. Low sighting rates of killer whales in the Azores (Pereira, 2008, Lisa Steiner, unpublished data) and in the Gulf of Mexico (O’Sullivan & Mullin 1997, Mullin & Hoggard 2000, Fulling *et al.*, 2003) and the fact that most attacks of killer whales on sperm whales have been reported from the Pacific (Jeferson *et al.*, 1991; Pitman *et al.*, 2001; Whitehead, 2003), support the idea that predation pressure is higher in the Pacific.

This combination of reduced intraspecific competition and possibly higher predation pressure in the Pacific, may favour the formation of larger groups compared to the Azores where reduced prey availability may increase the costs of grouping with other social units. However, the

sizes of social units are similar between the Pacific locations and the Azores. This suggests that these units are either less influenced by ecological factors, or under the influence of ecological factor that are similar among locations, and that the benefits of these associations are higher than the costs of forming them.

Killer whales represent another example of how ecological factors may influence social structure in cetaceans. Killer whales in the nearshore waters of the eastern North Pacific occur in two sympatric forms that show remarkable differences in their diets. The '*resident*' form feeds exclusively on fish while the '*transient*' predominantly feeds on pinnipeds and small cetaceans (Ford *et al.*, 1998). The differences in foraging specialization are also reflected in social structure and population genetics. Genetic studies show that both forms of killer whales represent monophyletic groups, suggesting that differentiation between them occurred only once (Barret-Lennard, 2000). Like sperm whales, killer whales form long term stable social groups. Pods (groups of whales that travel together more than 50% of the time, as observed over periods of years) of '*residents*' are made of one to three subpods. These subpods comprise of two to nine individuals of mixed age and sex which rarely separate from each other for more than a few hours. These subpods appear to contain a single matriline and result from lack of dispersion from natal groups by both sexes. '*Transients*' on the other hand, form pods containing between one and four individuals, but are most commonly found in groups of three. This is the group size at which individual energy intake rates are maximized, which are thought to result from a synergistic effect of increased prey detection and capture rate (Baird & Dill, 1996). In '*transients*', individuals of both sexes can either disperse or remain in their mother's pod (Bigg *et al.*, 1990; Baird, 2000). These differences in social structure have been suggested to relate to differences in the balance of costs and benefits of groups living associated with feeding on different prey (Baird, 2000). Due to the increasing costs of forming groups larger than three individuals, '*transients*' may benefit from dispersing from their natal pods, and dispersal may be conditional on the number of individuals already present in the natal pod (Baird, 2000). Even though groups of three individuals are favoured during foraging, '*transients*' occasionally form temporary groups of larger animals, which suggests that other advantages may be gained by individuals in larger groups when food related competition is reduced, or when cooperation may provide benefits in the capture of large or dangerous prey (Baird, 2000). In contrast, preying on fish may result in less constraint on the sizes of '*resident*' pods compared to '*transients*' who prey upon marine mammals. Less constrained by group sizes, '*residents*' of both

sexes may receive benefits in terms of inclusive fitness (Hamilton, 1964) by not dispersing and providing care for related calves (Waite, 1988). The costs associated with inbreeding from lack of dispersal in '*residents*' may be circumvented by mating between pods, rather than within them (Baird, 2000).

Although both sperm and killer whales form long term social units, their social systems show differences. Male dispersal seems to be obligatory in sperm whales and at least optional in '*transients*' and absent in '*residents*'. Predation may be a less important factor in killer whale social systems as they may have fewer predators than sperm whales. Even though different foraging specialisations have been proposed for different sperm whale clans in the Pacific (Marcoux *et al.*, 2007b), no differences in social structure are apparent; a social structure characterised by multi-unit groups seems to be present in all clans (Whitehead, 2003). However, I am not aware of any analysis that specifically looked for differences in social structure between clans. Sperm whales are not thought to be cooperative hunters, in the sense that several individuals increase their capture rate from cooperative handling of single prey, thus such benefits may not be a determinant of their social structure as in the case of '*transient*' killer whales.

Variation in the grouping of social units into larger groups dependent on ecological conditions, such as suggested in Chapter 4, has also been found in African savannah elephants (*Loxodonta africana*). Female savannah elephants' society is characterised by a multitiered structure with an increasing level of cohesion among individuals from upper to lower tiers (Wittemeyer *et al.*, 2005). In the first (*i.e.* lowest) tier, adult females and their calves represent the most regularly associating individuals, which coalesce into '*family units*' in the second tier, which in turn coalesce into '*extended family units*' in the third tier and in the fourth-tier '*episodical units*'. Wittemeyer *et al.* (2005) observed that the cohesion of second tier units, was little affected with different ecological conditions, whereas the formation of third and fourth tier units was significantly reduced in the dry season, which may relate to increased intraspecific competition. Wittemeyer *et al.* (2005) argued that second tier units are organized below the ecological threshold at which variability in the social costs and benefits of forming these units, can significantly affect their formation and cohesion. On the other hand, the balance of the costs and benefits of forming third and fourth tier social units is much more affected by ecological factors and their formation may be reduced when conditions are less favourable.

Sperm whales share many aspects of their life history with savannah elephants, perhaps

more than with other cetacean species, suggesting that these two species' social organization may well be the result of convergence under similar selection pressures. Both species are long lived, among the largest in their habitats (and there is thus little predation pressure on adults), both show male dispersal and in both females live in strictly or generally matrilinear social units (Lee & Moss, 1999; Whitehead, 2003). Equivalences between social units of both species can be drawn, with savannah elephant second tier units corresponding to sperm whale social units, and elephant third tier units corresponding to sperm whale multi-unit groupings found in the Pacific. As suggested for savannah elephants, the benefits of forming sperm whale social units may be less dependent on ecological conditions, while the balance of the costs and benefits of multi-unit group formation may be more affected by ecological factors.

Protection from predators in larger groups is potentially a benefit for both the savannah elephants' second tier and sperm whale social units. However mature sperm whale males are solitary, which indicates that the group living may not be necessary for protection from predators, although they are much larger than females making them more difficult to prey upon. The formation of long term relationships such as found in both species may enhance protection from predators by providing a more stable group compared to more variable associations, although many other species seem to find protection in numbers without long-term relationships. This would be specially useful in an environment where the presence of conspecifics may not be easily predicted such as the sperm whale's open ocean habitat. The benefits of both savannah elephants second tier and sperm whale social units may also be long-term, through investment in offspring (Wittemyer *et al.*, 2005; Whitehead, 2003). Except human caused mortality, most predation of savannah elephants seems to target juvenile individuals (Ruggiero, 1991; Wittemyer *et al.*, 2005). Sperm whale calves must also be an easier target for predation than the much larger adults. Both adult savannah elephants and sperm whales exhibit allomaternal care of calves (Lee, 1987; Whitehead, 1996; Payne, 2003; Gero, 2005). In groups with calves, adult sperm whale stagger their dives more than when no calf is present, reducing the time calves are unaccompanied by an adult at the surface (Whitehead, 1996). Savannah elephant calves are nursed by females other than their mothers (Lee, 1987) and calf mortality seems to decline as the number of allomothers in the family unit (*i.e.* second tier social unit) increases (Payne, 2003). These observations suggest that, in addition to potential benefits in protection from predators for themselves, the care and protection of calves may well be one of the main advantages provided by the formation of savannah elephant second tier and sperm whale social units.

Apart from mother-calf pairs, both sperm whale's social units and savannah elephant second tier units are probably the relationship levels where inclusive fitness (Hamilton, 1964) benefits are greatest, as members of these units are more likely to be related than in higher levels. This may also act to create and maintain relationships at this level, as has been suggested by Wittemyer *et al.* (2005) for savannah elephants.

As well as the more permanent benefits of elephant second tier and sperm whale social units, additional benefits may be gained from forming third and fourth tier units in elephants and multi-unit groupings in sperm whales, when the costs of forming these are reduced. Protection from predators may well be an advantage at these levels, because benefits such as dilution effect, increased vigilance and defence ability would increase with the number of animals. Protection from predators has been proposed as the main advantage of sperm whale multi-unit group formation (Whitehead, 2003). In the case of elephants, additional benefits of third and fourth tier units may include larger aggregations during the breeding season that may more easily attract mates and intragroup information exchange (Moss & Poole, 1983; Foley, 2002; Wittemyer *et al.*, 2005). Because individuals in larger groups also incur higher costs related with competition, both the formation of sperm whale multi-unit groups and elephant third tier units may be conditional on ecological conditions.

Aspects of sperm whale multi-unit formation suggest that, besides protection from predators, other advantages may be gained at this level of association. If the advantages of grouping sperm whale social units were restricted to protection from predators in large groups, no preference in association among units would be expected, or at least preference would be based on unit sizes. However, the formation of multi-unit groups in the Pacific is non-random, as groups tend to be formed with other units that share their vocal repertoire, even though sympatric units with different repertoires are found (Whitehead, 2003). This suggests that other advantages may be important at this level of association.

6.5. Coda repertoire variation

Previous studies in the Pacific Ocean have revealed that sympatric sperm whale social units could be grouped into clans with different dialects. These clans also showed differences in diet, habitat use, foraging, and reproductive success, suggesting that clan membership has implications in terms of individual fitness (Whitehead, 2003; Marcoux *et al.*, 2007a; 2007b). In Chapter 5, I

analysed the variation in coda repertoires in the North Atlantic and Gulf of Mexico and did not find sympatric dialects.

The parallel finding of differences in sperm whale social structure and coda repertoire variation between locations studied in the North Atlantic and Eastern Tropical Pacific suggests a link between these two aspects of sperm whale behaviour. In Chapter 5, I suggested that the differences in coda repertoire variation between ocean basins may be related to differences in social structure between the locations studied in both oceans. In the Pacific the differences in coda repertoires among clans may result from character displacement of signal parameters, driven by individual advantages gained by group formation between social units with similar foraging specializations. The absence of temporary multi-unit groups in the Atlantic may thus remove the need for vocal differentiation among units, and explain why marked differences among sympatric groups are not found. However a great variety of codas are still produced in the Atlantic, which indicates that they must have other functions besides simply advertising clan membership. In Chapter 3, I found support for identity transmission as a function for one of three coda types compared, and others have found evidence for the use of codas as social affiliation signals (Schulz, 2007). Different functions for different coda types may, at least partially, account for the variety of codas produced.

6.6. Foraging specialisation and the evolution of vocal dialects in cetaceans

The suggestion that sympatric foraging specializations may exist in the Eastern Tropical Pacific, and be absent in the North Atlantic, calls for a hypothesis that could explain these differences. A comparison with other species that also show sympatric foraging specializations may provide some insight. The cultural transmission of different foraging strategies was suggested to have initiated the division between fish-eating and mammal-eating killer whale forms (Baird *et al.*, 1992; Boran & Heimlich, 1999; Baird, 2000). The foraging specialization of killer whales pods in the eastern North Pacific may have occurred because resource variability and abundance allowed for niche partitioning - an abundance of fish and marine mammal prey that could support two foraging specializations simultaneously. This species also seems to exhibit foraging specialization in the productive waters of the Antarctic. There, ecotype A killer whales seem to feed mostly on Antarctic minke whales (*Balaenoptera bonaerensis*), whereas ecotype B is thought to prey

preferentially on pinnipeds, and occasionally on other cetaceans and penguins. Ecotype C killer whales are believed to prey mainly on fish and have been reported to interact with other marine mammals and penguins without any predation attempts (Pitman & Ensor, 2003; Krahn *et al.*, 2008). Killer whales in other locations do not seem to have such niche partitioning. For example in the Crozet Islands the same killer whales have been observed attacking fish, penguins, pinnipeds and large cetaceans (Guinet, 1991; 1992). In Hawaii, located in the oligotrophic North Pacific subtropical gyre, there are indications that killer whales do not exhibit foraging specializations, feeding both on marine mammals and cephalopods (Baird *et al.*, 2006). In other locations only one feeding specialization has been identified. For example in inshore and coastal Northern Norway killer whales seem to have specialized in eating herring (Simila, 1997).

Sperm whale clans may also result from cultural transmission of foraging behaviour, as suggested for killer whales. Using stable isotopes analysis, Marcoux *et al.*, (2007b) found evidence of differences in diet among clans in the same area and proposed that these are due to different foraging behaviours, with some groups using more benthic or inshore resources and others depending more on pelagic resources. Additional studies have reported differences between clans in terms of habitat use, foraging and reproductive success, indicating that clan membership likely has consequences in terms of individual fitness (Marcoux *et al.*, 2007a; Whitehead, 2003; Whitehead & Rendell, 2004). These observations are consistent with the idea of niche partitioning by different sperm whales clans.

All data describing sperm whale vocal clans, and a social structure characterized by temporary grouping of social units, originate from studies in the Eastern Tropical Pacific and coast of Chile (Christal *et al.*, 1998; Rendell & Whitehead, 2003b; Coakes & Whitehead, 2004; Jaquet & Gendron, in Press). As aforementioned, these areas are very productive because of the influence of ocean Eastern boundary, coastal and equatorial effects. In contrast, the Azores and the Sargasso Sea are much less productive (Frazel & Berberian, 1990; Longhurst *et al.*, 1995). The Gulf of Mexico's primary productivity is higher than the Sargasso Sea and Azores, but not as high as the Eastern Tropical Pacific (Figure 4.4; Chapter 4). It is plausible that higher levels of primary production in the eastern Pacific could cause higher abundance and diversity of sperm whale prey, which not only allow for the formation of larger groups as discussed above, but may also allow for niche partitioning and foraging specialization. Whales in less productive areas such as the Azores and the Sargasso Sea may depend on less abundant prey and consequently be subject to reduced niche space

that does not allow for foraging specialization.

Foraging specializations may be important in the differentiation of vocal repertoires for some species, as suggested here for sperm whales. In cases where there are advantages of grouping with animals that have the same foraging specialization, vocal signals can be used to communicate the foraging specialization to which they belong benefiting both receiver and transmitter. Red crossbills (*Loxia curvirostra*) provide an illustration of this. Red crossbills occur in nine sympatric forms that show variation in size and bill shape thought to correspond to foraging specializations on distinct conifer resources (Groth, 1988; 1993; Benkman, 1993, 2003; Benkman & Miller, 1996; Benkman *et al.*, 2001; Parchman *et al.*, 2006). Niche partitioning among crossbill forms may have been possible due to a variety of resources in sufficient abundance, in this case distinct conifer species. Distinct contact call subtypes constitute the most conspicuous differences between these different forms. These call subtypes are learned early in life and tend to remain stable during the life of the birds. Red crossbills respond selectively to contact calls of the subtype associated with their own foraging specialization (but see Sewall & Hahn, 2009 for evidence of erosion in call subtype selective response) and females preferably choose mates that produce the same call subtype as their own (Snowberg & Benkman, 2007). Apart from the reproductive advantages of mating with partners with the same adapted specialization, red crossbills have also been suggested to benefit from assorting with others from the same foraging specialization by pooling information about foraging success (Smith *et al.*, 1999). This grouping of individuals with similar requirement may also involve costs, as competition may increase, and other benefits associated with protection from predators may be important. Similarly, the differences between sperm whale clans in the Pacific may be used to signal social units' foraging specialisation, which would mediate the formation of multi-unit grouping among units with similar foraging specialisations. As suggested for eastern North Pacific killer whales and sperm whales, niche partitioning among crossbill forms may also have been possible due to a variety of resources in sufficient abundance to favour specialisation.

6.7. Sperm whale behavioural variability

We can expect sperm whale social behaviour to have evolved a balancing of the costs and benefits of group living approaching some kind of optimum. However sperm whales occupy a broad range of environmental conditions, and the behavioural strategies that maximise benefits in

spite of incurred costs in one set of ecological conditions, may not do so in another, and sperm whales would benefit from adaptively adjusting their behaviour accordingly. The differences in social structure between the Azores and the Pacific, which I suggested are related to differences in ecological conditions, may provide an example of behavioural flexibility in sperm whales. However, the mechanisms by which sperm whale behaviour may adapt to varying ecological conditions are unknown.

In the case of social structure, it is not known if individual sperm whales within a location change their behaviour facultatively according to the experienced conditions so that the average benefits for individuals of the emerging social structure are increased, or if the observed social structure results from fixed adaptations to average local conditions. In the example of elephants presented above, the same individuals seem to adapt the formation of third tier social units to variation in ecological conditions within their lifespan, while maintaining second tier units, suggesting that the first can be changed, but not the latter. Killer whales in the eastern North Pacific also seem to be capable of change at some levels of social association, but more constrained at others. 'Transient' pods seem to be constrained in their sizes but also to aggregate temporarily, perhaps when conditions are favourable. Sperm whale units in the Pacific can occasionally be found alone, not aggregated in larger groups (*e.g.* unit T described in Rendell & Whitehead, 2004), which suggests that the formation of multi-unit groups is not an absolute requirement. However sperm whale social structure studies have presented the average social structure, and have not investigated variation related to ecological conditions, precluding precise conclusions about a direct relationship between ecological conditions and the formation of multi-unit groups.

In the case of differences in vocal behaviour among Pacific clans, existing data support temporal stability (Rendell & Whitehead, 2005a), even though the sample period included years in which different ecological conditions (ENSO years) were shown to differentially affect the clans foraging success (Whitehead & Rendell, 2004). Because the differences in coda repertoires are likely to take a long time to develop, temporal stability of these differences is expected even if the benefits gained by the formation of groups among units of the same clan (as opposed to random) depended on experienced ecological conditions.

In the case of red crossbills, the vocal repertoire differences could be maintained genetically as mating takes place within forms. The sperm whale's low global nucleotide diversity, a result mainly of male dispersal (Lyrholm *et al.*, 1999; Engelhaupt, 2004), does not support inheritance of

locally adapted behaviour that would benefit the more spatially philopatric female social units. There is no evidence that males choose their breeding grounds and mating partners selectively to increase the probability of transmitting locally adapted genes. Other possible explanations for locally adapted behaviour in sperm whales are phenotypic expression of maternally inherited genes, phenotypic plasticity through norms of reaction and behavioural acquisition through social learning. These explanations are not mutually exclusive and several of these processes may act simultaneously. The formation of long term social groups which often show coordinated behaviour (*e.g.* movements and vocal output; Rendell & Whitehead, 2003b, Whitehead, 2003) suggests that social learning may be important in maintaining ecologically adapted behaviours.

The hypothesis about the influence of ecological variation in the social and vocal behaviour of sperm whales predicts that in locations in the Pacific where ecological conditions are characterized by reduced niche space and prey abundance, and lower predation pressure in comparison to the Eastern Tropical Pacific and Chile (*e.g.* in subtropical gyres) one would find comparatively reduced cultural diversity, similar to that observed in the North Atlantic, and a social organization characterized by the absence of multi-unit group formation. Conversely, locations with potentially more diverse and abundant food resources would exhibit sympatric cultural variants such as the Pacific clans and the formation of multi-unit groups.

6.8. Suggested future research

The studies presented here are only the first steps toward a proper understanding of the issues discussed above, and all areas addressed by this thesis can be characterised by a need for further investigation. The analysis of individual discrimination using within coda type variation presented in this study relied on a small dataset which did not include all members of the studied social unit. Further studies of the same unit used in this study (*Group of Seven*), as well as other units, are required to draw more precise conclusions on the presence of individual-specific information and its variation among coda types. An ongoing study in Dominica will likely provide additional data from the *Group of Seven* that will provide greater control of context and motivational variables, and verification of the hypothesis suggested in this thesis. The expansion of this research to other social units by assigning codas to individuals based on IPIs depends on the finding and being able to follow other social units showing distinct IPIs for each individual. The use

of automatic IPI estimation methods such as the ones tested in Chapter 3 will facilitate the finding of this fortuitous combination of factors by reducing the time required for measuring clicks from diving whales. An alternative means by which individual specific repertoires may be determined is through the use of sound recording tags deployed on known individuals (*e.g.* Johnson & Tyack, 2003). Future research on individual use of coda repertoires could be based on the deployment of these instruments, although the application of this method on a whole social unit would be an expensive and daunting task.

The finding of individual-specific variation in coda types is a prerequisite for its use by sperm whales for communicating individual identity. However, two additional steps are required to demonstrate that sperm whales use within coda type variation for this function. Both the ability of sperm whales to discriminate between codas of the same type produced by different individuals, and behavioural differences reflecting differential responses to different individuals, need to be demonstrated. Playback studies, where the behaviour of individual whales is monitored while being exposed to stimuli from known and unknown individuals and appropriate controls, are the most obvious methodology to study the use of codas for individual discrimination (Janik *et al.*, 2006; Rendell & Whitehead, 2005b).

Some of the hypotheses raised by this study assume temporal stability in coda repertoires. The proposed advantages gained by transmitting a signal identifying a foraging specialization would require some degree of temporal stability because vocal differences between social units with different foraging specializations, that only occasionally meet, would need to remain functional over time. The Pacific studies found that coda repertoires of social units are stable for at least 6 years (Rendell & Whitehead, 2005a). Although this period of time represents only a small proportion of a sperm whale's typical lifespan (>50 years) it supports some degree of temporal stability of repertoires in the Pacific. Also, the finding of the same coda type in recordings off Dominica made approximately 20 years apart also suggests temporal stability of coda repertoires in this region (Chapter 5). However, given the differences found between the Pacific and Atlantic studies one should be careful in extrapolating these observations into other areas, and the temporal stability of repertoires may well be another difference found between oceans. The data used in Chapter 5 will be further analysed to investigate the temporal variation of coda repertoires in the North Atlantic.

The aforementioned predictions that locations in the Pacific Ocean with similar ecological

variation (*e.g.* similar levels of primary production) would exhibit social structure and coda variation similar to that found for North Atlantic (*i.e.* absence of sympatric clans and multi-unit groups), require testing through the collection of data on sperm whale social structure and coda repertoire variation from other locations, and in varying ecological conditions. Such investigation is largely constrained by our limited knowledge of sperm whale ecology, which precludes the accurate determination of sperm whale ecological niches, in particular lack of knowledge of the spatial and temporal patchiness of their prey. Stable isotope analysis, which has proven to be an useful tool for detection of niche partitioning among sperm whale clans in the Pacific, will be useful in conjunction with coda repertoire analysis to aid in further investigation of this hypothesis. The study of variation in fatty acid signatures (Iverson *et al.*, 2004) could potentially also reveal niche partitioning between clans.

The aforementioned ideas give rise to some hypotheses that need testing. Future research should focus on these aspects to either support or dismiss the assumptions made. A key idea of the theories presented here is that in the Pacific social units benefit from preferentially forming groups with other units from the same clan. The potential advantages gained by this require investigation. The isolation of units from different clans, mediated by vocal behaviour, should also be investigated. Differing behavioural responses of social units to coda playbacks from the same and different clans would support the hypothesis of social unit assortment mediated by coda repertoire. Another major research challenge is the demonstration of learning in sperm whales. The size and life history of the species precludes studies in captivity similar to those on smaller cetaceans (*e.g.* bottlenose dolphins). In addition, logistics and ethical issues prohibit translocation experiments. Long term studies in which the behavioural output of known individuals is tracked in the field remains the only investigation method with which to verify the proposed rationale.

6.9. Conclusions

Found in every ocean on the planet, the sperm whale is the second most widespread marine mammal and an important component of the pelagic ecosystem. Within its range the species is subject to a wide variety of ecological conditions, from tropical highly productive areas, to oligotrophic subtropical gyres, to high latitudes with strong seasonality in productivity. Sperm whales may well be an example of how flexibility in social behaviour allows a species to adapt to a

wide range of conditions. The suggestions made in this thesis that sperm whale social structure varies according to ecological conditions, and that functional variation in vocal behaviour may relate to those changes, seems to support this idea. However, data are sparse and information from a variety of other locations are required.

The results presented in this thesis provide support for the communication of individual identity as one of the functions of sperm whale codas, but also suggest that different coda types may have different functions. The study of the function of codas is still in its infancy and faces many difficulties, not least the problems of assigning the recorded signals to their producer. Pioneering work by Schulz (2007) that investigated individual repertoires was an important advance. Future studies in other locations and targeting other social units are required. The use of IPIs for assigning of codas to individuals may well be an important tool in further developing our understanding of codas and these studies would benefit from the use of automatic IPI measurement methods such as those developed in this thesis.

Comparative studies across species and within species in different environments are a powerful tool for understanding the pressures that shape behaviour. The studies of sperm whale social structure and coda repertoire variation presented in this thesis provided a contrast to previous studies from the Pacific. The contrast between the findings from the Pacific and Atlantic study sites underlines the importance of comparative studies in the understanding of sperm whale behaviour and highlights the dangers of generalising behavioural patterns among regions. The contrasting results between oceans lead to new hypotheses and questions about the function and evolution of social structure and coda communication in sperm whales. However, these hypotheses rely on many assumptions and need to be tested by further research.

The sperm whale remains a mysterious animal that deserves study not only because of its important ecological role, but also as an example of how behaviour may help animals adapt to extreme environments. The difficulties of studying an animal that spends most of its life in the open ocean submerged and beyond visual perception no doubt contribute to our sparse understanding of this species. Although the sperm whale is not an easy subject to study, it is a fascinating one and the investigation of its biology will always provide a host of captivating questions to fill the lives of scientists willing to take on the challenges of its study.

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