THE PRODUCTION AND EXCHANGE OF SPERM WHALE CODA VOCALIZATIONS

by

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To Michael, who was with me even when I was away….

i carry your heart with me

i carry your heart with me (i carry it in
my heart) i am never without it (anywhere
i go you go, my dear; and whatever is done
by only me is your doing, my darling)

i fear
no fate (for you are my fate, my sweet) i want
no world (for beautiful you are my world, my true)
and it's you are whatever a moon has always meant
and whatever a sun will always sing is you

here is the deepest secret nobody knows
(here is the root of the root and the bud of the bud
and the sky of the sky of a tree called life; which grows
higher than soul can hope or mind can hide)
and this is the wonder that's keeping the stars apart

i carry your heart (i carry it in my heart)

e.e. cummings

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ABSTRACT

The sperm whale (*Physeter macrocephalus*) is a highly social animal that exchanges patterns of clicks ('codas') amongst members of long-term social units. Due to the difficulty of assigning codas to individual whales, little was known of the coda production of individuals or the exchange of vocalizations between them.

To address this problem, I developed a method for assigning recorded codas to whales using differences in the inter-pulse intervals of clicks. Applying this method to recordings of two social units – one studied off Dominica, the other off the Galàpagos Islands - revealed that sperm whales produced codas at regular 3-5 s intervals. Furthermore, whales synchronized their vocal output, resulting in duet-like sequences of overlap exchanges. I suggest that these exchanges affirm social relationships between unit members.

The coda repertoires of both studied units were highly redundant, indicating little potential for syntactic communication. Moreover, whales in both units tended to repeat one particular coda type, both in the sequences of individuals and in overlap exchanges. Given that units preferentially associate with other units with similar coda repertoires (i.e. from the same acoustic clan), I suggest that the repetition of a particular coda type functions to bond unit members and/or communicate clan affiliation.

Most whales in the Dominican social unit had similar coda repertoires, again suggesting that coda types function to advertize clan identity. However, the repertoires of two whales – a male calf and its mother – differed from those of others in the unit, including each other, suggesting that their repertoires signal individual identity. While adult females in the unit vocalized at approximately equal rates, the calf and a juvenile male vocalized less often. This is likely because they did not engage in overlapping exchanges, interactions that may have a social bonding function unnecessary for males that leave their natal unit.

To examine the distance between vocalizing whales, I developed an acoustic array consisting of remotely-piloted vessels. Deployment of the array in the Sargasso Sea in 2004 revealed that sperm whales engaged in overlapping coda exchanges both with nearby and comparatively distant whales. This again supports a social bonding function for overlapping exchanges. The acoustic array was also used to show that the waveform structures of coda clicks, like echolocation clicks, vary with the recording position relative to the orientation of the whale.

In summary, this thesis suggests that coda production functions to affirm social bonds between unit members (via coda overlapping and matching), advertize clan identity, and advertize individual identity for animals with an increased need to do so.

LIST OF ABBREVIATIONS AND SYMBOLS USED

2-D	two-dimensional
3-D	three-dimensional
ASCII	American Standard Code for Information Interchange
b	slope
°C	temperature in degrees centigrade
CV	coefficient of variation
dB	decibel
dB//1µPa	decibels relative to one micro-Pascal of pressure (peak-to-peak measure)
d.f.	degrees of freedom
DNA	deoxyribonucleic acid
ε_x	zonal error
ε_y	meridional error
ft	foot
FSK	Frequency Shift-Keying
GPS	Global Positioning System
h	hour
HWI	Half-Weight Index
Hz	Hertz, frequency in cycles per second
ICI	inter-click interval
IPI	inter-pulse interval
IQR	inter-quartile range
kHz	kilohertz, frequency in thousands of cycles per second
km	kilometre
µPa	micro-Pascal
m	metre

msec	millisecond
n	sample size
NMEA	National Marine Electronics Association
p0	initial pulse of a sperm whale click
p1	pulse subsequent to initial pulse (p0)
p2	pulse subsequent to p1
P	probability
Q	photograph quality for identification purposes
r^2	proportion of variability in a data set that is accounted for by a statistical model
RINEX	Receiver Independent Exchange Format Version
RMS	root-mean-square
RPV	remotely-piloted vessel
s	second
SD	standard deviation, used to measure the spread of data about the mean
t	*t* statistic, used to calculate probability in a *t*-test
TOAD	time-of-arrival-difference
UTC	coordinated universal time
V	volt
Z	*Z* statistic, used to calculate probability in a *Z*-test

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CHAPTER ONE

INTRODUCTION

INTRODUCTION

The communicative function of an interaction between animals with an obvious conflict of interest is often clear. Whether a signaler honestly or misleadingly communicates its intention, condition, or status, the nature of the conflict between signaler and receiver, in combination with the context in which it is given, often points to the communicative purpose of the signal (see Bradbury and Vehrencamp 1998). For example, the aggressive and/or territorial function of song overlapping between male songbirds is often indicated by the conflict of interest between the interaction participants (i.e. intrasexual competition for territory and mates) and the context in which it is given (i.e. between neighbouring males) (see Hall et al. 2006). And while a finer understanding of the communicative value of song overlapping is possible by studying the behaviour of individuals during interactions or through playback experiments (e.g. Burt et al. 2001), its general function is still indicated by knowledge of the conflict of interest between the interacting males. Therefore, even when the specific function of a signal is not entirely obvious (e.g. the tail flag of white-tailed deer, *Odocoileus virginianus*; Bildstein 1983), knowledge of the nature of the conflict between animals can nevertheless suggest the general purpose of signals exchanged between them, although researchers must consider that the presumed and intended receiver may not be the same (e.g. McGregor 1993). Communicative exchanges in which the conflict of interest can suggest the general function of the signal include those involved in mate attraction, territorial defense, aggression, social dominance, parent-offspring feeding interactions, and predator-prey interactions.

Although the functions of communicative signals can be less clear when there is a less apparent conflict of interest between signaler and receiver, they can often still be indicated by contextual cues, including the presence of predators, resources, and other individuals. For example, some social primates that mutually depend upon group members for food and protection produce specific calls in the presence of food (e.g. Hauser and Marler 1993) or predators (e.g. Seyfarth et al. 1980), indicating the function of their calls to alert conspecifics to the presence of the external referent. Moreover, in contexts of separation or isolation, social animals often exchange vocal signals, presumably to maintain contact with group members or coordinate group movement (e.g. Snowdon and Cleveland 1984; Oda 2002).

However, when there is little or no perceptible conflict of interest between interacting animals and few if any obvious external referents, behavioural signs, or contextual cues, the general purpose of exchanged signals can be ambiguous and require detailed experimental or field research to investigate their function. Moreover, the investigation of vocal interactions between animals with cooperative relationships is important for a number of reasons, including that human language is assumed to have evolved in a context of shared interest between participants (Számadó and Szathmáry 2006). Furthermore, because the evolution of human language has been suggested to be a result of kin-selection (Fitch 2004, 2007) and an increase in the complexity of social structure (Dunbar 1996; Nowak et al. 2000), the most logical place to look for comparable non-human communication systems is in the vocal exchanges between cooperative and highly related animals with complex social structures.

Animals that live in highly related, long-term social units would be particularly expected to have little conflict of interest between unit members. Although conflicts between unit members could arise during the establishment of dominance hierarchies or competition for food and mates, several species of social animals exchange vocalizations in the absence of food, potential mates, and aggressive behaviour, leading one to question their communicative function. African elephants (*Loxodonta africana*), for example, live in long-term matrilineal social units (Laws et al. 1975; Moss and Poole 1983; Poole et al. 1988) and exchange low-frequency rumbles between individuals both within and between units (Payne et al. 1986; Poole et al. 1988; Leong et al. 2003a; Soltis et al. 2005a). Although the subtle gradation of elephant rumbles has thus far precluded the detection of rumble classes or syntax in elephant communication (Soltis et al. 2005b) - and thus the identification of a complex and expressive communication system - captive elephants engage in overlapping and antiphonal exchanges primarily with long-term social affiliates (Soltis et al. 2005a), suggesting that vocal exchanges function in maintaining social relationships.

Like elephants, bottlenose dolphins (*Tursiops truncatus*) are highly social animals that exchange vocalizations with their kin and social associates (Lilly and Miller 1961; Tyack 1986a; Smolker et al. 1993). In contrast, however, dolphins produce discrete whistle vocalizations (Caldwell et al. 1990; McCowan et al. 1999), whistles that McCowan et al. (1999, 2005) have concluded follow syntactic rules (but see Suzuki et al. 2005). Given the relative lack of external referents in the marine environment (besides other individuals and prey resources) it is possible that dolphin whistles function to communicate about other individuals, non-present prey resources, or abstract concepts in a manner similar to that suggested for primitive human language (Számadó and Szathmáry 2006). However, due to the difficulty of assigning vocalizations to individuals in the field, the study of wild bottlenose dolphin whistle interactions has been limited to exchanges between separated individuals (Janik 2000). Exchanges are therefore suspected to function as isolation calls during periods of separation. Likewise, although killer whales (*Orcinus orca*) in matrilineal social units exchange a variety of discrete calls, the problem of distinguishing between the vocalizations of individuals has limited study to spatially separated whales, again leading to the conclusion that call exchanges function in group cohesion or coordination (Miller et al. 2004). While these studies have proven useful in suggesting a function for vocal exchanges between separated individuals, there is still a need to examine the vocal interactions of social, cooperative animals in close proximity to one another. The sperm whale (*Physeter macrocephalus*) is a highly social, cooperative, and vocal species that warrants study into the function of its vocal interactions for their own interest, as well as to determine whether its communication system resembles human language in possessing syntactic structure.

SPERM WHALE LIFE-HISTORY AND SOCIAL STRUCTURE

The sperm whale is a remarkable animal, an extreme in size, distribution, brain size, diving ability, and ecological importance (Rice 1989; Whitehead 2003a). The current estimate of worldwide consumption rates by sperm whales at about 100 million metric tons per year rivals that of the current annual catch of all human marine fisheries combined (Clarke 1980; Santos et al. 2001). Although this wide-ranging whale is a catholic predator that feeds on a variety of mesopelagic prey, it feeds primarily on squid, sometimes diving as deep as 1000 m to feed on giant squid (Whitehead 2003a). It has an extremely low birth rate, slow growth rate and maturation, and high survival, with little evidence of significant mortality from natural predators (Whitehead 2003a). The sperm whale exhibits the greatest sexual dimorphism of all the cetaceans with males reaching 18 m in length and 60 metric tons in weight while females generally reach 12 m in length and 15 metric tons (Rice 1989).

The sperm whale is particularly characterized by its huge nose, which makes up about 1/3 of its body length and body weight (Rice 1989; Madsen 2002) and gives the species the claim to the 'biggest nose on record' (Raven and Gregory 1933). Although researchers had previously proposed battering ram (Carrier et al. 2002) and buoyancy regulation (Clarke 1970, 1978) functions for the hypertrophied nasal complex, Norris and Harvey (1972) were the first to advance a sound generating function, a function that has since been corroborated by experimental evidence (Cranford 1999; Møhl 2001; Møhl et al. 2000, 2003). The nasal complex contains the spermaceti organ, junk bodies, and other organs associated with the production of the sperm whale's primary vocalization: the click (see Figure 1.1). The spermaceti organ likely evolved initially as a result of the fitness increase associated with the long-range biosonar detection of mesopelagic cephalopod prey (Madsen 2002).

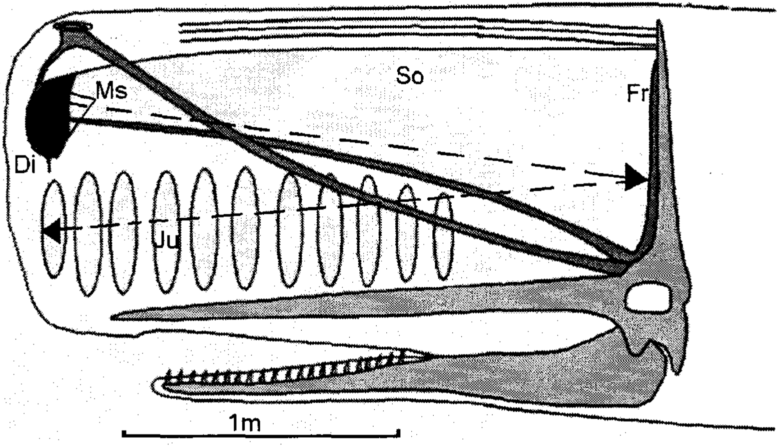

Figure 1.1. Schematic view of the head of a sperm whale depicting the path of a generated echolocation click (modified from Figure 1 of Madsen et al. 2002b). The dashed arrows indicate the sound path within the nasal complex according to the modified Norris and Harvey (1972) theory. Some sound energy is reflected back into the spermaceti organ where it reverberates between the two air sacs. Phonic lips/museau de singe (**Ms**); Junk bodies (**Ju**); Frontal air sac (**Fr**); Distal air sac (**Di**); Spermaceti organ (**So**).

Not only is there marked sexual size dimorphism in sperm whales, but the sexes also differ greatly in their geographic distribution and social structure. Male sperm whales leave their natal group at about 6 years of age (Richard et al. 1996) to form 'bachelor' schools and move to higher latitudes as they mature (Best 1979), while adult females, as well as juveniles and calves of both sexes, remain in tropical and sub-tropical waters in long-term, stable social 'units' consisting of 11-12 animals (Whitehead and Weilgart 2000). Although these social units are generally matrilineal in structure and remain stable in composition over periods of decades (Whitehead and Weilgart 2000), individuals sometimes move between units such that unrelated individuals may be found within them (Christal et al. 1998; Mesnick 2001). The most likely functions of these close-knit social units are group defense against killer whales and other predators (Pitman et al. 2001; Whitehead 2003a) and allomaternal care of calves (Whitehead 1996a), although other benefits could include communal knowledge of a large home range (Whitehead 1996a; Whitehead 2003a) and increased feeding success through group foraging (Best 1979). Sperm whale social units also form social 'groups' for several days with one or more other units, and are also thought to function in group defense or communal foraging (Whitehead and Weilgart 2000; Pitman et al. 2001). As the sperm whale evolved a complex social system with long-term associations between females, we might expect sperm whales to have also evolved a complex and perhaps syntactic communication system to manage the increase in social interactions and relevant communication topics that accompanied the increase in social complexity (see Dunbar 1996; Nowak et al. 2000). Accordingly, sperm whales appear to possess a highly complex communication system that merits closer examination.

SPERM WHALE VOCALIZATIONS

Sperm whale vocalizations consist of different types of broadband clicks, which appear to function in both social communication and echolocation. Clicks are generated by the forcing of air through a pair of phonic lips (i.e. museau de singe) at the anterior end of the nasal complex (see Figure 1.1), followed by the reflection of some sound energy between two air sacs at the ends of the spermaceti organ (Norris and Harvey 1972; Cranford 1999; Møhl et al. 2003), resulting in a multi-pulsed click structure (Backus and Schevill 1966). Much of the sound energy of echolocation clicks is redirected into the junk, where it is focused by lens-like junk bodies (Møhl et al. 2003) into a very loud and directional emitted click (Møhl et al. 2000, 2003). Although the most prevalent vocalization of sperm whales is the 'usual' click (i.e. echolocation click), which is produced in long click trains while whales forage at depth (Madsen et al. 2002a), whales sometimes produce short stereotyped patterns of clicks, termed 'codas' (Watkins and Schevill 1977; Whitehead and Weilgart 1991), generally while socializing at the water surface.

Codas can be classified into types based on the number and temporal spacing of clicks within the coda (Weilgart and Whitehead 1993; Rendell and Whitehead 2003a), and social units possess repertoires of coda types such that they can be classified into acoustic 'clans' based on their usage (or dialect) of particular coda types (Rendell and Whitehead 2003b). Clans span thousands of kilometres, are sympatric in their geographic distribution, and are likely a result of the largely matrilineal cultural transmission of information, including coda types (Rendell and Whitehead 2003b). Although the increase in coda vocalizations in the presence of calves and mature males and the strong correlation between behavioural activities and the rates at which codas are produced suggest that codas play a role in social interactions (Whitehead and Weilgart 1991), their function within social interactions is still not clear. The long-term associations and often high degree of genetic relatedness between unit members - which both suggest a low level of conflict of interest between these whales - together with the appearance of a complex Morse code-like communication system begs the question "What do sperm whales talk about?" Do they use syntax to discuss complex and abstract topics? Or is the function of coda communication much simpler than it appears to the casual listener?

It was initially suggested that codas function as individual signatures, with each individual producing a single characteristic coda type (Watkins and Schevill 1977; Watkins et al. 1985). Although evidence that whales share coda types indicates that this is not the case (Whitehead and Weilgart 1991; Rendell and Whitehead 2004), it is possible that individuals within social units produce different coda types at different rates and thus use coda repertoires to advertize individual identity. Moreover, because social units seem preferentially to form groups with other units within their own clan (Rendell and Whitehead 2003b) and coda dialects appear to persist over periods of years (Whitehead et al. 1998; Rendell and Whitehead 2003b), unit coda repertoires may play a role in unit or clan identification. Given that sperm whale coda clicks appear to be much louder (~190 dB//1µPa; P. Madsen, pers. comm.[1]) than required to communicate with another individual several metres away, one might hypothesize that codas function in broadcasting a signal, such as individual, unit, or clan affiliation. However, because previous research found that coda repertoires do not differ significantly between units within clans, codas likely do not function in advertizing unit identity (Rendell 2003).

Besides individual and clan identification, the production and exchange of loud codas could function in the advertizement of the social bond between unit members. Mated pairs in several species of animals broadcast a social bond by engaging in loud, often elaborate duets that advertize to listeners the time commitment - and thus social attachment - between the duet partners (Wickler 1980; Haimoff 1984; Geissmann 1999; Hall 2004). In addition, since duets and other vocal exchanges also function in social species to establish or affirm social bonds (e.g. Armstrong 1973; Richman 1978; Farabaugh 1982; Geissmann 1999; Geissmann and Orgeldinger 2000; Hall 2004; Rogers et al. 2006), *coda exchanges between sperm whales could also function to* reaffirm bonds between unit members, particularly after periods of separation during foraging. If coda production did function to advertize or reaffirm social bonds between members of a social unit, one might expect whales to engage in synchronous vocal production, coda overlapping, coda matching, or other duet-like exchanges to signal commitment to one another, although biased overlapping (non-reciprocal overlapping) could indicate that this behaviour functions in signaling dominance or aggression. Likewise, if codas functioned to bond members within a social unit, one might expect coda production to be relatively equal amongst unit members rather than dominated by one or two individuals. In contrast, vocal dominance by particular whales within a unit, could indicate that codas function to assert dominance (e.g. Tobias et al. 2004) or establish a social hierarchy within the group.

Alternatively, coda exchanges could simply function to permit the localization of separated unit members, since several species of animals engage in antiphonal vocal exchanges to monitor or locate group members when separated from one another (e.g. Snowdon and Cleveland 1984; Lamprecht et al. 1985; Masataka and Symmes 1986; Okayasu 1987; Sugiura 1998). If sperm whales use codas to localize unit members either to coordinate group movement or locate separated individuals, then one might expect whales to engage in alternating signal and response exchanges. Moreover, since the matching of vocalizations can permit a receiver to compare the degradation in signals and better localize the other individual (Krebs et al. 1981; McGregor and Falls 1984; Naguib and Wiley 2001), if coda matching were observed in sperm whale communication, it might be considered to function as a cohesion or contact call, as in bottlenose dolphins (Janik 2000) and killer whales (Miller et al. 2004). However, since coda overlapping would likely mask both the signal and response and thus obscure available information concerning location, a high degree of coda overlapping in coda recordings would likely negate a contact call function. Furthermore, if coda exchanges did function in locating separated individuals, one would expect them to occur only between individuals that are out of visual contact with one another. However, if exchanges occur both between whales that are far apart and whales in close proximity, then exchanges more likely function in social bonding or the exchange of referential information, although non-overlapping exchanges between distant whales could also function in contact calling.

Finally, specific codas could function to refer to external referents or internal motivational states. If so, then one might expect the coda types produced by a given whale to vary from one recording to the next, assuming that the recordings are made in different contexts. Moreover, given the similarity between the circumstances of coda production within social units and that suggested for the evolution of human language (i.e. low conflict of interest, high degree of relatedness, complex social structure), it is worth investigating whether sperm whale coda production could possess syntax, perhaps to refer to internal emotions, external referents, or other individuals. If sperm whales do possess syntax, then the coda repertoires of social units will likely contain a variety of coda types that are produced with a frequency that maximizes communication capacity (i.e. the repertoire is neither too redundant nor too diverse) (see McCowan et al. 1999). Furthermore, if sperm whales do possess syntax in their vocal communication, then one would expect to find rules in the ordering of codas within individuals' sequences and between whales in coda exchanges (e.g. see McCowan and Reiss 1999). Although previous research discovered non-random patterns in the types of codas that overlapped others or initiated coda interactions (Weilgart and Whitehead 1993), the analysis pooled different vocal clans, recordings, and individuals, such that the observed tendency for particular coda types to overlap others may have been an artifact of the coda repertoires of units or individuals or of the types of codas produced in different contexts.

To examine whether codas function in individual identification, social bonding, social dominance, contact calling, or syntactic communication, it is clearly necessary to examine coda output at the level of the individual. Unfortunately, it has been difficult to assign recorded codas to individuals within a social unit or group, thereby limiting our understanding of coda communication. Therefore, the purpose of this thesis was to investigate the potential functions of coda communication (summarized in Table 1.1) by studying the vocal output of individual sperm whales and the exchange of codas between them.

Table 1.1. A summary of the potential functions (rows) of sperm whale coda communication and the predictions made from the hypothesized functions (columns). The thesis chapter or reference that tested each prediction is provided in parentheses. Within the table, hypotheses that would be supported by a confirmed prediction are indicated by **Y** and hypotheses that would be rejected by a confirmed prediction are indicated by **N**. Hypotheses that might or might not be supported by a confirmed prediction are indicated by **Y/N** while hypotheses that are not related to a given prediction are left blank.

Function	Differences between whales in coda repertoires (Chapter 3)	Differences between units in coda repertoires (Rendell 2003)	Differences between clans in coda repertoires (Rendell and Whitehead 2003b)	Coda repertoires vary within whales between recordings (Chapter 3)	Whales overlap the codas of other whales (Chapter 4)	Biased coda overlapping (Chapter 4)	Whales match the codas of other whales (Chapter 4)	Biased coda matching (Chapter 4)	Whales engage in duet-like coda exchanges (Chapter 4)	Redundancy in coda repertoire of unit (Chapter 5)	Whales alternate coda production with other whales (Chapter 5)	Rules in the ordering of coda types within sequences (Chapter 5)	Coda production dominated by one or two individuals within the unit (Chapter 6)	Coda exchanges occur between whales that are out of visual contact (Chapter 8)	Coda exchanges occur between whales that are in close proximity (Chapter 8)
Individual identification	Y	Y/N	Y/N	N											
Unit identification	N	Y	Y/N							Y					
Clan identification	N	N	Y							Y					
Referential / contextual calling				Y											
Contact calling					N	N	Y/N	Y/N	Y/N	Y/N	Y		Y/N	Y	N
Affirmation of social bonds					Y/N	N	Y/N	N	Y	Y/N	Y/N		N	Y	Y
Display of dominance or aggression					Y/N	Y	Y/N	Y	N	Y/N	Y/N		Y		
Syntactic communication										N		Y			

To examine the coda output of individual whales, I originally planned to assign codas to individuals using an acoustic array to localize codas. After the first field season of deployments, however, it became apparent that unidentified technical difficulties with the array equipment were limiting the collection of usable data. Fortunately, during my second set of field studies, I encountered a fortuitous set of circumstances that allowed me to study individual coda output more thoroughly than I could have ever imagined. Off the island of Dominica in 2005, colleagues and I encountered a social unit of seven animals, the 'Group of Seven' (see Gero 2005), which remained in the area for the duration of our several month field season. Repeated encounters with this same unit over several weeks permitted the detailed description of the internal social structure of the unit (Gero 2005) as well as the recording of the same individuals on multiple occasions, both when vocalizing alone and when socializing with other unit members. In Chapter 2, I detail how I used these recordings, together with other recordings in which it was apparent that only two whales were in the area, to modify an existing method for estimating the size of vocalizing whales from the inter-pulse intervals (IPIs) of clicks (Rendell and Whitehead 2004; Marcoux et al. 2006) to distinguish between the codas produced by individuals within recordings. I further demonstrate in Chapter 2 that this modified method can be used in some cases, as with the Group of Seven, to assign codas to specific whales, thereby permitting the study of the repertoires, vocal output, and vocal interactions of particular individuals.

Although the finding of shared coda types within a sperm whale social unit disproves the hypothesis that whales each produce one coda type for individual identity (Rendell and Whitehead 2004), it does not exclude the possibility that individuals produce codas at different rates and thus have individual coda repertoires, which could explain differences in repertoires between clans (Freeberg 2001; Tyack 2001). Therefore, in Chapter 3 I use the codas assigned to Group of Seven whales to determine whether individuals within a unit possess individual-specific coda repertoires, thereby testing whether one function of coda production might be the advertizement of individual identity (see Table 1.1). As mentioned above, previous research found that while coda repertoires differ between clans (Rendell and Whitehead 2003b), they differ little between units within clans (Rendell 2003), indicating that codas could function to advertize clan but likely not unit identity, although differences in coda repertoires between individuals within a unit could call into question the finding of differences in coda repertoires between clans. Moreover, because sperm whales could use different coda types to refer to different behavioural contexts or referents, in Chapter 3 I test whether the repertoires of individuals vary between recordings (i.e. context) or whether codas produced by the same whale are consistent between recordings (Table 1.1).

In Chapter 4, I conduct permutation tests on codas assigned to individuals (or classes of individuals with similar IPIs) to determine whether sperm whales engage in overlapping and matching coda exchanges more often than expected, given the rates at which each whale produces each coda type. This could indicate that sperm whales produce codas to establish or reaffirm social bonds or perhaps locate one another during periods of separation (see Table 1.1). I also test whether overlapping and matching is reciprocal or biased in one direction, which could indicate that codas are used to communicate dominance or aggressive intentions. Moreover, in Chapter 4, I explore the function of a unique overlapping exchange, the 'echocoda', in which the clicks of two overlapping and matching codas alternate with one another (Weilgart 1990).

To determine whether coda communication contains some underlying syntax, in Chapter 5 I test the communicative capacity of coda production using information theory analysis and look for rules in the ordering of codas using permutation tests (see Table 1.1). Furthermore, because differences in the rates of coda production could indicate a vocal dominance or leadership function, in Chapter 6 I use permutation tests on the codas assigned to Group of Seven whales to compare the relative rates of coda production between individuals within a unit (see Table 1.1).

Because codas are often heard while sperm whales are in social clusters at the water surface, it can appear that whales are in relatively close proximity when producing and exchanging codas (pers. obs.). However, due to the difficulty of assigning codas to particular whales, the distances between vocally interacting whales have not been estimated with any convincing accuracy (see Watkins and Schevill 1972). In Chapter 7, I describe the acoustic array developed to localize sperm whale codas for this thesis. Despite the short duration of array recordings in the field, the calibration results indicate that the array is accurate and practical enough to permit the differentiation of whales' codas and thus the examination of several research questions concerning coda communication. In Chapter 8, I use the acoustic array described in Chapter 7 to localize sperm whale codas in the field and estimate the distance between whales making coda overlapping exchanges. This information is used to examine whether coda exchanges might function in social bonding or the localization of separated individuals (see Table 1.1).

Most sperm whale coda clicks recorded during the course of my fieldwork have clear pulse structures that permit the calculation of inter-pulse intervals and assignment to individuals within recordings. However, many recorded coda clicks have poorly defined waveforms that require their exclusion from analysis (see also Rendell and Whitehead 2004; Marcoux et al. 2006). Zimmer et al. (2005a) discovered that unclear pulse structures in usual clicks recorded in the far-field can be explained by off-axis effects and wondered if coda clicks might also suffer from off-axis effects. Chapter 9 details how I use the acoustic array described in Chapter 7 to compare the waveforms of coda clicks recorded from different aspects to address this question.

In Chapter 10 I summarize the findings of this thesis and discuss their implications for our understanding of sperm whale communication. I also suggest future studies that can build on these findings and address unanswered research questions.

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CHAPTER TWO

USING INTER-PULSE INTERVALS TO EXAMINE SPERM WHALE CODA COMMUNICATION AT THE LEVEL OF THE INDIVIDUAL

INTRODUCTION

A comprehensive understanding of vocal behaviour in a species requires knowledge of the vocal output of individual animals. Although studying the types and contexts of different vocalizations used by an animal population can provide some information on their function and use, a more detailed understanding of call function and the complexity of a species' communication system is not possible without knowledge of the way that vocalizations are exchanged between individuals (Bradbury and Vehrencamp 1998). For example, variation in the vocal output of 'codas' (short stereotyped sequences of clicks) by sperm whales (*Physeter macrocephalus*) while socializing at the surface permits the allocation of social units (stable, long-term groups of 11-12 females, calves, and immature animals of both sexes; Christal et al. 1998) into large, sympatric acoustic 'clans', which most likely result from the cultural transmission of vocal patterns (Rendell and Whitehead 2003b). Moreover, the tendency for units to preferentially socialize with other units of the same clan suggests that the clan represents a higher level within the complex social structure of this species (Rendell and Whitehead 2003b). However, without knowledge of the way that coda vocalizations are exchanged between individuals within a social unit, it is unclear whether coda production functions to identify members of the same acoustic clan, or if it serves some other communicative function. Neither is it clear how individuals contribute to group repertoires and how vocal output is divided between group members. Furthermore, although sperm whales appear to have a complex communication system, the existence of syntax (e.g. Robinson 1984; Hailman et al. 1985; McCowan et al. 1999), referential systems (see Zuberbühler 2000; Janik et al. 2006), or other complex phenomena in this species cannot be investigated without data on the way that individuals sequence their coda vocalizations.

The difficulty in determining which individual in a group is vocalizing is a common problem in studying vocal communication in mammals that spend the majority of their time underwater (Costa 1993). While recent advances in the use of passive acoustic localization have provided important tools for studying the movement, foraging behaviour, and communication patterns of vocalizing marine mammal species (e.g. Miller and Tyack 1998; Hayes et al. 2000; Janik et al. 2000; Møhl et al. 2001; Miller et al. 2004), these systems do not easily permit the discrimination of vocalizations made by pelagic cetaceans in very close proximity to one another. Furthermore, the use of non-fixed acoustic arrays can be expensive and cumbersome during fieldwork, particularly in the open ocean and during rough weather. Finally, acoustic arrays only provide information on the location of the vocalizing animal and thus do not readily permit the study of an individual's acoustic output in a social group between recordings and on different days.

A potentially more informative method of identifying vocalizing individuals is to use individually distinctive acoustic features that are stable not only within but also between recordings (e.g. van Parijs et al. 2003). Fortunately, the clicks of sperm whales do exhibit a fortuitous acoustic feature – the inter-pulse interval (IPI) – that is related to body length (Gordon 1991a) and is thus assumed to remain constant over periods of months in adults. Sperm whale clicks are multi-pulsed in structure (see Figure 2.1), a result of the reverberation of sound energy within the nasal complex of the spermaceti organ (Norris and Harvey 1972; Møhl 2001). Because the inter-pulse interval is directly related to the length of the spermaceti organ and thus body length (Gordon 1991a; Rhinelander and Dawson 2004; Teloni 2006), researchers have been able to measure the usual click IPIs of foraging whales to acoustically estimate the size of vocalizing whales (Adler-Fenchel 1980; Gordon 1991a; Leaper et al. 1992; Pavan et al. 2000; Drouot et al. 2004; Rhinelander and Dawson 2004; Teloni 2006).

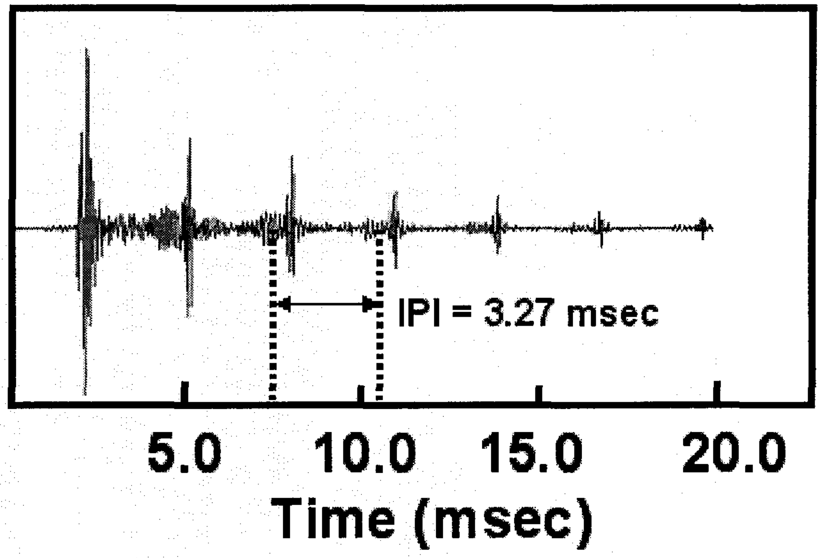

Figure 2.1. Illustration of the inter-pulse interval (IPI) in a single coda click with a clear multi-pulse structure.

Furthermore, this unique acoustic feature has been used in the study of coda communication to demonstrate that adult females produce the majority of codas (Marcoux et al. 2006) and that coda types are shared between individuals within a social unit (Rendell and Whitehead 2004). Nonetheless, this acoustic feature has not yet been realized as a useful tool to assign codas to specific individuals within a social group, which would allow the study of coda output at the level of the individual and thus provide more thorough information on the communication system of this species

One reason why Rendell and Whitehead (2004) did not assign codas to specific whales in a previous analysis is that the IPI distributions of recorded codas were continuous without completely isolated modes, thereby precluding the unambiguous assignment of codas to specific individuals (see Figure 4 of Rendell and Whitehead 2004). Likewise, the presence of a large number of whales during the time of recording increases the probability that at least some whales will be similar in size and thus have similar IPIs, again preventing the unequivocal assignment of codas. Finally, the use of IPIs to allocate codas to specific whales may have been avoided due to the high rate with which codas have been discarded in IPI analysis, a function of high intra-coda IPI variability (see Rendell and Whitehead 2004) and the poor pulse structure of some recorded clicks.

Recognizing the unrealized potential for using IPIs to study individual coda output, I took advantage of several fortuitous coda recordings in which only two whales were in the area to examine the causes of intra-coda IPI variation and to subsequently modify the IPI analysis method to minimize the IPI variation within codas and thus within whales. I then examined usual click and coda recordings made of known individuals recorded over several weeks to show that this method can, in some circumstances, be used to assign codas to individual animals, thereby permitting a more thorough examination of the sperm whale communication system.

METHODS

The IPIs of Codas in Two-Whale Recordings

I first analyzed four recordings for which I was confident that only two whales were in the area at the time of recording; because sperm whales produce large numbers of loud usual clicks (long click trains with inter-click intervals of approximately 0.2 - 2.0 s) while diving, when a sperm whale is in the area of a stationary research vessel, if a hydrophone cannot detect the whale producing usual clicks at depth, then the whale is most likely at or near the surface and either silent or producing codas and visible to observers (pers. obs.). Thus, the determination that there were only two whales in the area during recordings was made using both visual and acoustic observation before, during, and after the recording of codas. Two two-whale recordings were made off the coast of Dominica in February 2005 (recordings #020101 and #020703), one was made in the Sargasso Sea on June 10, 2005 (#20050610-1610b), and another was made in the Mediterranean Sea on July 20, 2005 (#20050720-0020). Codas were recorded using a custom-made towed hydrophone (frequency response: 0.1-30 kHz) connected to a FOSTEX VF-160 multi-track recorder, or via a Creative Audigy PCMCIA soundcard to a laptop computer, upon which recordings were made in the sound editing software ISHMAEL (Mobysoft). Recordings were made at a sampling frequency of 44.1 kHz or 96 kHz. Recordings were initially analyzed using Rainbow Click (see Gillespie 1997; Leaper et al. 2000; Jaquet et al. 2001; Rendell and Whitehead 2004), which detects sperm whale clicks under user supervision and stores them in a separate data file; the user can then designate clicks as belonging to a coda. I only analyzed codas that could be clearly identified aurally.

The software package Rainbow Click also outputs the digitized sound data for each click in each coda, and I used these data for the IPI analysis. I first used automated routines written in MATLAB® version 6.1.450, release 12.1 (MathWorks Inc. 2001) to implement Goold's (1996) cross-correlation and cepstrum methods for estimating the IPI of each click in each coda (as in Rendell and Whitehead 2004; Marcoux et al. 2006). These routines, which are detailed by Marcoux et al. (2006), calculate for each click both the maximum value of the waveform cross-correlation and the maximum value of the cepstrum, and take the median of each measure over each coda. They then compare the cross-correlation and cepstrum based estimates, accepting for each coda the estimate with the lowest within-coda inter-quartile range (IQR), and discarding codas in which neither cross-correlation nor cepstrum estimates of IPIs of the clicks in a coda has an IQR less than 0.02 msec.

The high percentage of coda discard that results from using this method (see Results and Rendell and Whitehead 2004) led me to examine the causes of within-coda IPI variability. Because codas are made over such short time periods (< 2 s) that within-coda IPI values are unlikely to be affected by major changes in orientation, as is the case for usual click IPIs (Zimmer et al. 2005a), intra-coda IPI variation must be due principally to measurement error. In an effort to reduce IPI distributions within two-whale recordings to two distinct modes, and thereby permit the assignment of codas in a recording to individuals, I considered the factors contributing to measurement error and modified the IPI analysis method to minimize intra-coda IPI variability and consequently intra-whale IPI variability.

First, intra-coda IPI variation was largely attributed to the calculation of IPIs of clicks with very poor pulse structure. Second, examination of the derivation of the IPI by this method revealed that unnecessary within-coda IPI variation resulted from taking the absolute *maximum waveform cross-correlation* (as suggested by Gordon 1991a) rather than simply taking the positive maximum waveform cross-correlation, since in some cases the negative maximum (i.e. maximum trough) was greater than the positive maximum (i.e. maximum peak) (as in Figure 2.2). This is because for some clicks, the absolute maximum cross-correlation is the time difference between the largest positive inflection of one pulse and the largest positive inflection of another pulse, while in other cases it may be the time difference between the largest positive inflection of one pulse and the largest negative inflection of another (or vice versa). Third, some intra-coda IPI variation was attributed to cases where the maximum positive cross-correlation was not necessarily the center of a symmetrical cross-correlation peak distribution, which is what is expected and found for clicks with a clear multi-pulse structure (as in Figure 2.2). Finally, IPI variation within codas was also caused by slight differences between clicks in the local maxima within broad cross-correlation peaks (see Figure 2.2).

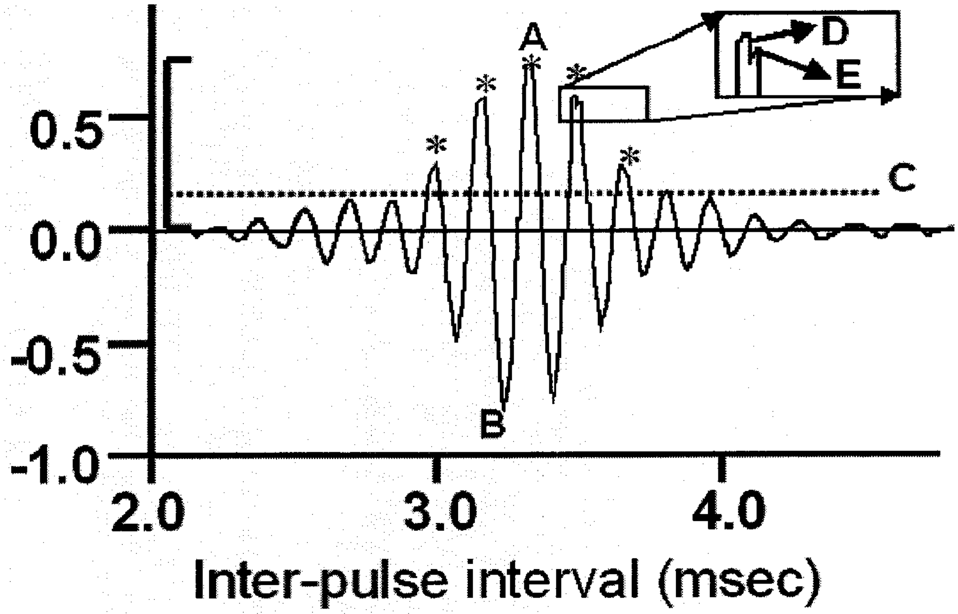

Figure 2.2. Illustration of the cross-correlation between pulses in the click depicted in Figure 2.1. The maximum positive cross-correlation (A) and the maximum negative cross-correlation (B) are identified. In this case (A) is also the median amongst the 5 greatest cross-correlation peaks (denoted by asterisks) as well as the midpoint amongst peaks that are at least 30% of the height (C) of the maximum cross-correlation. Two local maxima within a broad cross-correlation peak are denoted by (D) and (E).

To modify the analysis method to account for these sources of measurement error, I first reduced automation in the routines, allowing the user to discard clicks with poor click structure and select the section of the waveform to be cross-correlated, thereby permitting the avoidance of cross-correlating pulses with extraneous noise. Second, given that for clicks with a clear multi-pulse structure the time delay that results in the best overlap between adjacent pulses, and thus corresponds to the true IPI, results in a maximum cross-correlation peak in the center of the peak distribution (see Figure 2.2), I modified the routine to extract three values from each click: the time-delay giving the maximum waveform cross-correlation, the median time-delay amongst those giving the 5 largest positive cross-correlation values (see Figure 2.2), and the time-delay associated with the cross-correlation peak closest to the midpoint amongst peaks that are at least an arbitrary value of 30% of the height of the maximum peak (see Figure 2.2).

Because these three measures were all taken to estimate the same thing (the time delay that results in the best overlap between adjacent pulses), once these three values were calculated for each click in a coda, the routine calculated the single mode over all three measures for all the clicks in the coda. For example, a 4-click coda would yield three measured values per click and thus a total of 12 values from which the modal value was taken. The mode, rather than the mean, was taken because the lowest resolution of the recording system (~0.02 msec, see Rendell and Whitehead 2004) results in the allocation of calculated cross-correlation values into time classes with a width of approximately 0.02 msec and the method produces occasional highly aberrant values. Finally, to reduce intra-coda variation caused by slightly different minor peaks within broad cross-correlation peaks (see Figure 2.2), measured values within at least 0.05 msec of the mode were assigned the modal value; a criterion of 0.05 msec was used since cross-correlation peaks were approximately 0.10 msec in width. If more than 50% of a coda's measured values were within 0.05 msec of its mode, the coda was retained for analysis and the mode assigned as its IPI.

The IPIs of Group of Seven Usual Clicks

The Group of Seven is a social unit consisting of seven sperm whales (five adult females, one juvenile male, and one male calf) that was followed for a total of 41 days between January 16, 2005 and March 26, 2005 off the coast of Dominica (see Gero 2005). The animals were tracked visually during the day and acoustically at night using a directional hydrophone (see Whitehead and Gordon 1986). Sexes of these individuals were determined by the genetic analysis of sloughed skin samples (see Gero et al. submitted). Approximately three minutes after fluking, sperm whales produce very loud, clear, and slow-paced usual clicks as they make their descent into foraging dives (Gordon 1991a). While studying the Group of Seven, when a whale fluked alone, a photograph was taken of the fluke for photo identification purposes (see Gero 2005) and the first loud usual clicks produced were recorded by the method described above and were assumed to have been made by the photographed whale. In this way, usual clicks made during different foraging dives and on different days were assigned to each of the six eldest whales; the calf was not observed to fluke during the period of study. I used the modified IPI method described above to assign an IPI to each usual click recording by taking the modal IPI of the usual clicks of the diving whale. An IPI was assigned to each whale, excluding the calf, by taking the mode of the IPIs assigned to each of its recordings. The body lengths of whales were estimated from the IPIs of clicks using Gordon's (1991a) equation:

$$\text{Body length (m)} = 4.833 + 1.453 \times \text{IPI} - 0.001 \times \text{IPI}^2$$

The IPIs of Group of Seven Codas

While off the coast of Dominica, acoustic recordings were also made whenever sperm whales in the Group of Seven were spotted at the surface and codas detected on the towed hydrophone. Photographs were taken of whales while shallow diving and fluking during recordings, thereby providing information on the identity of whales observed at the time of recording (Gero 2005). Codas were recorded using the recording system described above and subsequently analyzed using Rainbow Click and the modified IPI analysis method described above. Acoustic analyses were carried out blind to the identities of whales visually observed at the time of recording.

RESULTS

The IPIs of Codas in Two-Whale Recordings

While the IPI analysis method used previously by Rendell and Whitehead (2004) and Marcoux et al. (2006) resulted in the discard of 70 of the 114 codas in the two-whale recordings, simply adjusting the IPI analysis routines to take the positive maximum cross-correlation rather than the absolute maximum reduced the number of discarded codas to just 41. Furthermore, modifying the IPI analysis method as described above not only reduced the discard rate even further to 27 of 114 codas, but also reduced the IPI distributions within each of the four recordings to two clear modes (e.g. Figure 2.3).

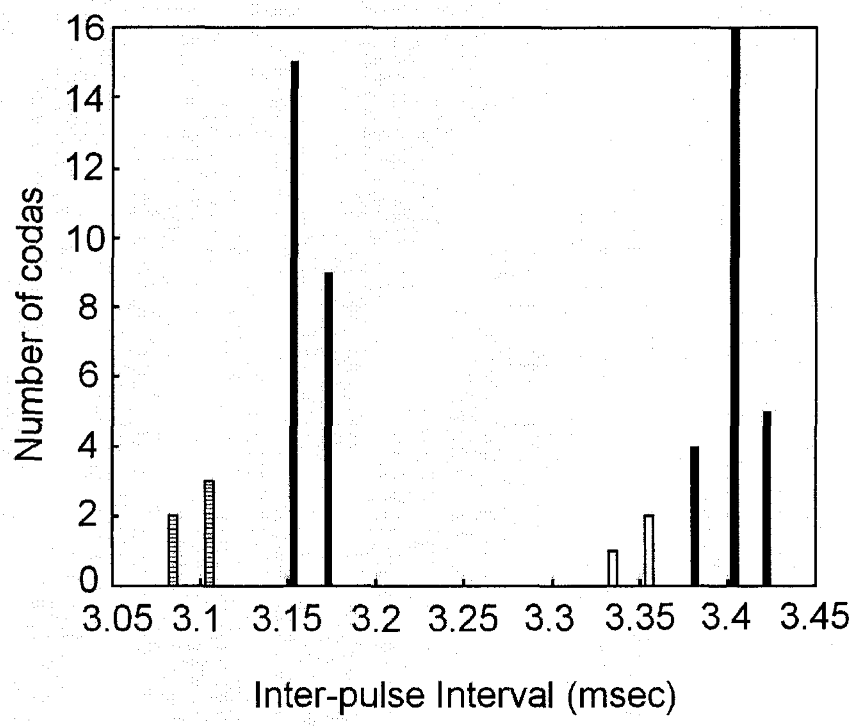

Figure 2.3. Distribution of coda IPIs (solid bars) in a recording (#020101) during which only two whales were in the area. The IPIs from usual click recordings of these two whales, whale #5130 (bars with horizontal stripes) and whale #5560 (open bars), are also presented. The IPIs were calculated using the modified IPI analysis method described in the Methods.

There was also a bimodal distribution when combining the four two-whale recordings and plotting a histogram of the differences in IPIs between codas within recordings (Figure 2.4). The first peak in Figure 2.4 is assumed to correspond to the differences in IPIs between codas made by the same whale and the second broader peak to the differences in IPIs between codas made by different whales. This histogram shows that intra-whale differences in IPIs were less than 0.07 msec, such that if two codas have IPIs within 0.07 msec of one another in a recording with a limited number of whales, it is likely that they were both produced by the same whale. Furthermore, the intra-whale differences did not exceed 0.1 msec, such that codas with IPI differences of 0.1 msec or greater between them were likely not made by the same whale.

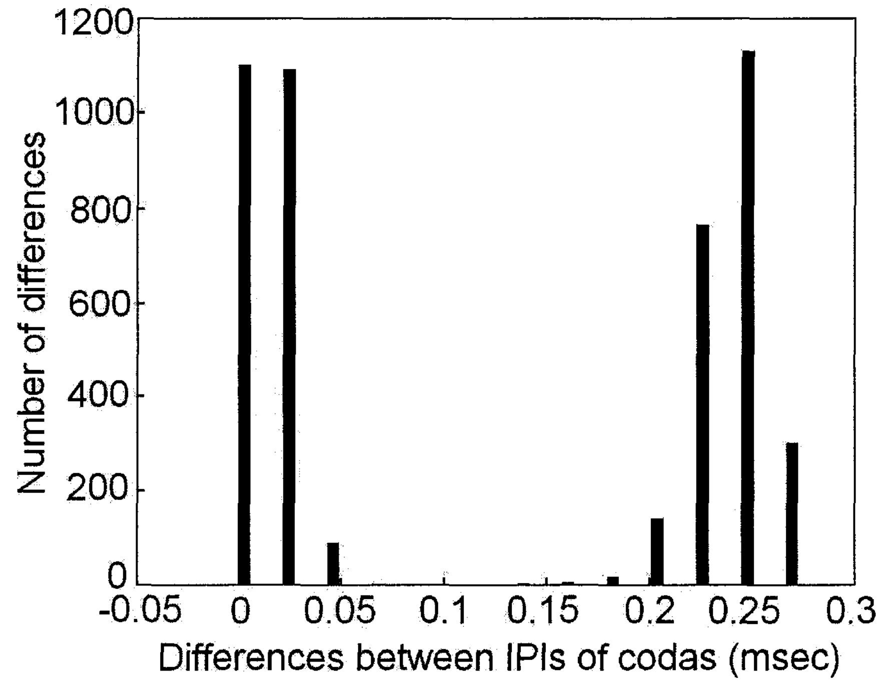

Figure 2.4. Distribution of the IPI differences between codas in four recordings in which only two whales were present.

In contrast to the results found using cross-correlation IPI values, extracting the cepstrum value resulted in IPI distributions for the two-whale recordings that were not nearly as bimodal, indicating that the cross-correlation method was much better at reducing intra-whale IPI variation. Similarly, even when discarding codas with IQRs less than 0.02 msec, the distribution of differences between cepstrum-determined within-recording coda IPIs for the combined two-whale recordings resulted in a much more dispersed distribution with no clear delineation between the coda differences for pairs of codas that were made by the same whale and those that were made by different whales.

The IPIs of Group of Seven Usual Clicks

Usual click recordings produced by the same whale had IPI estimates within 0.05 msec of one another (Figure 2.5). For example, the four recordings made of whale #5722 contained a total of 59 non-discarded usual clicks and had estimated IPIs of 3.22 msec, 3.22 msec, 3.22 msec, and 3.20 msec (Mode = 3.22 msec). Whale #5130 had a modal IPI of 3.11 (*n* = 5 recordings; 112 non-discarded clicks). Whale #5563 had a modal IPI of 3.08 msec (*n* = 4 recordings; 109 non-discarded clicks). Whale #5561 had a modal IPI of 3.31 msec (*n* = 4 recordings; 54 non-discarded clicks) and Whale #5560 had a modal IPI of 3.36 msec (*n* = 3 recordings; 80 non-discarded clicks). At 2.74 msec, the juvenile male (#5727) had the shortest modal IPI (*n* = 3 recordings; 133 non-discarded clicks). The estimated body lengths of these whales, as calculated from their IPIs, are also presented in Figure 2.5. Both IPI analysis and visual observation indicated that the juvenile male was smaller than the adult females.

The IPIs of Group of Seven Codas

From a total of 15 coda recordings, a subset of eight recordings met the criteria that during recording, the IPIs of recorded coda clicks were not within 0.2 msec of the estimated usual click IPI of more than one whale in the area. This conservative criterion was used to ensure that there would be no ambiguity as to which whale in the recording produced a given coda, since the above two-whale IPI analysis suggests that codas with IPIs greater than 0.1 msec in difference are likely not produced by the same whale.

All 108 of the codas from the eight recordings had IPIs within 0.1 msec of the mode usual click IPI of one, and only one, of the whales present during the time of recording (mean ± SD = 0.04 ± 0.02 msec; e.g. Figure 2.3). Figure 2.5 illustrates the distribution of usual click IPIs and coda click IPIs for 5 of the 6 eldest whales, excluding Whale #5563 which was not present for any recordings that met the criteria described above for the unambiguous assignment of codas to whales. There was a consistent difference in IPI estimates between usual and coda clicks for each whale (see Figure 2.5). A whale's modal usual click IPI was on average 1.3 ± 0.5% shorter than its assigned coda click IPIs ($n = 108$).

DISCUSSION

While the IPIs of sperm whale clicks have been used previously to estimate body size and study the production of codas within a group, I demonstrate here that they can also be used to study coda communication at the level of the individual whale. The utility of the IPI analysis method developed here for this purpose is demonstrated by the segregation of IPIs in the two-whale recordings into two distinct and non-overlapping modes, the consistency of the usual click IPIs between recordings within individuals, and the consistent relationship between the IPIs of coda clicks in a given Group of Seven recording and the mean usual click IPI of a whale present at the time of the recording. In addition, the modified method is advantageous over the method utilized by Marcoux et al. (2006) and Rendell and Whitehead (2004) in that it greatly reduces the number of discarded codas.

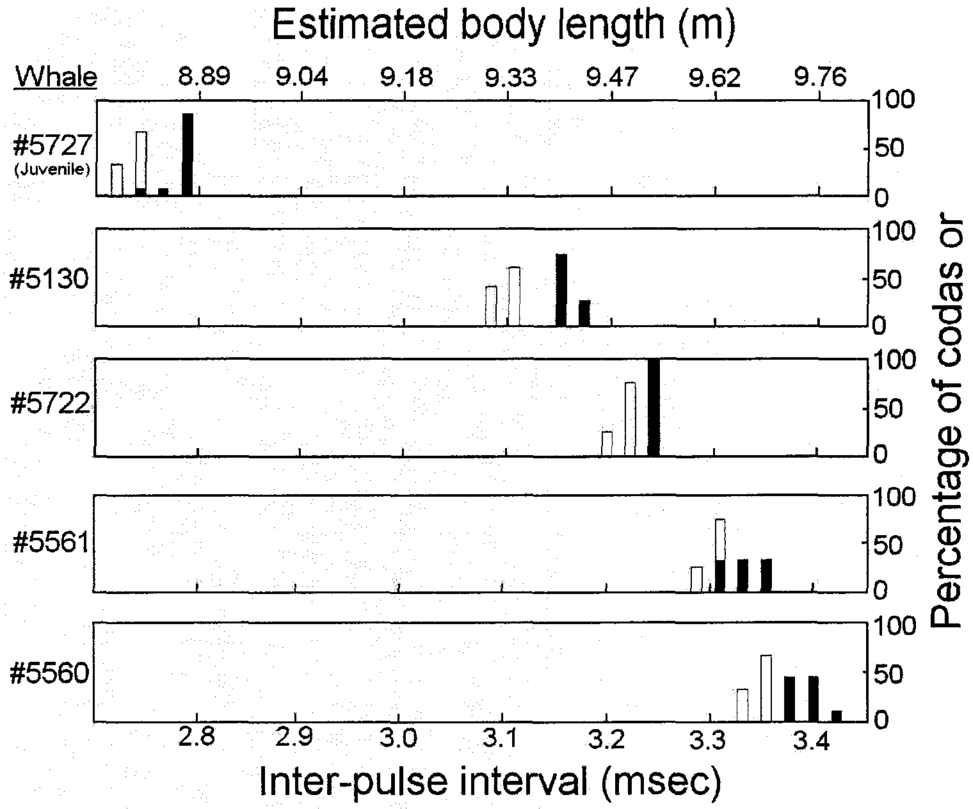

Figure 2.5. *Distributions of usual click IPIs (white bars) and coda click IPIs (black bars) for five of the whales in the Group of Seven. The estimated body lengths of these five whales, as derived from Gordon's (1991a) equation, are also presented. Whale #5563 was not included here because it was only present during one recording, which did not meet the criteria described in the Results for the unambiguous assignment of codas to whales. The IPI distributions are given in terms of percentage of total usual click recordings or percentage of total codas obtained for each whale.*

While the previously used method resulted in the discard of 62% of codas in the two-whale recordings, modifying the IPI analysis method to account for four factors that affected intra-coda variation reduced the discard rate to 24%. Similarly, while the previous IPI analysis of a sperm whale unit encountered off the Galàpagos Islands resulted in the discard of 89% of the analyzed codas (see Rendell and Whitehead 2004), analysis of the same unit's codas with the modified IPI method developed here results in the discard of only 31% of the codas.

Much of the rejection of usable codas that occurs when utilizing the previous method results from extracting the absolute maximum cross-correlation. This is because within some codas, for some clicks the maximum positive cross-correlation is greatest and for others the maximum negative cross-correlation is greatest. The extraction of the absolute maximum cross-correlation is based on Gordon's (1991a) suggestion that the IPI be calculated as the time difference between the largest positive deflection in the first pulse and the largest negative one in the second (or vice versa) because he found that successive pulses in a click were reversed in phase. However, because successive pulses in sperm whale clicks are believed to undergo reflections on both the frontal and distal air sacs (see Madsen et al. 2002b), they should be in phase with one another and the IPI should be calculated as the time difference between the largest positive deflections between successive pulses. In my results, taking the maximum positive rather than the absolute maximum cross-correlation clearly reduces intra-coda IPI variability, thereby reducing the number of discarded codas as well as reducing intra-whale IPI variability. This improves the consistency of IPIs between codas within whales and makes the discrimination of vocalizations between whales more viable. Intra-coda IPI variability is further reduced by taking the mode over several cross-correlation measures, rather than just the maximum value, and by combining local maxima that comprise broad cross-correlation peaks.

Even after making these modifications to the IPI analysis method, the cross-correlation of pulses within clicks with poor pulse structure still contributes to intra-coda IPI variation and thus the discard of codas in analysis. Given the effect of recording angle on coda click structure (see Chapter 9), clicks analyzed in this study with poor multi-pulse structure were likely recorded off the body axis of the vocalizing whale. And while no amount of signal processing can extract the IPI from a single click with poor pulse structure (Zimmer et al. 2005a), the manual rejection of clicks with obviously poor pulse structure during analysis can further reduce intra-coda IPI variation and thus the number of discarded codas.

It has been argued that the rarity of usual clicks with a clear multi-pulse structure disqualifies the extraction of IPIs from single clicks (Zimmer et al. 2005a; Teloni 2006) and instead favours the averaging of cepstral values over hundreds of clicks to obtain the correct IPI (see Teloni 2006). While this method is extremely useful in calculating the IPIs from usual click sequences with many clicks, codas are only 2-10 clicks long and so require an analysis method that can extract a correct IPI from just a few clicks. Furthermore, such a method necessitates the manual discard of clicks that lack a clear multi-pulse structure to ensure that clicks with complex pulse structures do not increase the intra-coda IPI variation and result in the unnecessary discard of a entire coda.

Fortunately, coda clicks are recorded in the far field, at least in my experience, with a clear multi-pulse structure much more often than usual clicks, thereby permitting the extraction of consistent IPIs from just a few coda clicks. Coda clicks may be recorded with a clear pulse structure more often than usual clicks not only because of the angle from which codas are generally recorded (see Chapter 9) but also because of differences in the production mechanism of coda and usual clicks. Codas are generally recorded while whales are at the surface, and, during my fieldwork, often from behind the vocalizing whales as they slowly move in one direction. Thus, coda recordings are often recorded on or near the body axis of the whale, which results in the recording of a click with a clear multi-pulsed structure (see Chapter 9). In contrast, usual clicks are generally recorded while the whale is at depth and off-axis, leading to a click structure that is less often clearly multi-pulsed in nature. Furthermore, because coda clicks have both a longer pulse duration and a lower decay rate than usual clicks (Madsen et al. 2002b), the distortion of the first pulse by water noise or acoustic overloading does not necessarily hinder the cross-correlation of subsequent pulses with one another as it can for usual clicks.

While Teloni (2006) argues that the manual discard of clicks by the user introduces user bias, I argue that this bias is only in the quality of the clicks analyzed and not in the values of accepted coda IPIs, and that this quality control is necessary in order to ensure that the correct IPI is extracted from such a small number of clicks. User bias concerning the quality of data to include in analysis is evident in many aspects of biology, including the discernment of peaks from cepstral analysis (see Teloni 2006) and the quality rating of photographs for photo-identification (see Arnbom 1987). In my analysis of Group of Seven coda IPIs, the discard of clicks with poor pulse structure never reduced the number of usable clicks in a coda to less than three clicks.

While the averaging of cepstrum values might be useful when large numbers of usual clicks are available, the lack of a delineated bimodal IPI distribution in two-whale recordings when using cepstrum values (and the lack of a clear delineation between modes in the histogram of intra-recording differences between codas) indicates that the modified analysis method involving the cross-correlation of pulses is much more suitable than cepstrum analysis for differentiating the codas made by different whales.

The distinct bimodal segregation of IPIs in the two-whale recordings demonstrates the efficacy of this method in examining the codas of individuals and indicates that codas with IPIs within 0.05 msec of one another are likely made by similarly-sized whales, and thus, in a small population, potentially the same whale. This criterion is similar to the average within-recording standard deviation of 0.065 msec (n = 4 recordings) in Teloni (2006) for usual clicks. My results also indicate that recorded codas with IPI differences greater than 0.1 msec are not likely made by the same whale. The assumption that each IPI mode in the two-whale recordings represents the codas made by one of the two whales was supported by the fact that no overlapping codas had similar IPIs, such that overlapping codas were made by differently sized whales.

The similarity criteria determined here will permit the study of coda matching, antiphonal calling, and the exchange of coda types in recordings where few whales are present and the IPIs segregate into distinct modes. Moreover, even though the utility of this method will be limited by the size of the recorded group, in recordings where several similarly sized whales are present and vocalizing, these criteria can still be used to determine if codas recorded in sequence were made by different whales, thus still revealing information on coda matching and antiphonal calling between different whales (see Chapter 4 and 5).

I was fortunate enough during field studies not only to make several two-whale recordings that permitted the establishment of these criteria, but also to record the usual clicks and codas of a small social unit over many days. This allowed me to assign codas to known photo-identified individuals based on the similarity between coda IPIs and the usual click IPIs of whales in the area. I was then able to use this data set to examine the rates of coda production within a unit (see Chapter 6), coda repertoires of individuals in this unit (see Chapter 3) and the exchange of codas between whales (see Chapters 4 and 5).

It is interesting to note that in the Group of Seven, the mean estimated usual click IPI of each whale was consistently shorter than its distribution of coda click IPIs (see Figure 2.5). This suggests that coda clicks and usual clicks are produced differently, with the sound energy of usual clicks traveling a slightly lesser distance within the nasal complex than coda click sound energy before being released into the water. It is currently believed that while coda clicks reverberate within the spermaceti organ between the distal and frontal air sacks to give rise to a prominent multi-pulsed structure (Madsen 2002), usual clicks travel a 'bent-horn' path from the spermaceti organ through the junk before being released into the water, with some residual energy reflected back into the spermaceti organ to give rise to a less pronounced, but still existent, multi-pulsed structure (Møhl 2001; Madsen et al. 2002b; Zimmer et al. 2005a). If usual clicks do exit via the junk rather than the spermaceti organ, then in large old males, which demonstrate a projection of the spermaceti organ beyond the anterior termination of the junk (Cranford 1999), usual clicks would be emitted into the water sooner (and thus have shorter IPIs) than coda clicks. Although in comparison to old males, females and immature males have spermaceti organs and junks of relatively equal length (Cranford 1999), perhaps slight differences in the lengths of the two organs explain the slight differences in the lengths of coda and usual click IPIs observed here. Alternatively, differences in the IPIs of usual and coda clicks could be a result of differences in the point of reflection on the frontal sac, conformational changes of the soft structures in the nasal complex, slight pressure effects of different depths on the production of the two click types, or other differences in their physiological production (P. Madsen, pers. comm.[2]).

While previous research has revealed that sperm whales have a complex communication system that involves the cultural transmission of repertoires (Rendell and Whitehead 2003b) and the seemingly non-random exchange of coda types (Weilgart and Whitehead 1993), the modified method of IPI analysis described here indicates that coda production can also be studied at the level of the individual, at least within small social groups, providing the opportunity to more thoroughly examine the functions of codas in the social behaviour of this remarkable animal. Furthermore, given the finding that a whale's coda click IPIs tend to be greater than its usual click IPIs, using this modified method to assign codas to whales also provides useful information concerning physiological differences in the ways that coda clicks and usual clicks are produced.

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CHAPTER THREE

INDIVIDUAL VOCAL REPERTOIRES WITHIN A SPERM WHALE SOCIAL UNIT

INTRODUCTION

Individual variation in the acoustic signals of conspecifics is presumed to function for a wide variety of species in the advertizement of individual identity. In species that live in colonies or form foraging aggregations, graded differences in call types are often used to advertize identity and to facilitate the reunion of parent-offspring pairs (e.g. Halliday 1983; Jones et al. 1987; McCulloch and Boness 2000) and mated pairs (e.g. Mathevon 1996; Lengagne et al. 1999). Moreover, in territorial species, individual-specific vocalizations often function in advertizing individual identity and asserting claim to territory (see Lambrechts and Dhondt 1995; Stoddard 1996). In co-operative groups, however, the acoustic signaling of individual identity can also function in the establishment and maintenance of social relationships between individuals (e.g. Caldwell et al. 1990; Tooze et al. 1990). For example, bottlenose dolphins (*Tursiops truncatus*) live in a fission-fusion social structure (Connor et al. 2000) and appear to utilize individual-specific 'signature whistles' (Caldwell et al. 1990) to facilitate relationships with individual dolphins (Janik 2000).

In contrast, a lack of individuality in vocal repertoires between conspecifics in a social unit may indicate that there is little necessity to acoustically advertize individual identity. While this may be because individual identity can be advertized via visual (e.g. Parr and de Waal 1999) or olfactory signals (e.g. Jäckel and Trillmich 2003), for animals that live in the marine environment where visual and olfactory cues are of limited value, a lack of individual-specific vocal repertoires may indicate that members of a species do not have strong individual-specific relationships. Instead, social animals that form equivalent associations with all members of their social group but interact differently towards members of different social groups (see Schusterman et al. 2000) would necessitate knowledge of a conspecific's group identity rather than individual identity, thus selecting for group-specific rather than individual-specific vocal repertoires. Study of the vocal repertoires of social marine species provides the opportunity to further investigate the correlation between the level of variation in vocal repertoires and their communicative function (Tyack 1986b; Tyack and Sayigh 1997). One such species worth examining then is the highly social and vocal sperm whale, *Physeter macrocephalus*.

Both the social structure and the communication system of the sperm whale are complex. Females, calves, and immature animals of both sexes live in long-term social units that persist for decades and consist on average of 11-12 animals in the Pacific (Christal et al. 1998). Acoustic recordings of sperm whale social units show different usage patterns (i.e. repertoires or dialects) of short stereotyped sequences of clicks (Weilgart and Whitehead 1997; Rendell and Whitehead 2003b) termed 'codas' (Watkins and Schevill 1977). Units preferentially associate with units possessing similar coda repertoires, such that these repertoires appear to represent a higher-order social structure, termed the acoustic clan (Rendell and Whitehead 2003b). Because acoustic clans are sympatric and are genetically similar to other clans, Rendell and Whitehead (2003b; Whitehead 2003a) have argued that differences in repertoires between clans most likely result from social learning. If true, sperm whale acoustic clans may represent the numerically largest example of culturally-defined cooperative groups outside of humans (Rendell and Whitehead 2003b).

Despite evidence that whales share some coda types within a social unit (Rendell and Whitehead 2004), it is still unknown whether sperm whales possess individual-specific coda repertoires and thus whether some variation in repertoires between units is a result of differences in coda repertoires between individuals (Freeberg 2001; Tyack 2001). Furthermore, if individuals in a unit do produce different coda types at different rates, then coda repertoires may function in individual identification and codas might be used in a manner similar to that theorized for bottlenose dolphin 'signature whistles' (Watkins and Schevill 1977; Watkins et al. 1985; see Tyack 1986b; Caldwell et al. 1990; Janik and Slater 1998; Sayigh et al. 1998). Conversely, if individuals in a unit do not possess individual-specific coda repertoires, then coda production may instead function primarily in the advertizement or assertion of clan affiliation.

The current lack of knowledge concerning the coda repertoires of individual sperm whales is largely a result of the difficulty of studying the individual vocal behaviour of free-ranging cetaceans (Janik et al. 2000). In Chapter 2, however, I demonstrated that a fortuitous feature of sperm whale clicks, the inter-pulse interval (IPI), which is related to the size of the sound-producing organ and hence the vocalizing whale's body length (Gordon 1991a), can be used to assign codas to particular whale sizes, and thus in some cases, to specific whales in small social units. Although coda clicks have a lower decay rate, lower directionality, more clearly defined pulse structure (Madsen 2002), and slightly longer IPIs than usual (echolocation) clicks (Chapter 2), both types of click permit the extraction of IPIs. Moreover, the modal IPI of a whale's usual clicks are generally within 0.07 msec of its modal coda click IPIs, thereby permitting the assignment of codas to whales whose modal usual click IPI is known (Chapter 2). In the current chapter, I used the IPIs of coda clicks to assign codas to individual whales in a well-studied social unit and to investigate whether sperm whales in the unit possess individual coda usage repertoires.

METHODS

Field Methods

A unit of seven sperm whales (five adult females, one juvenile male, and one male calf) was observed for a total of 41 days between January 16 and March 26, 2005 off the coast of Dominica. Animals were tracked visually during the day and followed acoustically at night using a directional hydrophone (see Whitehead and Gordon 1986). While studying this social unit, which was termed the 'Group of Seven' (see Gero 2005), when a whale fluked alone, a photograph was taken of its fluke for photo identification purposes and the first loud, clear, and slow-paced usual clicks (i.e. echolocation clicks) produced by the diving whale (see Gordon 1991a) were recorded and assigned to the photographed whale. Sloughed skin samples were collected in the slicks of individuals (Whitehead et al. 1990; Bérubé and Palsbøll 1996) and later analyzed for genetic determination of sex, haplotype, and pairwise relatedness (see Gero et al. submitted). Recordings were made from a towed hydrophone and recorded on a Fostex VF-160 multi-track recorder (see Chapter 2).

Assigning Codas to Individuals

Recordings were analyzed using Rainbow Click (see Gillespie 1997; Leaper et al. 2000; Rendell and Whitehead 2004) software. The modal IPI in each recording was calculated using a modified version of the custom-written MATLAB® (version 6.1; MathWorks Inc. 2001) routines described in Marcoux et al. (2005) and Rendell and Whitehead (2004) (see Chapter 2). This modified method extracts the maximum cross-correlation peak, rather than the absolute peak (cf. Gordon 1991a), for well-conditioned IPIs while allowing the user to discard clicks with a distorted pulse structure (see Zimmer et al. 2005a). The modal IPI was calculated for each recording and the usual click IPI for each fluking whale was calculated by taking the mode of the IPIs assigned to each of its recordings (see Chapter 2).

In addition to recordings of whales' first usual clicks, I also made 15 coda recordings of this unit and calculated the IPIs of coda clicks using the same IPI analysis method (see Chapter 2). Since IPI analysis of coda recordings in which only two sperm whales were in the area indicated that codas with IPIs greater than 0.1 msec in difference are likely not produced by the same whale (see Chapter 2), I initially used a subset of eight coda recordings in which the modal usual click IPIs of whales present at the time of recording were at least 0.2 msec different to unambiguously assign codas to individual whales based on the similarity of coda click IPIs and the usual click IPIs of present whales (see Chapter 2). I subsequently used the IPIs of these assigned codas to determine the modal coda click IPI for each fluking whale (Chapter 2). Unassigned codas were then assigned to a whale if its modal IPI was within 0.05 msec of the modal coda click IPI of a whale present at the time of recording and at least 0.1 msec dissimilar than the modal coda click IPI of every other whale present during recording (see Chapter 2). Because the modal coda IPIs of the adult females and juvenile male were all greater than 2.7 msec, codas that were observed with clear inter-pulse intervals of less than 2 msec while the calf was present were assumed to have been made by the calf (whale #5703).

Repertoire Comparisons

I used both categorical and continuous measures to examine differences between coda repertoires. Codas were assigned to categorical type using *k*-means cluster analysis methods described in Rendell and Whitehead (2003a,b, 2004). Each coda type was given a descriptive name based on the pattern of clicks. For example, '5R' denotes a coda with five regularly spaced clicks, while '5+1' signifies five regularly spaced clicks followed by a longer gap before the sixth click (Weilgart and Whitehead 1997). In this categorical method, two codas were similar (1) if they were assigned the same type and dissimilar (0) if they were of different types.

Additionally, two continuous measures of similarity were calculated for pairs of codas. For these, each coda was represented by the intervals between adjacent clicks ('inter-click intervals'), either using absolute time intervals or proportions relative to total coda length. The multivariate similarity of two codas with the same number of clicks was measured using the infinity-norm distance between the inter-click intervals (ICIs) and a basal similarity of 0.001 as in Rendell and Whitehead (2003a,b). The multivariate similarity of two codas containing different numbers of clicks was zero.

Using each of the three measures of similarity (category type, infinity-norm distance using absolute inter-click intervals, and infinity-norm distance using standardized inter-click intervals), I computed the average similarity of codas made by the same whale within recordings (within whales, within recordings) and compared this to the average similarity of codas made by the same whale but in different recordings (within whales, between recordings). Average similarity values were considered significantly different if the 95% confidence intervals calculated by jackknifing recordings did not overlap.

To determine whether coda repertoires were significantly different between whales, I compared the average similarity of codas made by the same whale in different recordings (within whales, between recordings) to the average similarity of codas made by different whales in different recordings (between whales, between recordings), thereby accounting for any autocorrelation in coda production within recordings. Under the expectation that the codas of the calf and juvenile male would differ from those of the adult females, I first used average similarities to compare the coda similarity of adult females, excluding the calf and juvenile. To examine the variation between whales when making a particular coda type, I also compared the average multivariate relative ICI coda similarities within and between adult females and between recordings for the most prevalent coda type. Next, to test whether the coda repertoire of the calf, juvenile, or any adult female differed from the general coda repertoire of the adult females in the unit, I compared the similarity of the codas of the calf, juvenile, and each adult female to the codas of the other adult females.

Finally, pairwise comparisons were conducted between each unit member to test whether the coda repertoire of a whale was significantly dissimilar than the coda repertoire of another particular whale. For all three similarity measures, I calculated average similarities between sets of codas assigned to pairs of whales and entered these similarities into an average linkage cluster analysis (e.g. Manly 1994). I tested the robustness of the resultant clustering using jackknifed resamples omitting each recording in turn. For a given branch I counted the number of jackknife resamples in which the branch contained exactly the same groups as the original clustering. I used routines custom-written in MATLAB® for all numerical analyses.

In addition, I tested whether coda repertoires correlated with genetic relationships by using Mantel tests (Mantel 1967; Schnell et al. 1985) and matrix correlation coefficients to examine the similarity of elements in matrices of the average similarities of whales' codas and a matrix of pairwise genetic similarity. Mantel tests were carried out using SOCPROG (2.2, H. Whitehead, Dalhousie University, NS, Canada) in MATLAB®.

RESULTS

Usual click recordings produced by the same whale had modal IPI estimates within 0.05 msec of one another, indicating the consistency of usual click IPIs made by the same whale on different days over several weeks (see Table 3.1). The coda click IPI value for each whale, as calculated using recordings in which codas could be unambiguously assigned to a present whale, is also presented in Table 3.1.

Table 3.1. The modal usual click inter-pulse intervals (IPIs) and coda click IPIs for fluking whales in the Group of Seven. The modal usual click IPI value (and SD) for each fluking whale was calculated from several recordings of their first usual clicks after fluking. The modal coda click IPI value (and SD) for each of these whales was calculated using recordings in which the assignment of codas to whales was unambiguous (see text for description of coda assignment). Individuals are labeled with letters denoting their age class or relationship with the calf (J – juvenile male, A – adult female, M – mother, B – babysitter).

Whale ID	Modal Usual Click IPI	Modal Coda Click IPI
5727 (J)	2.74 ± 0.01 msec (3 recordings, 133 clicks)	2.79 ± 0.01 msec (20 codas)
5130 (A)	3.11 ± 0.01 msec (5 recordings, 112 clicks)	3.15 ± 0.01 msec (36 codas)
5563 (A)	3.08 ± 0.01 msec (4 recordings, 109 clicks)	3.15 msec*
5722 (M)	3.22 ± 0.01 msec (4 recordings, 59 clicks)	3.24 ± 0.00 msec (2 codas)
5561 (B)	3.31 ± 0.01 msec (4 recordings, 54 clicks)	3.36 ± 0.02 msec** (3 codas)
5560 (A)	3.36 ± 0.01 msec (3 recordings, 80 clicks)	3.40 ± 0.02 msec** (47 codas)

*Although no modal coda click IPI was initially available for whale #5563 (due to the fact that it was only present during one recording, which did not meet the criteria described in the Methods for the unambiguous assignment of codas to whales), because its modal usual click IPI was very similar to that of another whale (#5130), it was assigned the same modal coda click IPI.

** Although whale #5561 and whale #5560 had modal coda click IPIs within 0.05 msec of one another, in recordings in which only one of these two whales was present (and thus the identity of the vocalizing whale was unambiguous), the modal coda click IPIs of whale #5561 were consistently less than or equal to 3.36 msec (n = 10 codas) and the modal coda click IPIs of whale #5560 were consistently greater than 3.36 msec (n = 43 codas). Codas in recordings in which both these whales were present were thus assigned to each of these whales using this criterion in addition to the assignment criterion described in the text. The use of these two criteria to discriminate between the codas made by these two whales is corroborated by the fact that in using them, for 35 pairs of recorded overlapping codas, the two codas in each overlapping pair were assigned to different whales (#5560 and #5561) whereas for no pairs of overlapping codas were both codas in the pair assigned to the same whale.

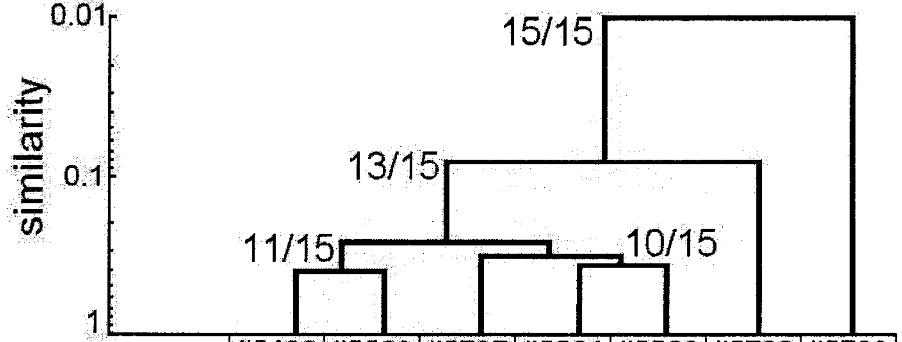
A total of 318 codas from 15 recordings were assigned to the seven individuals in the unit (see Figure 3.1). Using *k*-means classification methods, codas were categorized into 16 coda types with two coda types ('1+1+3' and '5R') making up more than 50% of the unit's coda repertoire. Neither the calf (whale #5703) nor its mother (whale #5722) produced the two most prevalent coda types. The coda type that was produced most often ('1+1+3') was the most prevalent in all of the other whales' coda repertoires, except for the juvenile male (whale #5727), which produced the most prevalent and second most prevalent coda types with equal frequency.

Overall, I found that the codas of adult females from different recordings (within whales, between recordings) were as similar as they were within them (within whales, within recordings), regardless of the similarity measure used (see Figure 3.2a-c). While the codas of the juvenile male did show less similarity between recordings than within them, particularly when comparing the categorical similarity of codas, this difference was not significant (see Figure 3.2e-g). Likewise, the average similarity of the calf's codas between recordings was not significantly different than the average similarity of its codas within recordings (see Figure 3.2h-j).

In examining coda repertoire variation between whales, overall the average similarity of codas produced by different females in different recordings (between whales, between recordings) was not significantly less than the average similarity of codas produced by the same females in different recordings (within whales, between recordings; see Figure 3.2a-c). Likewise, the average similarity of the juvenile male's codas with those of adult females in different recordings was not significantly less than the similarity of the juvenile's own codas between recordings (see Figure 3.2e-g). Although the average similarity of the calf's codas with those of adult females in different recordings was also not significantly different than the similarity of the calf's own codas between recordings, this finding was likely a result of the low number of calf recordings ($n = 2$) and the consequently large confidence intervals (see Figure 3.2h-j). Adult females were consistent in the way that they produced the most common coda type ('1+1+3') both between recordings and between individuals (see Figure 3.2d).

Average linkage cluster analysis of the similarities between repertoires indicated that when using either the categorical similarity of codas or the multivariate similarity of codas calculated with relative ICIs, the repertoires of the calf (whale #5703) and its mother (whale #5722) were the least similar to those of the other whales in the unit (see Figure 3.1). Furthermore, the calf's mother, whose coda type repertoire consisted solely of one coda type ('1+3'), was the only whale whose average categorical similarity between recordings (within whale, between recordings) was significantly greater than its average coda type similarity with codas of other whales in different recordings (between whales, between recordings). In contrast, using the multivariate measures rather than the categorical type similarity measure, no whale had an average coda similarity within whale between recordings that was significantly different than its average coda similarity between whales between recordings.

Although the limited number of calf recordings likely precluded the finding of an overall significant difference between the similarity of codas produced by the calf and the similarity of the calf's codas with those of other whales, pairwise comparisons revealed that the calf and its mother were the only whales that had significantly different coda repertoires than other whales; when using relative inter-click intervals whales #5561 and #5560 had significantly different repertoires than the calf and mother; when using absolute inter-click intervals the mother had a coda usage repertoire that was significantly different than all other whales except whale #5130; and finally, when using the average coda categorical type similarity measure, the mother's coda types were significantly different than all other whales and whales #5561 and #5560 both had coda types that were significantly different than those of the mother and calf.



coda type	#5130	#5563	#5727	#5561	#5560	#5722	#5703	
	(A)	(A)	(J)	(B)	(A)	(M)	(C)	**TOTAL**
2+1	0	0	2	0	0	0	0	**2**
4R	0	0	0	1	0	0	1	**2**
1+3	11	1	0	3	0	36	0	**51**
2+1+1+1	0	6	1	0	3	0	4	**14**
1+1+3	24	18	8	24	34	0	0	**108**
5R	0	4	8	34	41	0	0	**87**
5+1	0	0	0	0	0	0	12	**12**
6R	0	0	1	0	0	0	1	**2**
7R	1	0	1	0	6	0	0	**8**
6+1	0	1	0	0	0	0	4	**5**
6+1+1	0	0	1	0	0	0	1	**2**
1+1+6	0	0	0	0	3	0	0	**3**
8R	0	1	0	0	7	0	1	**9**
1+1+7	0	0	0	0	1	0	0	**1**
9R	0	1	0	0	5	0	3	**9**
9+1	0	0	0	0	1	0	2	**3**
no. of codas	**36**	**32**	**22**	**62**	**101**	**36**	**29**	**318**
no. of recs	**5(14)**	**1(0)**	**5(42)**	**5(45)**	**7(38)**	**4(26)**	**2(26)**	

Figure 3.1. Coda repertoires of Group of Seven sperm whales compared using average categorical similarity (top) and *k*-means classification methods (bottom). Numbers next to dendrogram branches indicate the number of jackknife resamples in which that branch was recreated (out of 15 recordings). Numbers in the top portion of the table indicate whale identification numbers and letters denote the individual's age class or relationship with the calf (C – calf, M – mother, B – "babysitter", J – juvenile male, A – adult female). Numbers in the classification table indicate the frequency with which each individual produced each coda type. Underlined numbers indicate that the coda type comprises at least 10% of the whale's coda type repertoire. The code 'R' indicates a coda with regular inter-click intervals and the code '+' indicates a gap between clicks. Numbers below each column are the number of codas recorded from each whale and the number of recordings made of each whale with the time interval (in days) between the whale's first recording and last recording in parentheses.

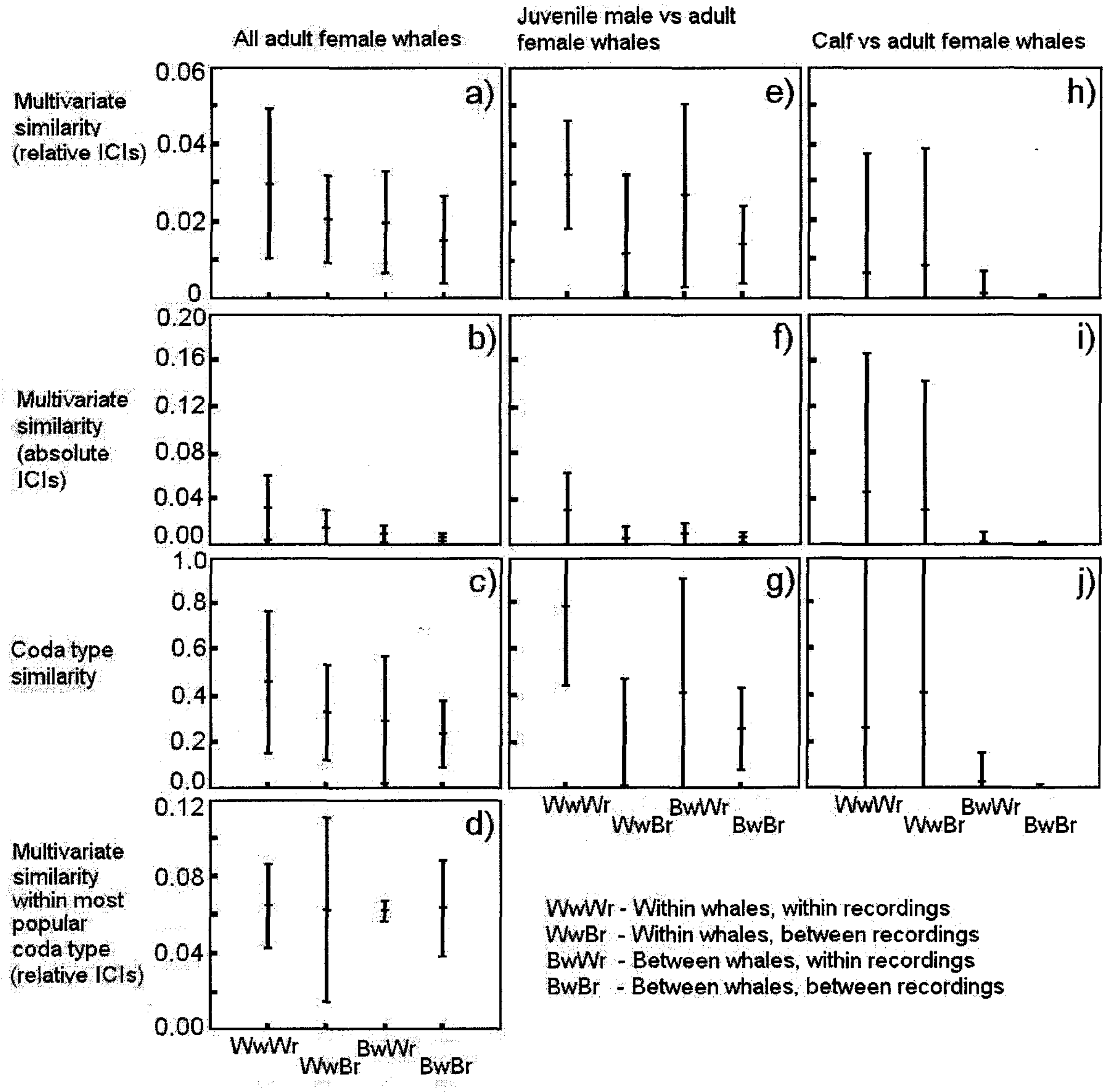


Figure 3.2. Average coda similarities calculated within whales within recordings (WwWr), within whales between recordings (WwBr), between whales within recordings (BwWr), and between whales between recordings (BwBr) using three different similarity measures: average multivariate similarity of codas using relative inter-click intervals (ICIs), average multivariate similarity of codas using absolute inter-click intervals, and average categorical similarity of codas as classified by *k*-means cluster analysis. Error bars are 95% confidence intervals calculated by jackknifing over recordings. Average coda similarities were compared for the adult females (a-c), the juvenile male in comparison to the adult females (e-g), and the male calf in comparison to the adult females (h-j). The average multivariate similarities of codas calculated using relative inter-click intervals were also compared for the most prevalent coda type ('1+3+3') within the adult females (d).

Genetic analysis indicated that all individuals in the social unit share the same mitochondrial DNA haplotype, suggesting that all of the seven whales originated from the same matriline (see Gero et al. submitted). Patterns of pairwise relatedness amongst the members of this social unit are presented in Gero et al. (submitted).

Matrix correlation and Mantel tests indicated that there was no correlation between genetic relatedness and categorical coda repertoire similarity (Mantel test matrix correlation = 0.405, $P = 0.118$), relative ICI coda repertoire similarity (Mantel test matrix correlation = 0.131, $P = 0.366$), or absolute ICI coda repertoire similarity (Mantel test matrix correlation = 0.171, $P = 0.269$).

DISCUSSION

These results indicate that the coda repertoires of individual whales are statistically indistinguishable between recordings made over several weeks and are generally similar between individuals in a unit, showing that codas cannot function exclusively in individual identification (see Watkins and Schevill 1977; Watkins et al. 1985; Tyack 1999). Moreover, the similarity in the way that adult females produced the most prevalent coda type ('1+1+3') indicates that individual variation in the production of this coda type is also not likely used in individual identification. The dissimilarity between the coda repertoires of the mother and calf with other whales in the unit, however, indicates that coda production by these individuals may function to alert their presence and location to other whales, particularly each other. While the other whales largely produced '1+1+3' and '5R' coda types, the calf primarily produced the '5+1' coda type and its mother solely produced the '1+3' coda type. Thus, while the codas of other females in the unit, particularly the two most common coda types, may function in clan identification, the coda repertoires of the calf and its mother may play some role in individual identification to permit their reunion. Although the recognition of individuals is accomplished in many mammalian species by individually-specific variation in graded calls (e.g. Cheney and Seyfarth 1980; McShane et al. 1995), this function is rarely achieved by individual differences in the repertoires of discrete calls (but see Janik and Slater 1998; Sayigh et al. 1998).

Although mature male sperm whales make very few codas in social contexts (Marcoux et al. 2006) and their codas can be highly limited in variety (see Pavan et al. 2000), my results indicate that the juvenile male in this social unit not only made several codas types, but also produced a coda repertoire similar to that of the adult females. Thus, mature males may also possess coda repertoires similar to those of females in their natal unit but produce codas at lower rates as they mature. The fact that the repertoire of the juvenile male was more similar to that of the adult females than was the repertoire of the male calf suggests that at some stage between infanthood and adolescence, sperm whales develop a coda repertoire that is similar to that of the unit as a whole.

While the dissimilarity between the repertoire of the calf and its mother with those of the other whales demonstrates that individual repertoire differences could potentially contribute to repertoire differences observed between units (see Freeberg 2001; Tyack 2001), the general repertoire similarity of whale repertoires suggests that repertoire differences between units that result from individual differences would be rare. Using IPIs to study the rates of coda production by individuals in a unit and the coda repertoires of individuals in other units will be useful in examining the contribution of individual repertoire variation to observed repertoire differences between units.

My finding of similar coda repertoires between most adults in the unit indicates that coda repertoires do not generally function in advertizing individual identity. Given that visual and olfactory cues likely play a limited role, if any, in individual identification in this species, the similarity of coda repertoires gives the impression that knowledge of the individual identities of vocalizing animals is of little importance in sperm whale social interactions and that associations between members of a unit are equivalent.

However, because members of this unit demonstrate preferred social associations and significant avoidances with other particular members of the unit (Gero 2005; Gero et al. submitted), sperm whales must use other cues besides coda repertoires to identify individual members in their social unit and mediate their individual-specific social associations. Other identifying signals could include the frequency structure of coda clicks, visual cues at short range, the IPIs of coda clicks, or combinations of these. While the use of IPIs as an indicator of body size and thus identity within a unit would be an honest signal, the presence of similarly-sized whales within a unit would diminish the value of IPIs in individual identification.

The similarities in coda repertoires between unit members and between units of the same clan (Rendell 2003) and the dissimilarities in coda repertoires between units from different acoustic clans (Rendell and Whitehead 2003b) suggest that coda repertoires function to signal clan identity or reinforce clan-specific bonds. Coda repertoires would therefore function in a similar manner to the presumed role of group-specific dialects in other species such as the killer whale, *Orcinus orca* (Ford 1991). Moreover, production of clan-specific repertoires rather than individual-specific repertoires within a unit may serve as a form of acoustic social grooming to reaffirm social bonds between members of the unit (see Dunbar 1996).

In contrast to the similarity of coda repertoires between most adults in this unit, the dissimilarity between the coda repertoires of the calf and its mother with the other whales suggests that the necessity of these animals to advertize personal identity is greater than the need to signal clan membership. While individual-identification of other unit members may be satisfied by subtler individual-specific signals, the requirement of the mother to localize, reunite with, and transfer milk to her calf appears to necessitate a more obvious means of individual identification for these whales. Again, even though whales could make use of IPIs to distinguish the identity of a vocalizing unit member, particularly the small calf, differences in coda repertoires would be much more obvious. In this way, the individual-specific repertoires of the calf and its mother resemble the case of bottlenose dolphins, which have been suggested to use signature whistle repertoires to locate (Smolker et al. 1993; Janik and Slater 1998) and address (Janik 2000) each other. I note, however, that while the mother's coda type repertoire is significantly dissimilar to that of the other whales, the coda type produced by the mother ('1+3') is acoustically similar to the most prevalent coda type in the unit repertoire ('1+1+3'), differing by the addition of just one click. I suggest, then, that while the mother's coda repertoire may function in individual identification within her unit, because the coda type she produces is acoustically similar to the most common coda type of the unit, her clan affiliation is still likely apparent both to her social affiliates as well as unfamiliar whales.

On the other hand, the coda repertoires of the mother and calf may differ from those of other whales in the unit not to impart some identification function but because their codas convey different referential, affiliative, or emotional signals than those of other individuals (e.g. Wong et al. 1999). Research is needed on individual whale repertoires in units with several calves and mothers in order to determine whether the repertoires of calves and mothers are in fact individually specific. Nevertheless, even if the coda types of calves and nursing mothers differ from those of other unit members as a result of different internal motivations, the byproduct differences in repertoires could be used as a means of effectively identifying these animals within the unit.

The correlation demonstrated in this unit between vocal repertoire similarity and the necessity for effective individual or group identification clearly illustrates the relationship between a communication signal and its function. My findings imply that there is flexibility in the coda repertoires of sperm whales that permits individuals to switch between repertoires depending on the need to broadcast individuality. If my predictions concerning the function of the mother and calf coda repertoires are correct, as the calf begins to forage on its own and the necessity for the mother-calf pair to localize one another decreases, their repertoires will become more similar to the repertoires of the other unit members. Given that the repertoires of the juvenile male and its probable mother, whale #5560 (Gero et al. submitted), are similar to the coda repertoires of the other adults, it seems likely that the repertoires of the calf and its mother will converge on the unit repertoire once the selective pressure to advertize their identities is alleviated and is outweighed by the need to advertize clan identity or affirm social bonds. Additional studies of the individual acoustic repertoires of other social cetaceans will be useful in examining the importance of vocal dialects in individual identification.

CHAPTER FOUR

OVERLAPPING AND MATCHING OF CODAS IN THE VOCAL EXCHANGES BETWEEN SPERM WHALES

INTRODUCTION

Temporally associated vocal exchanges have been observed in a variety of animal species including birds (e.g. Masataka and Symmes 1986; Catchpole and Slater 1995; Todt and Naguib 2000; Burt et al. 2001), frogs (e.g. Pallett and Passmore 1988; Jehle and Arak 1998; Gerhardt et al. 2000), primates (e.g. Sugiura 1998), and cetaceans (e.g. Janik 2000; Miller et al. 2004). While the timely response of one animal to another was initially believed to be a consequence of a facilitative release mechanism (Hinde 1958), subsequent studies on the vocal responses of interacting animals and the contexts of exchanges have revealed that dyadic vocal interactions are functional in animal communication.

Dyadic vocal interactions are often classified based on the temporal and pattern-specific characteristics of a receiver's response in relation to a conspecific's signal (Todt and Naguib 2000). In a temporal-specific response, a receiver adjusts the timing of its response relative to the initial signal so as to impart communicative meaning. Such responses include overlapping - in which a receiver replies by initiating its response before the end of the signaler's call - and non-overlapping countercalling - in which a receiver quickly replies with a response but not until after the end of the signaler's call. In a pattern-specific response, on the other hand, it is the call type or acoustic structure of the response compared to the initial signal that conveys meaning. One of the most obvious and prevalent forms of a pattern-specific response is call-matching, in which an animal responds to a conspecific's signal with a similar acoustic response (Geberzahn and Hultsch 2004; Janik 2005; Naguib 2005). Many responses involve both temporal-specific and pattern-specific components.

Although Brémond (1968) proposed that immediately responding to the vocalization of another animal, particularly in the form of a call-match, functions to simply address the initial signaler (Armstrong 1973), several communicative functions for this vocal response have since been advanced, with the specific function of a dyadic vocal exchange depending on the context of the interaction, the social system of the species, and the form of the exchange. In most territorial songbirds studied, temporally associated vocalizations appear to function primarily in territory defense, with both overlapping and song matching serving as acoustic threats (e.g. McGregor et al. 1992; Burt et al. 2001; Mennill and Ratcliffe 2004). In a few territorial birds, however, different vocal exchange types seem to have different functions, given the contexts in which they are used. For example, while overlapped matching appears to function as a threat in nightingales (*Luscinia megarhynchos*) and blackbirds (*Turdus merula*), non-overlapped matching appears to function in the confirmation of established social relationships (Todt 1981; Hultsch and Todt 1986 in Geberzahn and Hultsch 2004).

On the face of it, overlapping and call-matching in frogs also appear to have an acoustic threat function, since territorial males often overlap each other and exchange calls with similar note numbers (Arak 1983; Schwartz 1986; Pallett and Passmore 1988; Jehle and Arak 1998; Gerhardt et al. 2000). However, because male quacking frogs (*Crinia georgiana*) match the total number of notes played from two separated speakers (Gerhardt et al. 2000), the purpose of call-matching in this species, and perhaps other frog species, is likely not to direct an aggressive response to a particular male but to present to females a call that is at least as appealing as the signal just heard, thereby serving a mate attracting function (Gerhardt et al. 2000).

In contrast to non-social species, animals that live in social groups engage in vocal exchanges not with competitors to defend territory or attract mates but with other group members to permit localization during periods of isolation or to coordinate group movement (e.g. Masataka and Symmes 1986; Okayasu 1987; Sugiura 1998). Furthermore, because vocal exchanges in several social species tend to occur between affiliated animals (e.g. primates: Snowdon and Cleveland 1984; Biben et al. 1986; Mitani 1986; Masataka and Biben 1987; Biben 1993; Lemasson and Hausbenger 2004; elephants: Soltis et al. 2005a), countercalling and call-matching in social species might also be a means of maintaining contact with and/or reaffirming social bonds with social affiliates. Similarly, the exchange of vocalizations in duetting primate and bird species likely functions in resource defense, signaling commitment to a partner, or preventing the usurpation of oneself or a mate from a partnership (Geissmann and Orgeldinger 2000; Hall 2004).

For social marine animals, the localization of conspecifics and coordination of group movement are particularly dependent on acoustic signals, given the limitations of visual contact in the marine environment (Myrberg 1980). Not surprisingly then, studies of two social cetaceans, the killer whale (*Orcinus orca*) and bottlenose dolphin (*Tursiops truncatus*), suggest that these species use antiphonal calling, and call-matching in particular, in contact and cohesion calling to localize isolated conspecifics or maintain contact with group members while traveling and foraging (Tyack 1986b; Caldwell et al. 1990; Smolker et al. 1993; Janik and Slater 1998; Janik 2000; Miller et al. 2004).

One highly social cetacean, the sperm whale (*Physeter macrocephalus*), however, appears to engage in vocal exchanges not during periods of dispersion and foraging but during intervals of social behaviour when in apparently close proximity to one another (Chapter 8; see also Watkins and Schevill 1977; Whitehead and Weilgart 1991). Female sperm whales live in long-lasting social units (~10-12 individuals) with other females, calves, and juveniles of both sexes (Whitehead et al. 1991; Christal et al. 1998; Whitehead and Weilgart 2000). Although sperm whales spend much of their time foraging, they sometimes socialize at the water surface and produce short stereotyped patterns of broadband clicks termed 'codas' (Watkins and Schevill 1977; see Figure 4.1), which can be classified into types based on their inter-click intervals (ICIs) (see Rendell and Whitehead 2003a,b). Previous research has demonstrated that members of sperm whale social units share coda types (Rendell and Whitehead 2004) and coda type repertoires (Chapter 3). However, variation in coda repertoires between units permits their allocation into large, sympatric acoustic 'clans' (Rendell and Whitehead 2003b), which, given the tendency for units to preferentially socialize with other units of the same clan, suggests that the clan represents a higher social level within the complex social structure of this species (Rendell and Whitehead 2003b).

Although it has been observed that sperm whales exchange vocalizations in tight temporal sequences (Watkins and Schevill 1977) and that the non-randomized order of coda types within exchanges suggests a type of "conversation" (Weilgart and Whitehead 1993), the rates of coda overlapping and coda matching have not yet been estimated, a result of the difficulty in determining whether recorded sequential codas were produced by the same or different whales. Moreover, the function of echocodas - a seemingly unique form of coda overlapping in which the clicks of two matching codas alternate with one another (Weilgart 1990) (see Figure 4.1) - is still unclear.

The purpose of this study was to characterize the exchange of codas between individual sperm whales. I analyzed the coda vocalizations of two sperm whale units encountered in two different oceans and used differences in the inter-pulse intervals (IPIs) of coda clicks (see Chapter 2) to assign codas to individuals (or size classes) and then determine whether adjacent codas were made by the same or different whales. I used permutation tests of coda sequences to examine the rates of both temporal and pattern-specific vocal exchanges and test whether coda production by an individual whale is influenced by the coda production of other unit members. I also conducted Mantel tests to examine whether there were correlations between either coda overlapping or coda matching and pairwise genetic relatedness or social association index between whales. Moreover, to determine whether echocodas represent a unique coda response, I tested whether codas produced in echocoda exchanges were more similar in tempo (absolute ICIs) or rhythm (relative ICIs) than were other overlapping and matching codas. This paper provides the first description of the patterns of coda exchanges between individual sperm whales within social units.

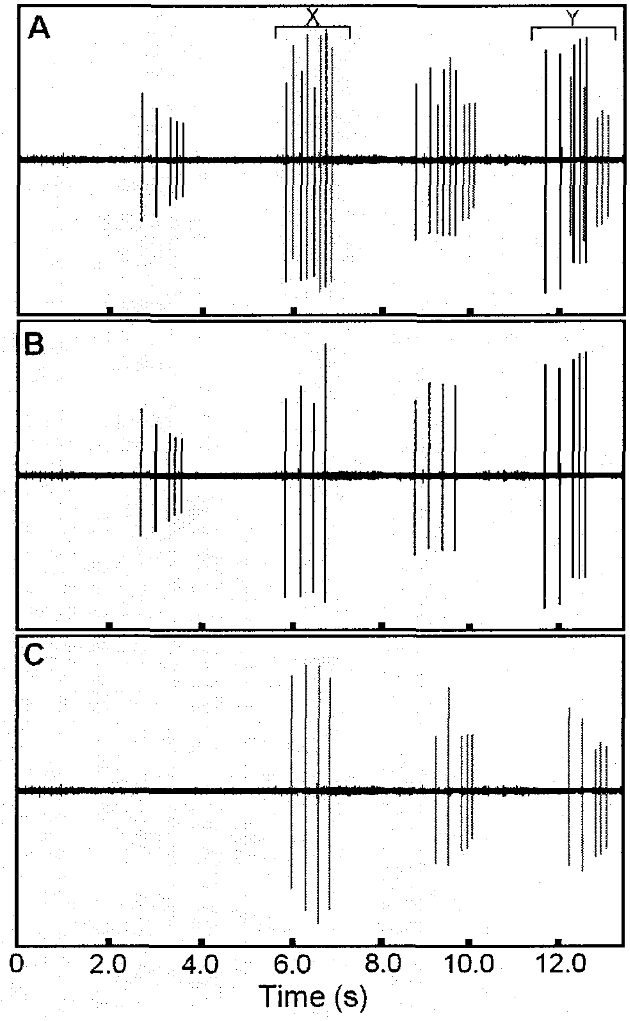


Figure 4.1. Waveform of a recording segment in which the coda of one whale is followed by three overlapping coda exchanges. The coda clicks in black have calculated inter-pulse intervals (IPIs) of 3.38-3.42 msec while the coda clicks in grey have IPIs of 3.15-3.17 msec, indicating that there are two individuals of differing sizes producing codas approximately every 3-4 s and that the codas of the first whale (in black) are overlapped by the second whale (in grey). Panel **A** shows the coda production of both whales while panels **B** and **C** show the coda production of each whale separately. The coda exchange (**X**) is an echocoda exchange since the two codas in the exchange not only overlap and match (are of the same type), but also alternate clicks. The coda exchange (**Y**) is an overlapping and matching coda exchange but is not an echocoda exchange since the clicks of the two codas do not alternate.

METHODS

Field Methods – Group of Seven

The Group of Seven is a social unit consisting of five adult females, one juvenile male, and one male calf (see Gero 2005) that were followed for a total of 41 days between January 16 and March 26, 2005 off the coast of Dominica. Animals were tracked visually during the day and followed acoustically at night using a directional hydrophone (see Whitehead and Gordon 1986). During daylight hours, individuals at the surface were approached and digital photographs of flukes were taken using a Canon D10 digital SLR for individual identification purposes (Arnbom 1987). Sloughed skin samples were collected from the slicks of whales (Whitehead et al. 1990; Bérubé and Palsbøll 1996) and analyzed to reveal the sexes and genetic relationships of these individuals (see Gero et al. submitted). I made 15 coda recordings of this unit as well as recordings of their usual clicks (i.e. echolocation clicks) when solitary whales fluked at the start of a foraging dive (see Chapter 2). Recordings were made from a towed hydrophone and recorded on a Fostex VF-160 multi-track recorder (see Chapter 2).

Field Methods - Unit T

Unit T is a social unit of nine female and immature sperm whales that were followed by Dr. Luke Rendell during four encounters for a total of 17 days between March 10 and April 12, 1999 around the Galápagos Islands (see Rendell and Whitehead 2004). As with the Group of Seven, this unit was tracked visually during the day and acoustically at night and photographed for individual identification. Sloughed skin samples were used to reveal that the five sampled unit members were largely unrelated (Mesnick 2001; Whitehead 2003a). During social periods, 21 recordings were made using an Offshore Acoustics hydrophone connected to a Sony TC-D5M cassette recorder and subsequently digitized at 44.1 kHz onto a standard desktop PC.

Photographic and Genetic Analysis

Photographic and genetic analysis of the Group of Seven was conducted by Shane Gero and Dan Engelhaupt (see Gero 2005; Gero et al. submitted). Photographs of individual Group of Seven whales were assigned a quality rating (Q) between 1 and 5 (Gero et al. submitted), with 1 indicating a very poor quality photograph and 5 indicating a very high quality photograph (Arnbom 1987; Dufault and Whitehead 1993). Only photographs with a $Q \geq 3$ were used in the analyses and the best photograph for each individual within each encounter was assigned an identification number subsequently matched between encounters using a computer-based matching program (Whitehead 1990). To identify associations between individuals within the Group of Seven, individuals were deemed to be associating if they were within the same cluster at the surface. Individuals were considered to be in the same cluster if they were within approximately 3 adult-body lengths (~40m) from any other cluster member and were coordinating their behaviour (Whitehead 2003b). A 2 hr sampling period and a "Half-Weight Index" (HWI) measure of association was used as it accounts best for any observer biases in photo-identification (Cairns and Schwager 1987). Relatedness values were calculated for each pair of Group of Seven whales using sloughed skin samples across 13 loci (Gero et al. submitted).

Acoustic Analysis

Recordings were analyzed using Rainbow Click software (see Gillespie 1997; Leaper et al. 2000; Rendell and Whitehead 2004) and the inter-pulse intervals (IPIs) of usual clicks and coda clicks were calculated using routines custom-written in MATLAB® version 6.1.450, release 12.1 (MathWorks Inc. 2001). The codas recorded of the Group of Seven were previously assigned to individuals based on the similarity of coda and usual click IPIs (see Chapters 2 and 3). Although codas were not assigned to specific individuals for Unit T, codas with IPIs less than 0.05 msec in difference between them were assumed to have been produced by the same whale. Codas in recordings with IPIs greater than 0.10 msec in difference were deemed to have been produced by different whales (see Chapter 2).

The intervals between clicks within a coda (inter-click intervals or 'ICIs') were output from Rainbow Click, standardized by coda length, and classified into types using *k*-means cluster analysis (see Rendell and Whitehead 2004). Histograms of the time differences between adjacent codas made by different whales indicated that the codas of both Group of Seven and Unit T whales were generally responded to by a different whale within 2 s (and often overlapped) or responded to approximately 5 s later (see Figures 4.2 and 4.3). Histograms of the time differences between adjacent codas made by individual whales (or whales with similar IPIs) indicated that whales generally produced codas every 3-5 s (see Figures 4.2 and 4.3). Moreover, when limiting the analysis to segments of recordings where the time intervals between the codas of individual whales were uninterrupted by the codas of other whales - and thus the temporal coda production of individuals could not be affected by the coda production of other whales - histograms still showed that whales produced codas primarily every 3-5 s, indicating that whales were consistent in the temporal patterning of coda production even when not engaging in exchanges with other whales. Together, these histograms illustrate the temporal patterning observed in many Group of Seven and Unit T recordings in that a coda was often overlapped or quickly followed by the coda of another whale within 2 s, followed by another bout of overlapping or 'exchanged' codas 3-5 s later (see Figure 4.1).

Given these distributions of time intervals for codas made by the same whale and by different whales, I defined a coda exchange as two in-sequence codas that were produced within 2 s of one another. I used the term 'overlapping coda' to describe second-in-sequence codas whose onset occurred after the onset of an initial coda but before the termination of the initial coda (see Soltis et al. 2005a). In contrast, 'adjacent coda' was used to describe second-in-sequence codas whose onset occurred within 2 s of the initial coda but after the termination of the initial coda. Accordingly, 'overlapping coda matches' were used to describe overlapping codas in which both coda types were of the same coda type, as determined by *k*-means cluster analysis, and 'adjacent coda matches' were used to describe adjacent codas that were of the same coda type.

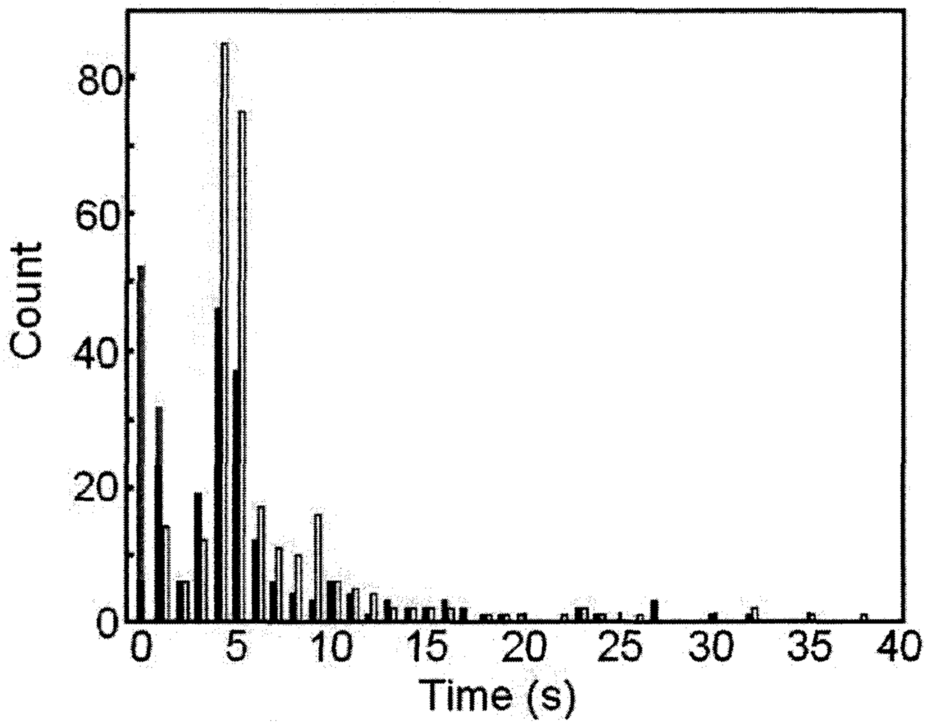


Figure 4.2. Histogram of the time intervals between contiguous codas made by whales in the Group of Seven. The grey bars represent the frequency of time intervals between overlapping codas made by different whales and the black bars represent the frequency of time intervals between adjacent but non-overlapping codas made by different whales. The white bars represent the frequency of time intervals between adjacent codas made by the same whale.

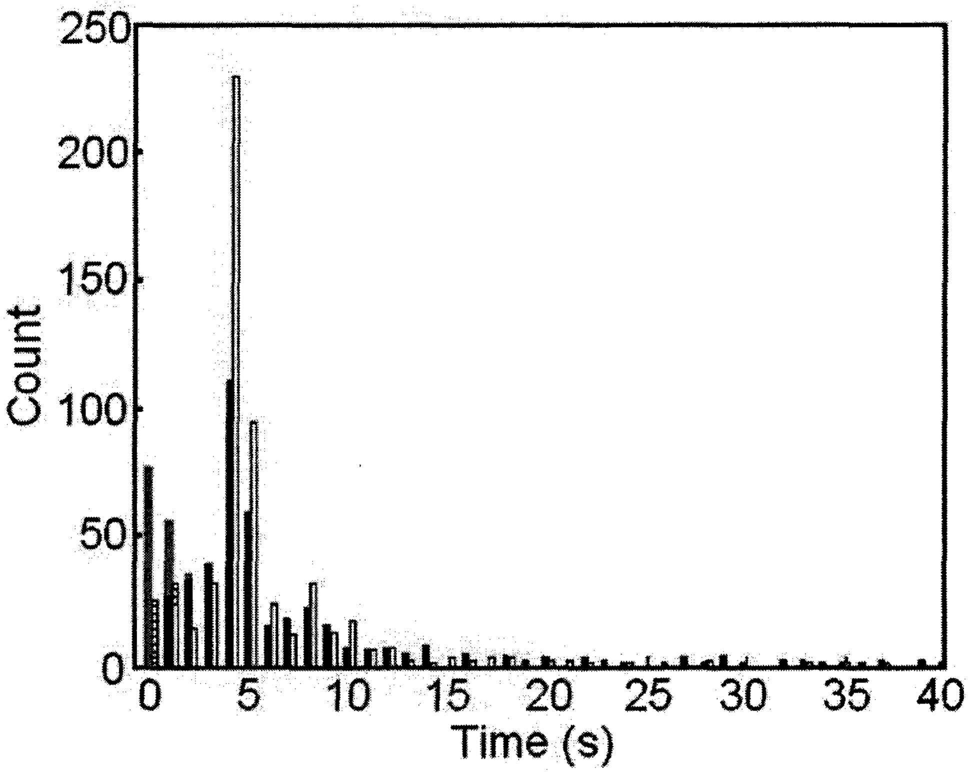


Figure 4.3. Histogram of the time intervals between contiguous codas made by whales in Unit T. The grey bars represent the frequency of time intervals between overlapping codas with dissimilar inter-pulse intervals (IPIs) (greater than 0.10 msec difference) and thus likely different whales, and the black bars represent the frequency of time intervals between adjacent but non-overlapping codas with dissimilar IPIs. The striped bars represent the frequency of time intervals between overlapping codas made by whales with similar IPIs (less than 0.05 msec difference) and the white bars represent the frequency of time intervals between adjacent codas with similar IPIs, and thus potentially produced by the same whale.

Non-Parametric Randomization Tests

I modified the non-parametric randomization techniques described in Miller et al. (2004) to test whether codas occurred within 2 s of each other more often than expected, given the rate and periodicity of coda production within each recording. Within the Group of Seven recordings, I tallied the number of coda exchanges, the number of overlapping codas and the number of adjacent codas by different whales within 2 s, and compared the observed tallies to the probability distribution from 10,000 randomizations that rotated the coda sequences of each whale a random amount of time. This method is similar to that used in Miller et al. (2004) to test for countercalling but, because I was able to distinguish the coda sequences of each whale in the unit, involves the rotating of each whale's coda sequences rather than just the call sequences of a focal animal. For Unit T, however, because the identities and coda sequences of individual whales were not known, within recordings I grouped codas with IPIs within 0.05 msec of each other (see Chapter 2) and within each permutation rotated the coda sequences of these grouped codas a random amount of time. These permutation tests were also used to test for countercalling and overlapping within particular coda types, whether there were tendencies for responding whales to have longer or shorter IPIs than the initial whale, and to test for countercalling and overlapping between individual whales in the Group of Seven.

The above permutation tests were used to examine countercalling irrespective of the types of codas produced. To test whether whales changed their coda-type production in response to the codas of other unit members, I examined the rate of coda-type matching of these two units using permutation tests that rotated the coda types but retained the timing of coda production. For each social unit, I tallied the number of coda matches, overlapping coda matches, and adjacent coda matches and compared the observed tallies to the probability distribution from 10,000 permutations that randomly rotated the coda types produced by each whale (or by each IPI group in the Unit T recordings) while still preserving the timing with which each whale produced codas as well as the ordering of coda types in the sequences of each whale. In order to account for any potential effects of vocal bouts (i.e. context) on the types of codas produced, I rotated the codas of individual whales within bouts separated by the bout criteria calculated as described below.

As with the permutation tests used for coda overlapping, this method is similar to the method used by Miller et al. (2004) to test for call-matching but involves the random rotation of each whale's coda types rather than just those of a focal animal. In addition, these permutation tests were used to test for matched countercalling and matched overlapping within particular coda types, to test whether there were tendencies for matching whales to have longer or shorter IPIs than the whales they matched, and to test for matched countercalling and matched overlapping between individual whales in the Group of Seven. The Hemelrijk Rr-test (Hemelrijk 1990), a Mantel test variant which ranks values within rows, was used to examine the similarity of elements in a matrix of the proportion of whale's codas that were overlapped and matched by other individual whales and the elements of its inverse, thereby testing for reciprocity in overlapping and matching between whales.

Determination of Bout Criteria

Using the time intervals between the codas of individual whales, I tested whether sperm whales produced codas in bouts by successively fitting the log-frequency distribution of intervals to one and two-process exponential models (Sibly et al. 1990; see Miller et al. 2004). For the Group of Seven, the two-process model fit the interval distribution well ($r^2 = 0.928$) and better than the one-process model (Akaike information criterion for one-process model = 126.59; information criterion for two-process model = 80.99). Likewise, for Unit T, the two-process model fit the distribution of time intervals with similar IPIs well ($r^2 = 0.884$) and better than the one-process model (Akaike information criterion for one-process model = 123.79; information criterion for two-process model = 102.48). Using Slater and Lester's (1982) bout criterion interval calculation, which minimizes the total number of time intervals misclassified into bouts, I calculated a bout criterion interval for the Group of Seven of 35 s and for Unit T of 21 s

However, because coda production in sperm whales appears to be highly regular with whales producing a coda approximately every 3-5 s (see Figures 4.2 and 4.3), the calculation of the bout criterion by the method suggested by Sibly et al. (1990) is likely affected by the non-random distribution of time intervals within these 'bouts'. When represented as a cumulative frequency in proportions, I found that the time intervals between codas within Group of Seven whales fit a Poisson distribution with an initial mean of 5 s very well ($r^2 = 0.944$). I then fit the data to a Poisson distribution truncated by an exponential model (a two-process curve) with an initial mean of 5 s and cutoff of 15 s and found that this model did not add any additional information to the model (Akaike information criterion for one-parameter model = -54.89; information criterion for two-parameter model = -52.89). Under a Poisson distribution with a calculated mean of 5.5 s, 95% of the time intervals were less than 9 s, suggesting that the sequences of regularly produced codas can be conservatively separated by intervals larger than 9 s. Similarly, for Unit T, the two-parameter model did not provide any additional information beyond a Poisson distribution. Under a Poisson distribution with a mean of 4.8 s, 94% of Unit T time intervals were less than 8 s, suggesting that sequences can be conservatively separated by intervals larger than 8 s. Non-linear models were fitted to the data using nonlinear regressions in which parameters were estimated using least-square regression in SPSS, version 10.1 (2000, Chicago, Illinois, U.S.A.).

Overlapping, Matching, Genetic Relatedness, and Social Associations

Mantel tests (Mantel 1967; Schnell et al. 1985) and matrix correlation coefficients between the elements of the genetic relatedness matrix and a matrix of the proportion of whale pairs' codas that were in overlapping exchanges were calculated in order to determine whether highly related whales were in overlapping exchanges together more than distantly related whale pairs. Similarly, I calculated Mantel tests and matrix correlation coefficients between the elements of the social association matrix (see Gero 2005) and the overlapping exchange matrix to determine whether the association indices were correlated with patterns of overlapping. In addition, these tests were repeated testing for correlations between matching exchanges and both genetic relatedness and association indices. The calculation of HWI, Mantel tests, and Hemelrijk Rr-tests were carried out using SOCPROG (2.2, H. Whitehead) in MATLAB®.

Echocoda Exchange Analysis

To determine whether codas in echocoda exchanges were more similar (in tempo and rhythm) to one another than were overlapping and matching codas in non-echocoda exchanges, I calculated the multivariate similarity (using both absolute and relative ICIs) between pairs of codas in echocoda exchanges (see Figure 4.1) and between pairs of codas in matching, overlapping non-echocoda exchanges (see Figure 4.1) and compared these similarities using *t*-tests and by calculating 95% confidence intervals by bootstrapping with replacement. I reasoned that if codas produced as echocodas were simply overlapping and matching codas whose clicks happened to occur within the inter-click intervals of the first coda, then codas in echocoda exchanges should not be any more similar to one another in either tempo (absolute ICIs) or rhythm (relative ICIs) than codas in non-echocoda overlapping and matching exchanges.

RESULTS

Overlapping and Antiphonal Calling – Group of Seven

Of the 421 codas in the 15 Group of Seven coda recordings, 318 (76%) were confidently assigned to a whale in the unit (see Chapters 2 and 3). Of these 318 assigned codas, 71 (22%) occurred in the following 2 seconds of a coda produced by a different whale. I compared this observed value to the distribution expected from rotating the coda sequences of each whale within each recording a random amount of time and tallying the number of codas within 2 seconds of a coda by a different whale. The observed value exceeded the expected mean ± SD of 52.4 ± 7.6 codas generated by 10,000 randomizations and was significant ($P = 0.027$), indicating that coda production by whales in the Group of Seven was closely synchronized. Moreover, since the number of observed overlapping codas (50) was significantly greater than expected (mean ± SD: 23.9 ± 5.3; $P < 0.001$) but the number of observed adjacent codas within 2 seconds was not (observed = 21; expected mean ± SD = 28.6 ± 6.2; $P = 0.210$), the close production of codas by different whales appeared to be a result of coda overlapping and not adjacent antiphonal calling.

Although the Group of Seven produced 16 different coda types (see Chapter 3), only 5 different coda types were overlapped in these recordings. The most common coda type of the Group of Seven ('1+1+3') was the most overlapped coda type (27 overlaps/50 total overlaps) while the second most common Group of Seven coda type ('5R') was the second most overlapped coda type (17/50 total overlaps). No coda type, however, overlapped another coda or was overlapped by another coda more often than expected ($P > 0.172$).

Coda overlapping exchanges in which the overlapped whale had a longer IPI than the overlapping whale were no more likely to occur than exchanges in which the overlapping whale had a longer IPI ($P = 0.496$). However, there were trends in the rates in which different whales overlapped other whales in the unit. Although the calf, the juvenile, and one adult (whale #5563) were in as many overlapping exchanges as expected, whale #5130 overlapped the codas of whale #5560 more than expected ($P = 0.018$), whale #5560 overlapped whale #5561 more than expected ($P < 0.0001$), and whale #5561 overlapped whale #5722 more than expected ($P = 0.001$). Nonetheless, randomized permutation tests did not find significantly different rates in which one whale overlapped the other within these pairs of whales ($P > 0.25$). Likewise, a Hemelrijk Rr test of the rates in which pairs of whales overlapped and were overlapped by one another, standardized for the rates with which whales produced codas when in recordings together, was significant (Rr test matrix correlation = 0.645; $P = 0.003$), indicating that whales tended to overlap individuals that overlapped them.

There was no significant correlation between genetic relatedness and the rates with which individuals were in overlapping exchanges (Mantel test matrix correlation = -0.06, $P = 0.26$; see also Figure 4.4). Similarly, there was no significant correlation between the Half-Weight Index of social association and the rates with which individuals were in overlapping exchanges (Mantel test matrix correlation = 0.06, $P = 0.19$; see also Figure 4.5). Thus, sperm whale pairs that were closely related or socially associated were not more likely to engage in overlapping exchanges.

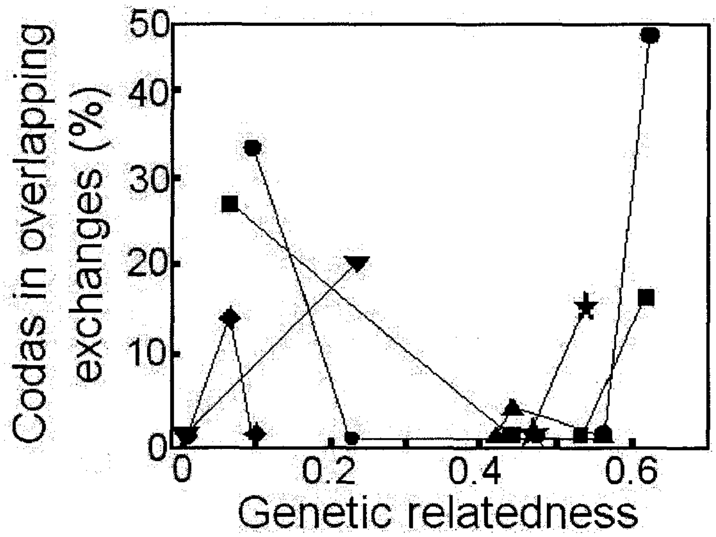


Figure 4.4. Relationship between genetic relatedness and percentage of a whale's codas produced in overlap exchanges with other unit members (excluding the calf). Each line represents one whale, and the identical symbols on each line represent the genetic relatedness to, and percentage of codas engaged in overlapping exchanges with, the other whales in the social unit. Each symbol marks the coordinate indicating the percentage of codas produced in recordings with a particular whale that were in overlap exchanges with that whale, and the genetic relatedness to each whale as determined using sloughed skin samples across 13 loci. Generally, there were no relationships between the genetic relatedness between pairs of whales and the percentage of a whale's codas that were in overlap exchanges with each other whale.

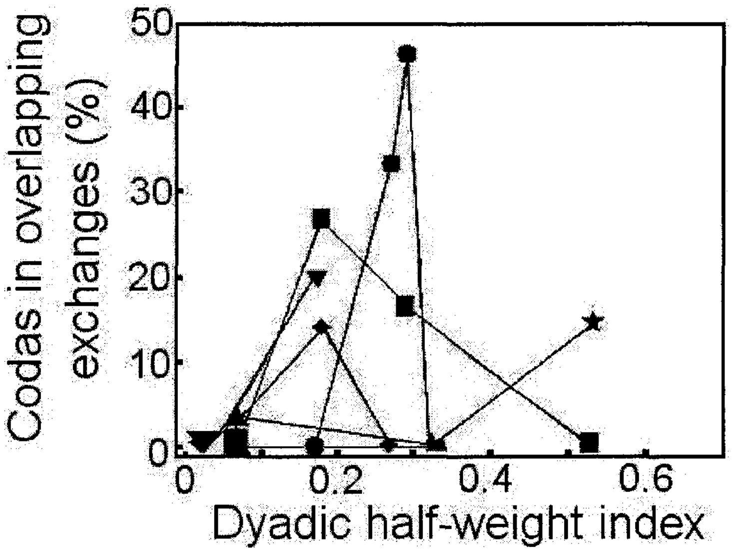


Figure 4.5. Relationship between social association and percentage of a whale's codas produced in overlap exchanges with other unit members. Each line represents one whale, excluding the calf, and each symbol marks the coordinate indicating the percentage of codas produced in recordings with a particular whale that were in overlap exchanges with that whale, and the Half-Weight Index of social association with each whale. Generally, there were no relationships between the social association between pairs of whales and the percentage of a whale's codas that were in overlap exchanges with each other whale.

Coda Matching – Group of Seven

The observed number of codas that were matched within 2 seconds (48) significantly exceeded the expected mean ± SD of 42.7 ± 1.7 generated by 10,000 randomizations ($P < 0.008$) that rotated the coda types of each whale within bouts (see Methods). Although the observed number of 41 overlapping coda matches was significantly greater than the expected mean ± SD of 36.1 ± 1.81 ($P = 0.026$), the number of antiphonal non-overlapping coda matches was not (observed = 7; expected mean ± SD = 6.6 ± 0.9; $P = 0.559$).

Of the 16 different coda types produced by the Group of Seven, only three types were coda matched; coda type '1+1+3' was matched 28 times, coda type '5R' was matched 19 times, and coda type '1+3' was matched once. Only coda type '1+1+3' was overlap matched more than expected (observed = 26; expected mean ± SD = 22.3 ± 1.6; $P = 0.013$). When coda overlaps that involve the matching of this coda type were excluded from the analysis, overlapping coda matching occurred as often as expected (observed =15, expected mean ± SD = 14.0 ± 0.8, $P = 0.284$).

Coda matching exchanges in which the matched whale had a longer IPI than the matching whale, and thus was likely larger, were no more likely to occur than the reverse ($P = 0.820$). This non-significant result was true for both overlapped and adjacent matching exchanges ($P = 0.952$ and $P = 0.203$). While most whales in the Group of Seven were in coda matching exchanges as often as expected, one pair of whales, #5560 and #5561, were in matching exchanges with each other more often than expected (observed = 30; expected mean ± SD = 14.6 ± 5.1; $P < 0.001$). However, as with overlapping exchanges, whale #5560 did not overlap match whale #5561 any more often than the reverse ($P = 0.565$). Likewise, a Hemelrijk Rr test on the rates in which whales matched codas and were coda matched by different whales returned a significant result (Rr test matrix correlation = 0.828; $P = 0.004$), indicating reciprocity in matched overlapping. As with overlapping exchanges, there was no significant correlation between the rates with which individuals were in matching overlap exchanges with other unit members and genetic relatedness (Mantel test matrix correlation = -0.02, $P = 0.25$) or social associations (Mantel test matrix correlation = 0.09, $P = 0.21$).

Overlapping and Antiphonal Calling – Unit T

Of 621 codas in 21 Unit T recordings, 575 (93%) were confidently assigned an IPI. Of these 575 codas, 127 (22%) occurred within 2 seconds of a coda produced by a different whale. This observed value significantly exceeded the mean ± SD of 112.9 ± 7.1 generated by 10,000 randomizations ($P = 0.038$) (see Methods). Moreover, similar to coda production in the Group of Seven, the closely synchronized production of codas appeared to be a result of coda overlapping rather than adjacent calling since the number of observed overlapping codas (87) was significantly greater than the expected mean ± SD of 58.3 ± 7.2 ($P < 0.001$) but the number of observed adjacent codas within 2 seconds (40) was significantly less than the expected mean ± SD of 54.5 ± 7.2 ($P = 0.037$).

Of the 19 coda types with fewer than 11 clicks that were recorded of Unit T, 15 different types were overlapped. Even though the two most common coda types in Unit T ('2+2' and '2+1') were also the most commonly overlapped coda types, individually they were not overlapped any more often than expected ($P > 0.05$). There were no trends in the overlapping of coda types except that coda type '5R' overlapped other codas more often than expected (observed = 12, expected ± SD = 6.1 ± 1.6; $P = 0.001$). However, even when overlaps of this coda type were excluded from the analysis, coda overlapping still occurred at a rate higher than expected (observed = 82, expected mean ± SD = 53.9 ± 7.3, $P < 0.0001$). In Unit T, as in the Group of Seven, coda overlapping exchanges in which the overlapped whale had a longer IPI than the overlapping whale were no more likely to occur than exchanges in which the overlapping whale had a longer IPI ($P = 0.182$).

Coda Matching – Unit T

The observed number of 51 codas that were matched within 2 seconds significantly exceeded the expected mean ± SD of 33.8 ± 5.0 generated by 10,000 randomizations ($P = 0.004$) (see Methods). This was true for both overlapped coda matching (observed = 32; expected mean ± SD = 24.9 ± 3.6; $P = 0.024$) and adjacent coda matching (observed = 19; expected mean ± SD = 13.1 ± 2.6; $P = 0.029$). Although 9 of the 19 coda types produced by Unit T were coda matched, only 4 types were coda matched more than once. Coda type '2+1' was by far the most commonly matched coda type (30 coda matches/51 total observed coda matches) and it was the only coda that was matched and overlap matched more than expected ($P < 0.001$ and $P = 0.006$). When matches of this most commonly matched coda type were excluded, coda overlap matching did not occur at a rate any higher than that expected ($P = 0.809$).

As in the Group of Seven, Unit T coda matching exchanges in which the matched whale had a longer IPI than the matching whale were no more likely to occur than the reverse ($P = 0.756$). Again, this non-significant result was true for both overlapped and adjacent matching exchanges ($P = 0.856$ and $P = 0.566$).

Echocoda Exchange Analysis

Although codas in Group of Seven echocoda exchanges were slightly more similar to one another in terms of infinity-norm absolute ICI similarity than were codas in overlapping and matching coda exchanges that were not echocodas, this difference was not significant ($t = 1.826$, d.f.= 39, $P = 0.08$; Figure 4.6). In contrast, Group of Seven codas in echocoda exchanges were clearly not any more similar in infinity-norm relative ICI similarity than were overlapping and matching codas not in echocoda exchanges ($t = -0.243$, d.f.= 39, $P = 0.81$; Figure 4.7). Moreover, in Unit T, codas in echocoda exchanges were not any more similar to one another, in terms of infinity-norm absolute or relative ICI similarity, than were codas in overlapping and matching coda exchanges that were not echocoda exchanges (absolute ICI similarity: $t = -0.360$, d.f.= 30, $P = 0.72$, Figure 4.6; relative ICI similarity: $t = -0.623$, d.f.= 30, $P = 0.54$; Figure 4.7).

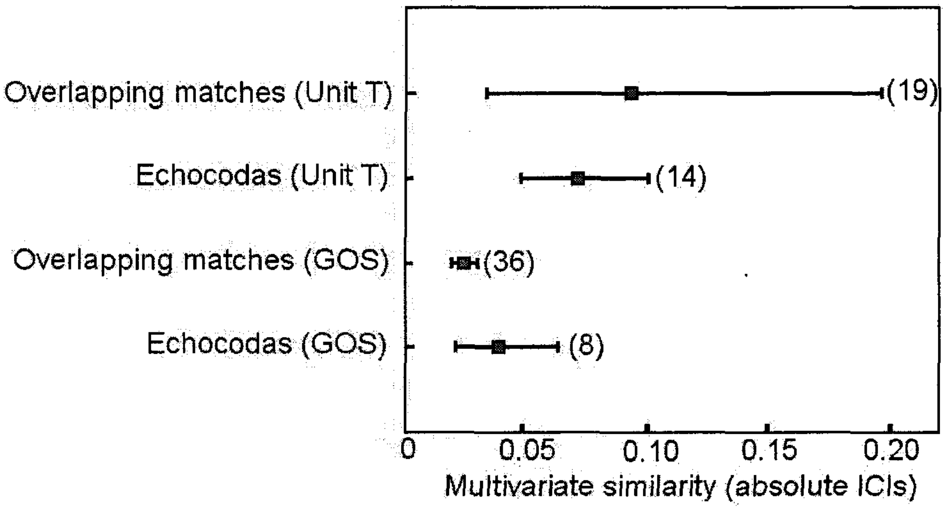


Figure 4.6. Average Group of Seven (GOS) and Unit T coda similarities between codas (with absolute inter-click intervals) in echocoda exchanges and between codas in overlapping, matching coda exchanges that were not echocoda exchanges. The 95% confidence intervals were calculated from 1,000 bootstrap resamples. The number of overlapping matches and echocoda exchanges recorded from each unit are provided in parentheses.

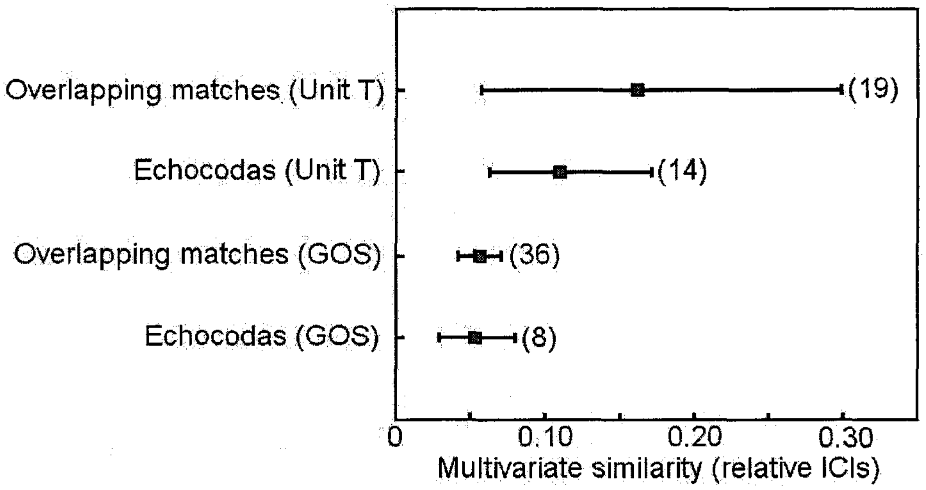


Figure 4.7. Average Group of Seven (GOS) and Unit T coda similarities between codas (with relative inter-click intervals) in echocoda exchanges and between codas in overlapping, matching coda exchanges that were not echocoda exchanges. The 95% confidence intervals were calculated from 1,000 bootstrap resamples. The number of overlapping matches and echocoda exchanges recorded from each unit are provided in parentheses.

DISCUSSION

The results presented here indicate that although individual sperm whales regularly produce codas at 3-5 s intervals, the timing of their coda production is affected by the timing of coda production of other social unit members. In the Group of Seven, 22% of codas were followed within 2 s by a coda of another whale and 16% were overlapped by a coda of another whale, more than 2 times more often than expected by chance. Likewise, in Unit T, a social unit in a completely different geographic area than the Group of Seven, 22% of codas were followed within 2 s by a coda of another whale and 15% were overlapped by a whale's coda with a considerably different IPI, a rate of 1.5 times more often than expected by chance. This tendency to overlap the codas of other whales resulted in bouts of coda overlapping exchanges. Moreover, given that coda overlapping in both social units occurred significantly more often than expected but adjacent countercalling within 2 s did not, it appears that countercalling in sperm whales in these units is largely a result of coda overlapping rather than antiphonal calling.

To ensure that the regularity of coda production and tendency to overlap codas is not limited to these two units and instead a widespread phenomenon in sperm whales, I conducted additional analysis on a subset of eight sperm whale recordings made in another completely different geographic area, the Sargasso Sea, when both visual observation (see Chapter 2) and IPI analysis indicated that only two whales were in the area and producing codas. As with the Group of Seven and Unit T, I found that individual whales in these recordings generally produced codas every 3-5 s (see Figure 4.8) and engaged in overlapping exchanges more often than expected (observed = 41; expected mean $\pm$ SD = 20.0 $\pm$ 4.7, $P < 0.001$), suggesting that this behaviour is prevalent in sperm whale vocal communication.

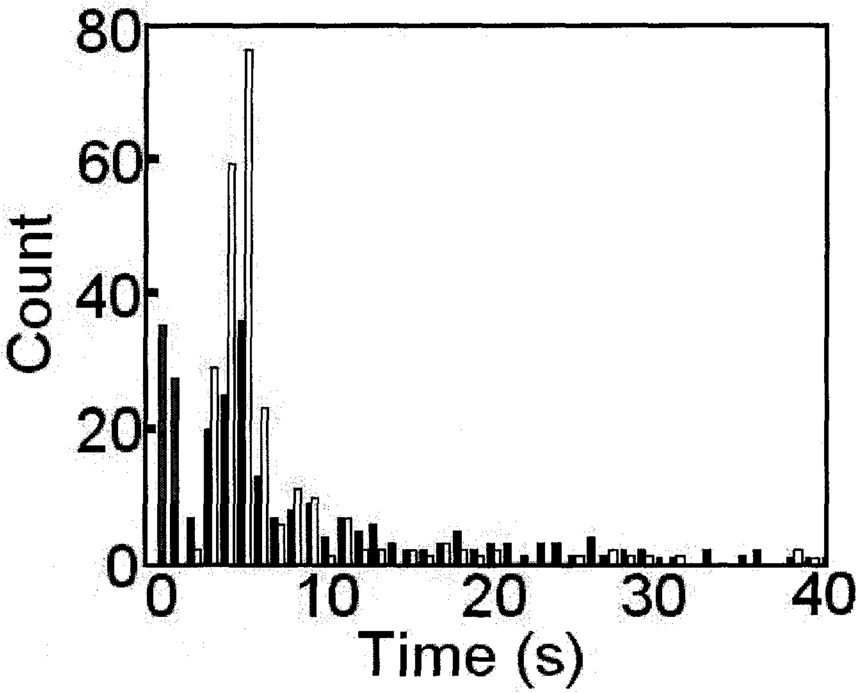


Figure 4.8. Histogram of the time intervals between contiguous codas made by whales in eight two-whale recording sessions made in the Sargasso Sea. The grey bars represent the frequency of time intervals between overlapping codas made by whales with dissimilar inter-pulse intervals (IPIs) (greater than 0.10 msec difference) and the black bars represent the frequency of time intervals between adjacent but non-overlapping codas with dissimilar IPIs. The white bars represent the frequency of time intervals between adjacent codas with similar IPIs (less than 0.05 msec difference) There were no overlapping codas with similar IPIs.

My analysis also indicates that within the vocal exchanges of Group of Seven and Unit T whales, the type of coda produced by a responding whale was influenced by the coda type produced by the immediately preceding whale. In the Group of Seven, 68% of coda exchanges and 82% of coda overlapping exchanges involved a whale being coda matched by another whale. In Unit T, 41% of coda exchanges and 38% of coda overlapping exchanges involved a whale being coda matched by another whale. In both units, however, coda matching in overlap exchanges appeared to be largely a result of the matching of one particular type, coda type '1+1+3' in the Group of Seven and coda type '2+1' in Unit T. In contrast, while coda matching appeared to be a result of matching particular types, coda overlapping did not appear to be the result of the overlapping of just one particular coda type.

By comparing the form and context of sperm whale coda exchanges to countercalling in other species, it is possible to make inferences about the possible functions of this vocal behaviour in sperm whales. Given that codas were produced and exchanged in both the Group of Seven and Unit T when no sexually mature males were present, it seems clear that coda exchanges do not function, at least not exclusively, in mate attraction. Furthermore, since coda overlapping and coda matching do not appear to be accompanied by agonistic interactions or an escalation in aggression (cf. Dabelsteen et al. 1996, 1997; Beecher et al. 2000; Langemann et al. 2000; Burt et al. 2001; Anderson et al. 2005), and since sperm whales are not territorial but likely cooperative with other members of their social unit, it seems highly unlikely that coda exchanges function as an acoustic threat.

In two social cetaceans that engage in vocal exchanges, the killer whale and the bottlenose dolphin, countercalling likely permits the signaler and responder to locate one another in the visually obstructive marine environment (see Janik and Slater 1998; Janik 2000; Miller et al. 2004). By immediately responding to a vocal signal, particularly in the form of a call-match, animals may provide location information to receivers as well as provide themselves with an auditory template for estimating the degradation difference between the two calls, thereby permitting a more accurate estimate of the distance between the two callers (Krebs et al. 1981; McGregor and Falls 1984; Naguib and Wiley 2001). Alternatively, by immediately responding to a call, responders may simply indicate that they are in close enough proximity to the signaler to detect the call and, if responding with a call-match, that they are near enough to discern the call type.

Because temporarily isolated bottlenose dolphins tend to produce highly distinctive 'signature whistles' (Tyack 1986b; Janik and Slater 1998; Caldwell et al. 1990;

but see McCowan and Reiss 2001), and because dolphins are capable of copying new whistles and incorporating them into their repertoires (Richard et al. 1984), whistle matching observed in wild dolphins (see Smolker et al. 1993; Janik 2000) has been suggested to function in maintaining contact between specific vocalizing animals (Janik 2000) either as an isolation call or cohesion call. Because killer whale calls are exchanged between members of a social group while traveling and foraging, it is similarly believed that call-type matching may function in this species as a cohesion call to coordinate pod movements (Miller et al. 2004). Likewise, the almost continuous production of loud, usual clicks while echolocating for prey may permit sperm whales to continuously monitor the locations of their unit members and thus better coordinate foraging formations and timing of surfacing (Tyack 1998; Jaquet et al. 2001).

Sperm whale coda vocalizations, however, are exchanged not during periods of isolation or coordinated foraging but generally during social periods at the water surface after separation during dives (Whitehead and Weilgart 1991), while in very close proximity to one another and often within visual range (see Chapter 8). During this time, whales generally move very slowly through the water or engage in social displays, including lobtails, breaches, side-flukes, and spyhops (Whitehead and Weilgart 1991). Moreover, my findings indicate that sperm whale coda exchanges generally involve coda overlapping, such that unless sperm whales are capable of simultaneously vocalizing and evaluating differences in call degradation between the signal and response, a skill not yet proven in songbirds, coda overlapping would likely 'jam' both the initial and responding signal and prohibit a whale from accurately localizing the source of the responding coda. Therefore, given the close proximity of coda-exchanging sperm whales, the social context in which codas are exchanged, and the high rate of coda overlapping, coda exchanges do not likely function as either a contact call or cohesion call in sperm whales.

Given that coda exchanges do not likely function as an acoustic threat, mate attracting signal, isolation call, or cohesion call, and given that sperm whales exchange codas during periods of social activity, it seems most likely that coda exchanges function to mediate social relationships between unit members. The fact that only a few pairs of individuals in the Group of Seven exchanged overlapping and matching codas more often than expected could imply that whales engage in vocal exchanges to assert dominance over lower ranking whales, if there were a social hierarchy within sperm whale social units. However, in both the Group of Seven and Unit T, whales were just as likely to be overlapped or coda matched by a whale with a longer IPI as by a whale with a shorter IPI, indicating that if a dominance hierarchy does exist and is related to body size, then overlapping and matching likely does not serve to signal dominance over or subservience to the other whale. Furthermore, in the pairs of Group of Seven whales that engaged in overlapping and matching more than expected by chance, individual whales did not overlap or coda match the other whale in the pair significantly more than the reverse, indicating reciprocity in the overlapping and matching of codas, and suggesting another social function to exchanges than that of asserting dominance.

The sperm whale and elephant share many similarities in terms of brain and body size, ecological success, social structure, and vocal behaviour (Weilgart et al. 1996) such that the functions of social behaviours in elephants may be comparable to the functions of similar behaviours in sperm whales. Female African elephants (*Loxodonta africana*) live in small matrilineal social units with other females, juveniles, and calves (Laws et al. 1975; Moss and Poole 1983; Poole et al. 1988) and produce temporal clusters of ‘rumbles’ with other members of their social group (Payne et al. 1986; Poole et al. 1988; Leong et al. 2003b; Soltis et al. 2005a). Similarly, sperm whales live in small social units, though not strictly matrilineal (Christal et al. 1998; Mesnick 2001), and likewise exchange vocalizations with unit members. Given the similarities in the social structure of elephants and sperm whales and the comparable contexts of vocal exchanges, one might expect parallels in the function of countercalling between these two groups. Similar to my finding that sperm whale overlapping and matching is reciprocal and thus does not likely serve a dominance function, Soltis et al. (2005a) found that the relative dominance rank of calling elephants does not affect the probability of vocal response, likewise suggesting a function to countercalling other than to signal dominance. Accordingly, Soltis et al. (2005a) found that females were more likely to respond to the rumbles of their most affiliated partners in the social group than to less affiliated group members, implying that rumble exchanges serve an affiliative function in elephants. Although my finding of reciprocal overlapping and coda matching between pairs of whales likewise suggests that these behaviours function in affiliative social bonding, I found no correlation between overlapping or matching and either genetic similarity or association index. Therefore, if countercalling does function in social bonding in sperm whales, either countercalling serves to establish or reinforce social bonds between whales irrespective of their relatedness or social relationship or else the strength of the social affiliation between pairs of whales is related to some other variable (e.g. duration of social relationship).

Female sperm whales are presumed to live in social units in order to provide group defense against killer whales (Whitehead 2003b), provide allomaternal care of calves (Whitehead 1996a), provide communal knowledge of a large home range (Whitehead 2003a), and perhaps increase feeding success through group foraging (Best 1979). If the maintenance of social cohesion were important to achieving these functions and increasing the overall fitness of the unit, then reaffirming and strengthening the relationships between individuals in a unit would be imperative. It was previously suggested that the production of codas at the surface functions to reestablish social bonds between whales after the period of separation while foraging at depth (Whitehead and Weilgart 1991). However, the wide variety of coda types produced by a unit and the apparent functionality of both unit and individual coda repertoires (see Rendell and Whitehead 2003b; Chapter 3) indicate that codas likely serve a number of purposes, including clan identification and individual identification in the case of a mother and calf (see Chapter 3). I propose that the affirmation of social bonds is achieved not simply by coda production but by the overlapping and matching of codas. By overlapping the coda of another whale, the responder might indicate that it is in close enough proximity to the other whale to detect the coda, process what it is hearing, and respond even before the first whale has terminated its signal. Moreover, if two whales are side by side, an overlapping coda might redundantly indicate the close proximity of the responding whale and thus assure the initial signaler of the nearness and strong union between the two animals.

However, since many coda overlaps occurred within just a fraction of a second after the initiation of another whale's coda (e.g. see Figure 4.1), it seems unlikely that responding whales are capable of detecting, processing, and responding to another whale's coda in such a brief period of time (Weilgart 1990). Instead, since sperm whales generally tend to produce a coda every 3-5 s (see Figures 4.2, 4.3, and 4.8), I suggest that a sperm whale is capable of anticipating the temporal patterning of another whale's coda production and thus coordinates its coda production so that subsequent codas of the two whales overlap. To investigate this hypothesis, I examined the Group of Seven recordings and noticed that 96% of coda overlap exchanges were preceded 3-5 s earlier by a coda made by one of the two whales in the overlap exchange (excluding cases where the identity of a vocalizing whale in the preceding 3-5s interval was unknown). This suggests that the high rate of observed coda overlaps occurs because sperm whales synchronize their coda production with the temporal coda production of other whales. Furthermore, I conducted additional permutation tests and found that whales in overlapping exchanges, in both the Group of Seven and Unit T, matched a coda type made 3-5 s earlier by their overlapping partner more often than expected ($P < 0.001$). In fact, whales in overlapping exchanges matched codas made by their overlapping partner 3-5 s earlier more often (Group of Seven: 53 coda matches; Unit T: 44 coda matches) than codas that they overlapped (Group of Seven: 41 coda matches; Unit T: 32 coda matches). Again, this suggests that the timing and type of coda produced by a whale is influenced by a coda produced 3-5 s earlier by another whale and that the similarity in the coda types of overlapping codas is an artifact of the matching of the recently-produced type.

This phenomenon in which a sperm whale synchronizes its vocal output with an already vocalizing sperm whale such that some vocalizations overlap one another is remarkably similar to the synchronization of vocalizations in Gelada monkeys (*Theropithecus gelada*; Richman 1978). In a range of social interactions, a Gelada monkey will attempt to produce sounds closely synchronous to the tempo and rhythm of the sequence of sounds already being produced by another monkey (Richman 1978). As a result, the onset of a second monkey's sound in a sequence will often occur within a fraction of a second of the onset of the first monkey's sound in the sequence (Richman 1978). Because the onset time difference between vocalizations is often smaller than the expected reaction time for primates (~150 msec; Donders 1868; Teichner 1954; Broadbent and Gregory 1962), Richman (1978) argues that the second monkey responds not directly to the onset of the first monkey's sound but to the onset of the *previous* sound in the vocal sequence of the first animal and that this action requires some sort of internal time mechanism to determine the rhythm and tempo of the first monkey's vocal output.

In the Group of Seven and Unit T recordings, many of the recorded coda overlap exchanges (34% and 21% respectively) had onset time differences between the codas of less than 150 msec, indicating that many of the overlap responses occurred within a time period that is likely less than the reaction time possible for sperm whales. Together with the temporal regularity with which sperm whales produce codas and the observation that whales frequently match a coda produced 3-5 s earlier by its overlap exchange partner, the occurrence of remarkably short onset time differences between codas in exchanges strongly suggests that sperm whales, like Gelada monkeys, respond not directly to the vocalization that they overlap but to the *previous* vocalization in the vocal sequence of the other animal. Alternatively, the synchronization of coda production between whale pairs could be a combination of responding to a previous coda and to the overlapped coda, particularly if the timing of a previous coda prepares a whale to overlap an upcoming coda.

As a result of the apparent synchronization in coda production, 72% of coda overlap exchanges in the Group of Seven recordings were a part of sequences comprised of two or more overlap exchanges between two whales (e.g. see Figure 4.1), with exchange sequences ranging from 2 to 8 exchanges in length (mean ± SD = 2.1 ± 1.8 exchanges). Moreover, these values are underestimates of the length of sequences and percentage of codas in sequences since several sequences were disrupted by exchanges containing codas that were not confidently assigned to a whale or codas that were not overlapping but adjacent to one another within a 2 second lag. When I excluded such exchanges, 91% of coda overlap exchanges were in exchange sequences, with a mean sequence length of 3.1 ± 2.1 exchanges. These observations suggest that pairs of sperm whales within a social unit synchronize the timing of their coda production to produce sequences of temporally associated coda exchanges, resulting in duet-like vocal chains between whales. Although it is also possible that the production of temporally associated codas could be a result of responses by both animals to some external stimulus, the temporal regularity of both codas by solitary whales and overlap exchanges by pairs of whales and the lack of any obvious acoustic cue in recordings indicates that this is highly unlikely and instead favours the hypothesis that sperm whales are able to anticipate and overlap the vocal output of other individuals.

Additionally, since codas in echocoda exchanges were not any more similar in rhythm or tempo to one another than were codas in overlapping and matching exchanges that were not echocoda exchanges, it seems that the echocoda is not a special class of overlapping response but simply an overlapping and matching exchange in which the clicks of the second whale's coda occur between the clicks of the first. It is possible, however, that sperm whales produce overlapping and matching coda responses with the optimal goal of producing an echocoda, a response perhaps facilitated by, if not entirely a result of, the ability of whales to anticipate the timing of subsequent coda production by other whales. The anticipation of vocal production and subsequent overlapping of codas being produced in sequences therefore results in strings of overlapping coda exchanges, some of which occur as echocoda exchanges.

Even though further analysis of these exchange sequences is required to characterize their structure and identify any organizational rules, the general arrangement of these sequences conforms well with a recent definition of duets as "overlapping bouts of vocalizations given by paired individuals such that their elements within those bouts have a high level of alternation, or a low coefficient of variation of the intervals between their elements or both" (Hall 2004 adapted from Farabaugh 1982). While primate and avian duets generally occur between paired males and females (Geissmann and Orgeldinger 2000; Hall 2004), sequences of overlapping codas between female sperm whales may provide some of the pair-bonding functions suggested for mated pairs. For example, the apparent effort or attentiveness required to achieve precise temporal coordination with a duetting partner may indicate an individual's commitment to a partnership (Wickler 1980) and strengthen a social bond between duetting animals. Furthermore, precision in vocal production may signal to others the proximity of the duetting individuals to one another, if close proximity is required for greater precision (Hall 2004). In addition, coda overlapping may function as an acoustic form of social grooming (see Dunbar 1996), not only reaffirming the proximity between whales but also inducing opiate production and thus a sense of connection between overlapping partners (see Terry 1970; Keverne et al. 1989). Just as long sequences of Gelada monkey vocalizations provide a consistent rhythm and permit the synchronization of vocal output between animals, presumably as a vocal grooming function to maintain social relationships (Richman 1978), the consistent rhythm of sperm whale coda production and consequent synchronization of coda vocalizations into sequences of overlapping exchanges may also function to establish and cultivate relationships between whales.

While coordinated overlapping may function to affirm social bonds between sperm whales, call-matching may also serve a similar social bonding function in this species. In the orange-fronted conure (*Aratinga canicularis)*, a social parrot, birds were observed to increase the similarity between their response calls and playback when they also demonstrated an increased non-aggressive response towards the speaker, suggesting that call-matching in this species might represent an affiliative signal to communicate desire to join another flock (Vehrencamp et al. 2003). In sperm whales, coda matching of a recently produced coda may indicate the sharing of coda types in whales' repertoires as well as the attentiveness of responding individuals to the vocalization type just produced. Moreover, just as some bird species use temporal and pattern specific matching both separately and in concert as an escalated signal (e.g. McGregor et al. 1992; Langemann et al. 2000; Otter et al. 2002), the contextual similarity of coda overlapping and matching suggests that sperm whales use these signals both independently and cooperatively to impart a stronger form of the same or similar signals.

While call-matching in songbirds and frogs involves matching a variety of song types and note numbers (e.g. Stoddard et al. 1992; Geberzahn and Hultsch 2004; Burt and Vehrencamp 2005), coda matching in sperm whales appears to involve the matching of just a few coda types. If the production of certain vocalizations in a species or group are specific to particular contexts and/or the context can be induced by particular vocalizations (e.g. alarm calls), then it would not be unexpected for animals to respond to these context-specific calls with similar calls, resulting in apparent but not actual call-matching (e.g. right whale 'up calls': Clark 1983). I argue that true call-matching is characterized by the matching of many equivalent call types and that the signal is communicated by the match in the two calls, not solely by the type of call produced in response.

In order to confirm that observed call-matching is not simply an artifact of context-specific calling, it is necessary that researchers take into account not only the repertoires of individuals (e.g. Burt and Vehrencamp 2005), but also the vocal repertoires produced by individuals in particular recording contexts (e.g. Miller et al. 2004). Because sperm whales in the social units studied here matched codas more often than expected even when controlling for the repertoires of individuals within bouts, it appears that sperm whales do engage in coda-matching and not simply context-specific calling. However, coda matching appears to be largely restricted to one or two coda types, a likely outcome of the limited overlap of coda type repertoires between individuals (see Chapter 3). This suggests that while sperm whales alter their coda type production within bouts to match a particular type, whales do not match a variety of coda types more than expected and are simply responding in kind to the one type that elicits that response. Thus, while songbirds match a variety of song types such that the signal is not simply the type of song produced but the fact that the initial signaler is matched, in sperm whales it appears that coda matching may simply be a result of repeating a popular coda type in the unit repertoire when it is heard.

Coda matching in sperm whales therefore appears to be similar to the 'matching' of 'up calls' in right whales and of alarm calls in vervet monkeys in that whales are responding to a particular coda type with the same type rather than matching a variety of types at a rate higher than that expected (given the number of each type produced in that context). However, coda matching differs from the vocal 'matching' that is observed in those species since it is not simply context-specific calling, as a variety of coda types are produced within the same context (i.e. bout) and matching occurs at a higher rate than expected given the frequency of that type in the bout. I suggest that the tendency for whales to coda match then is a communication signal that indicates the sharing of that particular coda type in their repertoire and likely functions in cooperatively reaffirming the mutual clan membership of the matching animals

In summary, the results of this study indicate that despite the temporal regularity of coda production by individual whales, sperm whale coda production is influenced by the timing and types of codas produced by other unit members. Although patterns in overlapping and matching do not seem to be correlated with relatedness or social affiliation, the context of these behaviours, the reciprocity in coda overlapping, and the sequencing of overlap exchanges into 'duet-like' chains strongly suggest that coda overlapping and matching function to reinforce social bonds between whales. The fact that coda matching was largely caused by the matching of just one coda type in each unit could be a result of limited overlap in the repertoires between individuals but also function to reaffirm clan affiliation amongst unit members and strengthen social bonds. Future playback studies on sperm whales that broadcast codas at regular 3-5 s intervals will likely prove useful in further examining the structure, syntax, and function of the overlap exchange sequences observed in these units. Furthermore, while call-matching between foraging or traveling killer whales has been suggested to function in cohesion calling (Miller et al. 2004), further study of vocal exchanges between individuals in close proximity might also suggest an affiliative function.

CHAPTER FIVE

THE COMMUNICATION CAPACITY OF SPERM WHALE CODA PRODUCTION

INTRODUCTION

Animals have evolved a wide variety of signals that function in the transfer of information. From the waggle dance of the honeybee (*Apis mellifera*, von Frisch 1967) to the elaborate duets of gibbons (*Hylobates syndactylus*, Geissmann 1999), communication plays a critical role in the foraging, mating, defense, and parental care of animals (Bradbury and Vehrencamp 1998). But while it is recognized that animal communication, like human speech, is an integral component of social interactions, philosophers and linguists have long argued that human language differs from animal communication, and that it is a defining feature of humankind that distinguishes us from other animals. As articulated by the linguist Noam Chomsky, "when we study human language, we are approaching what some might call the 'human essence', the distinctive qualities of mind that are, so far as we know, unique to man" (Chomsky 1968).

For many years, researchers agreed with Darwin, Descartes, and Aristotle that animal vocalizations differ from human language in that they merely reflect changes in the signaler's affective state and do not refer to external environmental objects (Hauser 2000). More recently, however, it has become clear that some nonhuman primate vocalizations do involve symbolic communication, encoding information about both affective state and external referents (Seyfarth et al. 1980; Dittus 1984; Gouzoules et al. 1984; Cheney and Seyfarth 1990; Macedonia 1991; Marler et al. 1992; Zuberbühler et al. 1997; Hauser 2000). This evidence partially, but not entirely, bridges the philosophical divide between human and non-human communication.

In addition to symbolic communication, one of the qualities that all human languages share is their 'creative' aspect, the capacity of speakers to produce and understand an infinite number of previously unheard sentences (Chomsky 1965). Now that it is recognized that some animal species are capable of using referential communication (Green and Marler 1979), some have argued that it is the ability to communicate creatively that distinguishes human language from non-human communication (Aitchison 1998). Indeed animal communication is generally non-syntactic in that signals encode entire circumstances rather than discrete meaningful components that can be recombined to generate new messages (Nowak et al. 2000). The incredibly expressive capacity of human language, on the other hand, is made possible by syntax, which allows the generation of an infinite number of sentences using a finite number of words and phonemes (Chomsky 1965; Nowak et al. 2000).

However, research on birds, primates, and dolphins suggests that some animal vocalizations are in fact syntactically organized and more closely resemble human language than previously thought. Perhaps the best-studied combinatorial communication system in animals is that of the black-capped chickadee (*Parus atricapillus*) (Hailman et al. 1985; Hailman and Ficken 1986; Hailman et al. 1987). This species utilizes a repertoire of just four note-types to combinatorially generate an unlimited number of different calls with a given note-type predictably followed by a repetition of itself or by a particular note-type later in a fixed sequence (Hailman et al. 1985). Similarly, a predictable ordering of calls and whistle types has been found in wedge-capped capuchin monkeys (*Cebus olivaceus*) and bottlenose dolphins (*Tursiops truncatus*) (Robinson 1984; McCowan et al. 1999). Furthermore, Symmes and Biben (1988) found that squirrel monkeys (*Saimiri sciureus*) fulfill the three criteria which they proposed as indicators of primitive conversation: a) turn-taking; b) rules in the ordering of signals; and c) reactionary changes in the vocal patterns of a caller as a result of the vocal response given by a listener.

Given the increasingly apparent similarities between some animal communication systems and human language, researchers have subjected these systems to formal quantitative tests that have been used traditionally in linguistic analyses (Hailman et al. 1985; Hailman and Ficken 1986; McCowan et al. 1999). Zipf's rules and Shannon's entropic orders have been used to examine the frequency of occurrence and interaction of signals not only in a variety of human languages, but also in several animal communication systems (Zipf 1949; Hailman et al. 1985; McCowan et al. 1999). For example, Zipf's statistic, which is the regression slope of the log frequency of a signal in a repertoire against the log of its rank, has been used to measure the structure of human and animal repertoires and their potential capacity for information transfer (see Zipf 1949; Hailman 1994; Hailman et al. 1985, 1987; Hailman and Ficken 1986; McCowan et al. 1999, 2005). Furthermore, the 'chick-a-dee' call system of the black-capped chickadee has been found to have computable syntax and therefore qualifies as a language by structural linguistics (Hailman and Ficken 1986).

The evolution of syntactic language in humans has been suggested to be a result of an increase in the complexity of social structure (Dunbar 1996; Nowak et al. 2000). As early humans began to interact more socially, the accompanying increase in the number of relevant communication topics likely selected for a syntactic communication system that could formulate messages that had not been learned beforehand (Nowak et al. 2000). Given this proposed relationship between social structure and syntax, it seems likely that animal species that engage in a high degree of social interaction might also exhibit some form of syntactic communication. Therefore, in an effort to examine the similarities between human language and animal communication, it would be productive to quantitatively analyze the communication systems of other social and seemingly intelligent animals, such as odontocetes and primates. Furthermore, studying the communicative structure and vocal exchanges of such species may provide insight into the evolution of human language (Symmes and Biben 1988).

One cetacean species that demonstrates a complex social system is the sperm whale (*Physeter macrocephalus*). While male sperm whales leave their natal unit and travel to higher latitudes as they mature, females remain in tropical and sub-tropical waters where they live in social units consisting of approximately 10-12 adult females, as well as juveniles and calves of both sexes (Whitehead et al. 1991). These social units, which are generally stable in composition (Whitehead and Weilgart 2000), are thought to have evolved as an adaptation to provide allomaternal care and group defense (Whitehead 2003b). In turn, sperm whales may have also evolved a complex and perhaps syntactic communication system to manage the increase in social interactions and relevant communication topics that accompanied the increase in social complexity. Furthermore, sperm whales, which feed on widely distributed and temporally variable prey resources, may benefit from the combined memory of members of the social unit (Whitehead 1996b) and necessitate a complex communication system to share information and traditional knowledge (see Whitehead 2003a).

In keeping with these hypotheses, not only do sperm whales exhibit a complex social system, but whales in social units also appear to have a complex communication system in that short stereotyped patterns of broadband clicks, termed codas (Watkins and Schevill 1977; Whitehead and Weilgart 1991), are exchanged between whales while socializing at the water surface. Codas can be classified into types based on the number and temporal spacing of clicks within the coda (Weilgart and Whitehead 1993). Although it was initially suggested that codas function as individual signatures (Watkins and Schevill 1977; Watkins et al. 1985), evidence that different whales produce the same coda types (Whitehead and Weilgart 1991; Rendell and Whitehead 2004) and that whales in a social unit have generally similar coda repertoires (Chapter 3), indicate that this is not the case. Rather, units of sperm whales possess coda repertoires and can be classified into acoustic 'clans' based on their usage of particular coda types (Rendell and Whitehead 2004).

During periods of socialization, sperm whales appear to alternate and overlap codas in a conversational fashion (see Chapter 4). By using the inter-pulse intervals

(IPIs) of coda clicks to distinguish among the vocalizations of whales within recordings, I previously found that sperm whales in social units tend to engage in overlapping exchanges with other individuals and produce codas at regular intervals of 3-5 s, sometimes resulting in duet-like sequences of overlapping exchanges (Chapter 4). Although previous research discovered non-random patterns in the types of codas that overlapped others or initiated coda interactions (Weilgart and Whitehead 1993), the analysis pooled different vocal clans, recordings, and individuals, such that the observed tendency for particular coda types to overlap others may have been an artifact of the coda repertoires of units or individuals or of the types of codas produced in different contexts. Clearly, to investigate whether there are syntactic rules in the production of codas, it is necessary to examine coda output at the level of the individual. In this chapter, I used the assignment of codas to individuals using similarities in inter-pulse intervals (see Chapter 2) to examine the complexity of sperm whale coda communication and the potential for the transfer of information between vocalizing whales. Coda communication complexity was examined by calculating the Zipf slope for the repertoires of two social units, by testing for sequential dependencies in the ordering of codas both within individual whale sequences and between whales in coda exchanges, and by testing whether sperm whales engage in conversational turn-taking.

METHODS

Field Methods – Group Of Seven

The Group of Seven is a social unit consisting of five adult females, one juvenile male, and one male calf (see Gero 2005) that were followed for a total of 41 days between January 16 and March 26, 2005 off the coast of Dominica. Animals were tracked visually during the day and followed acoustically at night using a directional hydrophone (see Whitehead and Gordon 1986). During daylight hours, individuals at the surface were approached and digital photographs of flukes were taken using a Canon D10 digital SLR for individual identification purposes (Arnbom 1987). Sloughed skin samples were collected from the slicks of whales (Whitehead et al. 1990; Bérubé and Palsbøll 1996) and analyzed to reveal the sexes and genetic relationships of these individuals (Gero et al. submitted). I made 15 coda recordings of this unit as well as recordings of their usual clicks (i.e. echolocation clicks) when solitary whales fluked at the start of a foraging dive (see Chapter 2). Recordings were made from a towed hydrophone and recorded on a Fostex VF-160 multi-track recorder (see Chapter 2).

Field Methods – Unit T

Unit T is a social unit of nine female and immature sperm whales that was followed by Dr. Luke Rendell during four encounters for a total of 17 days between March 10 and April 12, 1999 around the Galápagos Islands (see Rendell and Whitehead 2004; Chapter 4). As with the Group of Seven, this unit was tracked visually during the day and acoustically at night and photographed for individual identification. Sloughed skin samples were used to reveal that the five sampled unit members were largely unrelated (Mesnick 2001; Whitehead 2003b). During social periods, 21 recordings were made using an Offshore Acoustics hydrophone connected to a Sony TC-D5M cassette recorder and subsequently digitized at 44.1 kHz onto a standard desktop PC.

Acoustic Analysis

Recordings were analyzed using Rainbow Click (see Gillespie 1997; Leaper et al. 2000; Rendell and Whitehead 2004) software and the IPIs of usual clicks and coda clicks were calculated using routines custom-written in MATLAB® version 6.1.450, release 12.1 (MathWorks Inc. 2001) and detailed elsewhere (Chapter 2). The codas recorded of the Group of Seven were previously assigned to individuals based on the similarity of coda and usual click IPIs (Chapters 2-4). For Unit T, although codas were not assigned to specific individuals, codas within recordings were assumed to have been made by different whales if their modal IPIs were at least 0.10 msec apart (see Chapter 2). The intervals between clicks within a coda ('inter-click intervals') were output from Rainbow Click, standardized by coda length, and classified into types using *k*-means cluster analysis (see Rendell and Whitehead 2004).

Zipf Relation

For both the Group of Seven and Unit T, I calculated the Zipf relation for each social unit by regressing the log (base 10) rank of coda types against the log of their frequency of occurrence as in the work of Zipf (1949, 1968) for human languages and McCowan et al. (1999) for bottlenose dolphin whistles. I compared the regression slopes to data sets of 10,000 randomly generated codas using the same number of coda types as found in each unit (see McCowan et al. 1999). Moreover, to ensure that the slopes of log rank vs. log frequency were not affected by coda matching between whales (see Chapter 4), I also calculated the Zipf slopes for each unit using a subset of codas for which transitions between codas produced by the same whale (or similarly-sized whale) were not interrupted by a coda produced by another whale.

Ordering of Coda Types in Intra-Whale Coda Sequences

Although the data set of Group of Seven codas was sufficiently large to reliably calculate first-order entropic measures and Zipf statistics, the data subset of uninterrupted coda sequences used to examine rules in the ordering of codas consisted of just 184 codas of 15 different coda types, resulting in a calculated sample size per cell of 0.57 for second-order entropy analysis (first-order Markov chain) (see McCowan et al. 1999). This value is well below the minimum of 10 samples per cell suggested by some researchers for reliable calculations of higher entropic orders (Hailman and Hailman 1993). Consequently, I used non-parametric permutation tests rather than calculations of higher-order entropies (cf. McCowan et al. 1999) to examine whether there were trends in the ordering of coda types within the coda sequences of individual Group of Seven whales.

I tallied the within-whale coda type transitions between codas that occurred within 5 s of each other (i.e. within coda sequences) and compared the number of observed transition types (as well as the number of coda-type repeats) to the numbers expected from 10,000 permutations that randomized whales' coda types within bouts of coda production, thereby accounting for any potential effect of vocal bouts (i.e. context) on the types of codas produced. The time intervals between a whale's codas fit a Poisson distribution better than a two-process exponential model (see Chapter 4) and under this distribution (with a calculated mean of 5.5 s) 95% of the time intervals were less than 9 s, suggesting that the bouts - consisting of codas produced at regular intervals of 3-5 s - were separated by time intervals larger than 9 s (see Chapter 4). Therefore, in permutations, coda types were rotated within bouts separated by a bout criterion of 9 s. I also repeated this analysis without limiting transitions to those occurring within 5 s, thereby including transitions between sequences of codas.

To ensure that coda type transitions were not influenced by the coda types of other whales, I limited this analysis to transitions that were uninterrupted by the codas of other whales. However, to examine whether whales repeated themselves more or less when uninterrupted by other whales, I also compared the observed percentage of coda transitions that were coda type repeats when whales were not interrupted to the percentage of transitions that were repeats when whales were interrupted by another whale.

Similar analysis of the ordering of coda types within whale sequences was not conducted on the Unit T coda recordings, as I could not confidently conclude that two adjacent codas with similar IPIs were made by two different whales.

Ordering of Coda Types Between Whales

To examine whether there were trends in the ordering of coda types between whales in overlapping coda exchanges, I tallied the coda type transitions between overlapping codas and compared the observed number of each transition type to that expected from 10,000 permutations that rotated the coda types of each whale within bouts separated by 9 s (see Chapter 4 and above). Moreover, since previous analysis suggested that whales might alter their coda production in response to a previous coda produced by its 'duet' partner (see Chapter 4), I examined the coda type transitions between a coda produced by a whale in an overlapping exchange and a coda produced by the other whale in that same overlapping exchange but produced 3-5 seconds earlier. I also repeated these transition tests for Unit T recordings, examining the transitions in coda types between codas with IPIs that were sufficiently different enough (>0.10 msec) to ensure that they were produced by different whales (see Chapter 2). In the analysis of the time intervals between codas by Unit T whales, a two-parameter model did not provide any additional information beyond a Poisson distribution (see Chapter 4). Furthermore, under a Poisson distribution with a mean of 4.8 s, 94% of the time intervals between Unit T codas were less than 8 s. Therefore, in permutations of Unit T coda recordings, coda types were rotated within bouts separated by a bout criterion of 8 s.

Turn-taking

To examine whether individual sperm whales in the Group of Seven took turns producing codas and thus exchanged vocalizations in an alternating, conversational manner, I tallied the number of times that a coda was followed by the coda of a different whale and compared the observed number to the expected number from 10,000 permutations in which the temporal patterning of each individual's coda production was rotated within recordings (as in Miller et al. 2004 and Chapter 4). This was repeated excluding the codas of the calf in the Group of Seven. I also used these permutation tests to test for turn-taking in the recordings of Unit T, comparing the observed and expected number of times that a coda was followed by a coda with an IPI that was dissimilar enough (greater than 0.10 msec difference between the IPIs) to be certain that the two codas were made by different whales.

RESULTS

Zipf Relation – Group of Seven

Although the sample size of analyzed Group of Seven codas (318 codas of 16 coda types) was much smaller than that reported for human languages and dolphin whistles (see McCowan et al. 1999), the sample of codas used met the suggested 'rule of thumb' (at least 10 times the number of signal types) for calculating first-order entropy measures (Hailman and Hailman 1993; see McCowan et al. 1999). When log rank of coda type was regressed against log frequency of occurrence, the slope for the Group of Seven coda data was –1.61. This calculated slope was significantly steeper than –1.00 ($t = 5.23$, d.f.= 14, $P = 0.001$), indicating that the recorded coda repertoire of this unit was repetitious in that the most prevalent coda types were produced very frequently. When the codas produced by the calf were excluded, the slope was even steeper (slope = -2.11), suggesting that the repertoire of the calf contributes some coda type diversity to the unit repertoire and that the coda repertoire of the older animals is highly repetitious. Accordingly, when the coda repertoire of the calf was analyzed alone, the calculated Zipf slope (-1.19) was much shallower than that for the adults and not significantly different from –1.00 ($t = 1.64$, d.f.= 7, $P = 0.146$). Moreover, given that the calf's coda repertoire was highly undersampled (29 codas of 9 coda types) and given that extreme undersampling has the effect of increasing the slope (the higher-ranking signals are over-represented in a smaller sample), the observed slope of the calf would be expected to become even flatter if the calf's coda repertoire were sufficiently sampled.

To ensure that the steepness of the Zipf slope was not an artifact of coda matching, I also calculated the Zipf slope for Group of Seven codas that were uninterrupted by the codas of other whales. The value of the Zipf slope for this subset of the data was –1.57, a value that was significantly different from –1.00 ($t = 3.36$, d.f.= 12, $P = 0.006$). Likewise, when the calf was excluded from this subset of data, the Zipf slope ($b = -1.79$) was significantly steeper than –1.00 ($t = 2.49$, d.f.= 9, $P = 0.035$; see Figure 5.1a).

Zipf Relation – Unit T

With a sample of 575 codas from 19 coda types, the Unit T codas also met the suggested requirement for calculating first-order entropies. Like the Zipf relation for the Group of Seven codas, the regression slope for the codas of Unit T was also steep (slope = -1.53) and significantly different than –1.00 ($t = 3.63$, d.f.= 17, $P = 0.002$). Moreover, when limiting the analysis to a subset of the data of uninterrupted coda sequences, the Zipf slope was –1.46 and still significantly different than –1.00 ($t = 5.02$, d.f.= 13, $P < 0.001$; see Figure 5.1b).

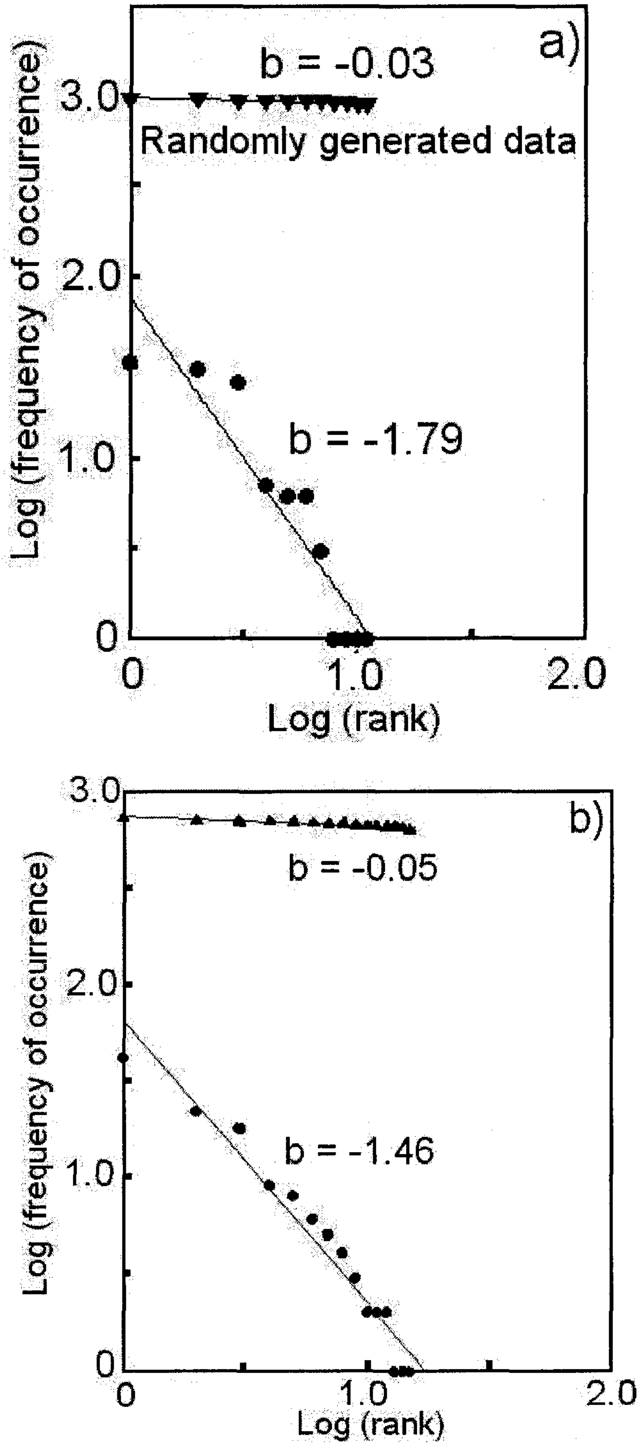


Figure 5.1 Regression of log(rank) versus log(frequency of occurrence) and lines of best fit for the coda repertoire of uninterrupted sperm whales in the Group of Seven (excluding the calf) (a) and uninterrupted sperm whales in Unit T (b). Zipf's slopes of randomly generated data from each coda repertoire are also shown for comparison.

Ordering of Coda Types in Intra-Whale Coda Sequences – Group of Seven

Of the 85 intra-sequence coda transitions in Group of Seven recordings that were not interrupted by a coda of another whale, 74 (87.1%) were transitions to the same coda type. I compared this observed value to the distribution expected by chance from randomizing the coda types of each whale within coda bouts and tallying the number of coda transitions that were transitions to the same type. The observed number of repeats exceeded the expected mean ± SD of 62.3 ± 2.1 codas generated by 10,000 randomizations and was significant ($P < 0.001$), indicating that whales tended to repeat themselves within coda sequences. Moreover, within uninterrupted coda sequences, the only transition types that occurred significantly more than expected were from coda type '5R' to type '5R' (observed = 28, expected = 23.1 ± 1.3, $P < 0.001$) and from coda type '5+1' to type '5+1' (observed = 6, expected = 2.1 ± 1.1, $P < 0.001$) (see Table 5.1). Furthermore, the tendency for a whale to repeat a coda type was also observed when all uninterrupted transitions between whales' codas were included, not just those within coda sequences (observed repeats = 101, expected repeats = 89.9 ± 2.4; $P < 0.001$; Table 5.2).

Additionally, whales tended to repeat coda types in sequences regardless of whether they were interrupted by another whale or not; the percentage of coda type transitions that were coda repeats when whales were uninterrupted by the coda of another whale (87.1%) was not significantly different from the percentage of coda type transitions that were coda repeats when whales were interrupted by the coda of another whale (85.5%; $Z = 0.288$; $P = 0.77$).

Ordering of Coda Types Between Whales – Group of Seven

In examining the transitions from one coda type to another within overlapping coda exchanges, no coda type overlapped another coda type ($P > 0.376$) or was overlapped by another coda type ($P > 0.105$) more often than expected. The only overlapping transition type that occurred significantly more often than expected was from coda type '1+1+3' to '1+1+3' (observed = 26; expected = 22.3 ± 1.6; $P = 0.013$; see Table 5.3). Likewise, the only significant transition type from a coda produced by one whale to a coda produced by a different whale in a subsequent overlapping exchange between the same two whales was from coda type '1+1+3' to coda type '1+1+3' (observed = 37; expected = 32.3 ± 2.4; $P = 0.028$, see Table 5.4).

Ordering of Coda Types Between Whales – Unit T

In examining the transitions from one coda type to another within overlapping coda exchanges, coda type '5R' overlapped other codas more often than expected (observed = 12; expected = 6.1 ± 1.6; $P = 0.001$) and was overlapped by other codas less often than expected (observed = 5; expected = 8.4 ± 1.6; $P = 0.035$). No other coda types overlapped other codas ($P > 0.184$) or were overlapped by other codas ($P > 0.055$) more often than expected. Three transition types within overlap exchanges occurred significantly more often than expected by chance; '3R' to '1+2', '2+1' to '2+1', and '2+4' to '5R' (see Table 5.5). For coda type transitions from a coda produced by one whale to a coda produced by a different whale in a subsequent overlapping exchange between the same two whales, the only two transitions that occurred significantly more often than expected were from coda type '2+1' to type '2+1' (observed = 28; expected = 17.3 ± 3.6; $P = 0.002$) and coda type '6R' to type '4R' (observed = 2; expected = 0.4 ± 0.6; $P = 0.042$) (see Table 5.6).

Turn-taking – Group of Seven

Within the Group of Seven, a coda was followed by a coda produced by a different whale 133 times and by a coda produced by the same whale 127 times, indicating that 49% of the time a whale repeated itself with another coda before being responded to by another whale. I compared the observed number of times that a whale's coda was followed by another coda from itself to the distribution expected by chance from rotating the coda sequences of each whale within each recording a random amount of time. The observed value of 127 repeats was less than the expected mean ± SD of 143. 7 ± 11.2 generated by 10,000 randomizations but not significant ($P = 0.133$), suggesting that whales were not engaging in antiphonal coda exchanges. Moreover, when the calf's coda production was excluded, the observed number of times that a whale repeated itself (110) was again not significantly less than that expected by chance (122.4 ± 11.9; $P = 0.291$).

Turn-taking – Unit T

Similar to the turn-taking results for the Group of Seven, the observed number of times that a Unit T coda was followed by a coda that was unmistakably produced by a different whale, rather than a similarly-sized whale, was not significantly greater than that expected by chance (observed = 241; expected = 229.9 ± 10.5; $P = 0.312$).

Table 5.1. Uninterrupted intra-whale intra-sequence coda type transitions in the Group of Seven. The numbers in the table indicate the number of observed transitions from a preceding coda type (rows) to a following coda type (columns). Underlined transition numbers denote transition types that occurred significantly more often than expected when using permutation tests that randomized coda types within coda bouts separated by 9 s. The mean numbers and standard deviations of expected transitions for those that occurred significantly more often than expected are provided below the table.

Following coda type

Preceding coda type

	2+1	1+3	2+1+1+1	1+1+3	5R	5+1	7R	6+1	6+1+1	1+1+6	8R	1+1+7	9R	9+1
2+1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1+3	0	11	0	0	0	0	0	0	0	0	0	0	0	0
2+1+1+1	0	0	0	1	0	0	0	0	0	0	0	0	0	1
1+1+3	0	0	0	24	0	0	1	0	0	0	0	0	1	0
5R	0	0	0	0	28[a]	0	0	0	0	0	0	0	0	0
5+1	0	0	1	0	0	6[b]	0	0	0	0	0	0	0	0
7R	1	0	0	0	0	0	1	0	0	0	0	0	0	0
6+1	0	0	0	0	0	1	0	0	0	0	1	0	0	0
6+1+1	0	0	0	0	0	0	0	1	0	0	0	0	0	0
1+1+6	0	0	0	0	0	0	0	0	0	0	0	1	0	0
8R	0	0	0	0	0	0	0	0	0	0	2	0	0	0
1+1+7	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9R	0	0	0	0	0	0	0	0	0	0	0	0	2	0
9+1	0	0	0	0	0	0	0	0	1	0	0	0	0	0

[a] Mean expected number of transitions = 23.1 ± 1.3
[b] Mean expected number of transitions = 2.1 ± 1.1

Table 5.2. Uninterrupted intra-whale coda type transitions in the Group of Seven (including transitions between sequences). Underlined transition numbers denote transition types that occurred significantly more often than expected when using permutation tests that *randomized coda types within coda bouts separated by 9 s. The mean numbers and standard deviations of expected* transitions for those that occurred significantly more often than expected are provided below the table.

Preceding coda type	Following coda type														
	2+1	1+3	2+1+1+1	1+1+3	5R	5+1	6R	7R	6+1	6+1+1	1+1+6	8R	1+1+7	9R	9+1
2+1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1+3	0	24	1	0	0	0	0	0	0	0	0	0	0	0	0
2+1+1+1	0	0	3	2	0	0	0	0	1	1	0	0	0	0	1
1+1+3	0	2	2	28	0	0	0	2	0	0	0	0	0	1	0
5R	0	0	0	1	30[a]	0	0	1	0	0	0	0	0	0	0
5+1	0	0	1	0	0	6[b]	0	0	0	0	0	0	0	0	0
6R	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
7R	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0
6+1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0
6+1+1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
1+1+6	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
8R	0	0	0	0	1	0	0	1	0	0	0	4[c]	0	0	0
1+1+7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9R	0	0	0	0	0	0	1	0	0	0	0	2	0	3	0
9+1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

[a] Mean expected number of transitions = 26.9 ± 1.0
[b] Mean expected number of transitions = 2.4 ± 1.0
[c] Mean expected number of transitions = 1.5 ± 0.8

Table 5.3. Coda type transitions between whales in Group of Seven overlap exchanges. Underlined transition numbers denote transition types that occurred significantly more often than expected when using permutation tests that randomized coda types within coda bouts separated by 9 s. The mean numbers and standard deviations of expected transitions for those that occurred significantly more often than expected are provided below the table.

	Following coda type									
Preceding coda type	**4R**	**1+3**	**2+1+1+1**	**1+1+3**	**5R**	**7R**	**6+1**	**1+1+6**	**8R**	**9R**
4R	0	0	0	0	0	0	0	0	0	0
1+3	0	0	0	0	5	0	0	0	0	0
2+1+1+1	1	1	0	0	0	0	0	0	0	0
1+1+3	0	0	1	26[a]	1	0	0	1	0	0
5R	0	1	1	0	15	0	0	0	0	1
7R	0	0	0	0	0	0	0	0	0	0
6+1	0	0	0	0	0	0	0	0	0	0
1+1+6	0	0	0	1	0	0	0	0	0	0
8R	0	1	0	0	0	0	0	0	0	0
9R	0	0	0	0	0	0	0	0	0	0

[a] Mean expected number of transitions = 22.3 ± 1.6

Table 5.4. Group of Seven coda type transitions between a coda produced by a whale and a coda produced by a different whale in an overlap exchange 3-5 s later with the same initially vocalizing whale. Underlined transition numbers denote transition types that occurred significantly more often than expected when using permutation tests that randomized coda types within coda bouts separated by 9 s. The mean numbers and standard deviations of expected transitions for those that occurred significantly more often than expected are provided below the table.

Following coda type

Preceding coda type

	1+3	1+1+3	5R	1+1+6	8R	9R
1+3	0	0	5	0	1	0
1+1+3	0	$\underline{37}$[a]	0	1	0	0
5R	4	1	16	0	0	1
1+1+6	0	2	0	0	0	0
8R	0	0	0	0	0	0
1+1+7	0	1	0	0	0	0
9R	0	0	0	0	0	0

[a] Mean expected number of transitions = 32.3 ± 2.4

Table 5.5. Coda type transitions between whales in Unit T overlap exchanges. Underlined transition numbers denote transition types that occurred significantly more often than expected when using permutation tests that randomized coda types within coda bouts separated by 8 s. The mean numbers and standard deviations of expected transitions for those that occurred significantly more often than expected are provided below the table.

Following coda type

Preceding coda type	3R	2+1	1+2	3+1	4A	4R	5R	4+1	6R	2+4	7R	2+5	8S	8RB	9R	9S	10R
3R	0	1	3[b]	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2+1	0	18[a]	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
1+2	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3+1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4A	0	1	0	1	6	2	3	2	3	2	0	1	0	0	0	0	0
4R	0	0	0	0	1	1	0	0	0	2	0	0	0	0	0	0	0
5R	0	0	0	1	1	0	1	2	0	0	0	0	0	0	0	0	0
4+1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
6R	0	0	0	0	4	0	2	2	1	3	0	0	0	0	0	0	0
2+4	0	0	0	0	7	0	4[c]	1	2	2	0	0	1	0	0	0	0
7R	0	0	0	0	2	0	1	0	2	0	0	0	0	0	0	0	0
2+5	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0
8S	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
8RB	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
9S	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
9R	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
10R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0

[a] Mean expected number of transitions = 7.8 ± 2.8

[b] Mean expected number of transitions = 0.4 ± 0.6

[c] Mean expected number of transitions = 0.8 ± 0.9

Table 5.6. Unit T coda type transitions between a coda produced by a whale and a coda produced by a different whale in an overlap exchange 3-5 s later with the same initially vocalizing whale. Underlined transition numbers denote transition types that occurred significantly more often than expected when using permutation tests that randomized coda types within coda bouts separated by 8 s. The mean numbers and standard deviations of expected transitions for those that occurred significantly more often than expected are provided below the table.

Following coda type

Preceding coda type

	3R	2+1	1+2	3+1	4A	4R	5R	4+1	6R	2+4	7R	2+5	8S	9R	9S
3R	1	0	2	0	1	0	0	0	0	0	0	0	0	0	0
2+1	1	28[a]	2	0	1	0	0	0	1	1	0	0	0	0	0
1+2	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
3+1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0
4A	0	1	0	0	8	2	5	5	2	6	0	0	0	0	0
4R	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
5R	0	0	0	0	5	0	1	2	1	3	0	0	0	0	0
4+1	0	0	0	0	4	0	1	0	2	1	0	0	0	0	0
6R	0	0	0	1	3	2[b]	1	1	2	2	1	0	0	0	0
2+4	0	1	0	1	5	0	3	0	0	3	1	1	0	1	0
7R	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
2+5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8S	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1
9R	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9S	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

[a] Mean expected number of transitions = 17.3 ± 3.6

[b] Mean expected number of transitions = 0.4 ± 0.6

DISCUSSION

Because sperm whales possess a variety of different coda types within both their unit and individual coda repertoires (Rendell and Whitehead 2004; Chapter 3) and because individuals appear to engage in 'conversational' exchanges of codas while socializing at the water surface (Weilgart and Whitehead 1993), recordings of socializing sperm whales can give the impression that sperm whale coda communication contains some underlying syntactic structure and thus possesses the capability of meaningful information transfer. However, the results presented here concerning the diversity of coda types within the repertoires of social units, the ordering of codas both between whales and within the sequences of individuals, and the apparent lack of turn-taking in vocal exchanges between individuals all suggest that sperm whale coda production contains little capacity for information transfer, at least when compared to animal species that appear to use syntax and conversational turn-taking to convey information.

Zipf Relation

Zipf's statistic measures the comparative potential communication capacity of a repertoire using a first-order entropic relation. While bottlenose dolphin whistle production and a variety of human languages possess Zipf slopes approaching –1.00 (see McCowan et al. 1999), indicating a balance between repertoire redundancy and repertoire diversity and thus a high potential for transferring communication, the steep slopes reported here for both the Group of Seven and Unit T repertoires suggest that sperm whale unit repertoires are highly repetitious in that a message is represented by only a few signals and therefore, less communication complexity is conveyed. In other words, sperm whales appear to strongly favour the production of one or two coda types, producing other coda types only rarely. Given the tendency for sperm whale units to socialize preferentially with other units of the same acoustic clan (Rendell and

Whitehead 2003b), I suggest that sperm whales produce a large number of the few coda types that might be used to identify clan affiliation, such that the types of codas produced by whales are related to the function of clan identification rather than the more complex functions of syntactic or referential communication.

However, in contrast to the relative lack of signal diversity in the repertoire of Group of Seven adults, the repertoire of the calf in this unit demonstrated a Zipf slope that was shallower than that of the adults and not significantly different from –1.00. This indicates that the calf's repertoire is more diverse and less redundant than that of the adults in the unit, a pattern that has been observed in the vocal repertoires of young animals in other species. Infant bottlenose dolphins less than 1 month of age showed a more diverse repertoire than that of adult dolphins (infant Zipf slope = -0.82; adult Zipf slope = -0.95) (McCowan et al. 1999) and human infants of 22 months possessed a Zipf slope (-0.82) that is much shallower than that of human adults (-1.00) (Zipf 1949, 1968). Although the Zipf statistic for the Group of Seven sperm whale calf was not as shallow as that of bottlenose dolphin or human infants and not significantly different than –1.00, because the calf's repertoire was highly undersampled and because undersampling has the effect of increasing the steepness of a slope, increased sampling of this whale's repertoire would result in an even shallower slope, indicating an even more diverse repertoire for the calf in this unit. In which case, the more highly diverse vocal repertoires of sperm whale calves and infant dolphins compared to the repertoires of conspecific adults might indicate an exploratory vocal behaviour similar to that of babbling in human infants.

Ordering of Coda Types in Intra-Whale Coda Sequences

The results of permutation tests revealed that within coda sequences, sperm whales in the Group of Seven tended to repeat a coda type that they had just produced, indicating that not only is coda production in this unit highly unified (as revealed by Zipf slope analysis) but it is also highly repetitious temporally. Since the only coda transitions that occurred significantly more often than expected were transitions to the same type, this suggests that there is little syntax in sperm whale coda production. While the syntactic organization of discrete signal types, as observed in human languages and some non-human communication systems, can provide the capacity to create an infinite number of meaningful messages - and so provide enormous communication potential (Chomsky 1965; Nowak et al. 2000) -, the tendency for whales to repeat themselves within coda sequences suggests that coda production provides little communication capacity in comparison to the communication systems of humans and perhaps bottlenose dolphins.

Within Group of Seven coda sequences, the most frequently observed coda type transition was the repetition of coda type '5R' (Table 5.1), a coda type that was not only one of the two most common coda types in the unit's repertoire but also one of the most prevalent in the repertoires of most individuals in the unit (Chapter 3). Although the other most prevalent coda type ('1+1+3') was not repeated significantly more often than expected within bouts (Table 5.1), when conducting permutation tests that randomized coda types within recordings as a whole, coda type '1+1+3' was repeated more often than expected (observed = 24; expected = 13.3 ± 1.9; $P < 0.001$). Furthermore, permutation tests also revealed that the coda type produced solely by the calf, coda type '5+1' (Chapter 3), was repeated in coda sequences more often than expected (Table 5.1), indicating that both the adults and the calf in this unit repeated coda types within coda chains. The calf's mother did not show any more transitions than expected as she only made one coda type, '1+3', and so always repeated herself (Chapter 3).

While the repetition of call types in animal communication systems had previously been suggested to be a consequence of a facilitative release mechanism

(Hinde 1985), because whales in the Group of Seven only repeated a few coda types rather than all codas in the unit repertoire, it seems more likely that the repetition of specific coda types is functional. One explanation for the function of coda repetition is that sperm whales repeat particular coda types within sequences to ensure that the coda type, and thus its communicative significance, is effectively conveyed to the intended receiver(s). Since sperm whale social units tend to preferentially associate with other units with similar coda repertoires (Rendell and Whitehead 2003b), perhaps particular coda types (e.g. '1+1+3' and '5R' in the Group of Seven) function in identifying a unit's clan membership and so are repeated by individuals within the unit to ensure the sufficient advertizement of clan affiliation to whales in other units as well as fellow unit members. Moreover, if the content of a coda type communicates an honest signal, then repetition of that coda type may function to emphasize the honesty of the signal. The calf and its mother in the Group of Seven, whales that likely possess a higher necessity for individual identification than other whales in the unit (see Chapter 3), may repeat those coda types that distinguish themselves from the other whales in the unit as a means of effectively communicating individual identity.

Although the repetition of a variety of presumably equivalent signal types has been suggested to function in a few species in communicating intention or aggression (e.g. banded wren, *Thryothorus pleurostictus*; Molles and Vehrencamp 1999), as mentioned above, in the sperm whales studied here only a few coda types were repeated by whales. Thus while some songbirds may communicate aggression by repeating a variety of equivalent songs (i.e. 'staying on type'), the signal communicated by sperm whales is likely the coda itself rather than the repetition of a coda type. Instead, if a coda type represents a particular motivational or behavioural state, such as anger, affection, or isolation, repetition of that coda type might communicate an escalated intensity of that motivation or emotion. Moreover, if in representing a positive behavioural state, the production of a particular coda type induces the release of endorphins, whales might repeat that coda type to elevate and maintain their pleasurable experience. Similarly, if particular coda types represent social attachment to members in a social unit or clan, then production of those types may function, not specifically to advertize unit or clan affiliation, but to communicate affection for unit members, a behaviour that might generate opiate production and therefore encourage repetition of that coda type.

Ordering of Coda Types Between Whales

Just as Group of Seven sperm whales tended to repeat coda type '1+1+3' within the coda sequences, the only coda transition between whales in this unit that occurred more often than expected were matches of this coda type. This suggests that coda matching (like coda type repetition) is not a consequence of a general facilitative release mechanism and instead suggests that coda type '1+1+3' may play an important role in the communication system of this social unit. As in the Group of Seven, matches of one particular coda type ('2+1') were by far the most common coda type transition between whales in Unit T, both within and between overlapping exchanges. Although several coda transitions between whales in Unit T were not coda matches, only two other transition types within overlapping exchanges (and only one between exchanges) occurred significantly more often than expected when randomizing coda types within coda bouts (see Tables 5.5 and 5.6).

While call matching in some species can function in the localization of isolated or separated callers (Masataka and Symmes 1986; Okayasu 1987; Sugiura 1998), given the overlapping structure and social contexts of coda matching in sperm whales, it seems most likely that this behaviour plays a role in affirming social relationships (Chapter 4). Moreover, if particular coda types act to advertize unit or clan affiliation, then matching those particular coda types either within or between overlapping exchanges may function to confirm mutual clan affiliation with other unit members and therefore solidify social bonds between them. Conversely, if those coda types were to represent cooperation or kinship with unit members, then the matching of those coda types between whales, as with the repetition of types within individuals' sequences, might potentially be opiate-inducing, generate positive feelings of inclusion, and therefore encourage further matching and repetition of those codas. As a result, the high proportion of particular coda types in the coda repertoires of a social unit might not be an adaptation to advertize clan affiliation but rather a byproduct of the repetition and matching of specific coda types that function in social bonding within the unit.

Turn-taking

Several species of animals, including pygmy marmosets (*Callithrix pygmaea;* Snowdon and Cleveland 1984), European starlings (*Sturnus vulgaris*; Chaiken 1990), Pinon jays (*Gymnorhinus cyanocephalus;* McArthur 1982), cliff swallows (*Hirundo pyrrhonota*; Beecher et al. 1985), quail (*Colinus virginianus*, *Lophortyx californicus*, and *L. gambelii*; Stokes and Williams 1968), Japanese greater horseshoe bats (*Rhinolophus ferrumequinum nippon*; Matsumura 1981), and bowhead whales (*Balaena mysticetus*; Clark et al. 1986), appear to exhibit antiphonal vocal exchanges between members of a pair or group seeking to establish or maintain contact. Alternating vocalizations may improve selectivity in connecting a signaler and receiver (Schleidt 1973) and the avoidance of acoustic overlap may prevent signal information (Stokes and Williams 1968), particularly location information (see Marler 1959), from being masked. Antiphonal vocal exchanges are thus thought to function, at least in these species, as a means of maintaining acoustic contact with social affiliates in a noisy environment. For example, pygmy marmosets appear to have a conversational rule system that results in non-overlapping turn-taking, a mechanism that likely functions in keeping social affiliates aware of each other's locations while foraging out of sight of one another (Snowdon and Cleveland 1984). Likewise, the fact that European starling parents engage in antiphonal calling exchanges with their nestlings when separated from them but not during feeding periods in the nest, again suggests that antiphonal calling functions to permit exchange participants to monitor the locations of one another (Chaiken 1990). However, because individuals in some animal species, such as humans and squirrel monkeys, engage in antiphonal turn-taking primarily when in close proximity to one another, this vocal behaviour might function in intimate contexts in the establishment and maintenance of social relationships (Symmes and Biben 1988) and/or the exchange of information.

In contrast to the turn-taking described in the species above, the results of the permutation tests conducted on sperm whale coda production indicate that sperm whales in these social units do not generally wait for another individual to produce a coda before producing another coda itself, indicating that female sperm whales do not engage in conversational turn-taking in their coda exchanges. Furthermore, given the tendency for sperm whales to overlap the codas of other unit members and thus acoustically obscure both the preceding and responding codas (see Chapter 4), it seems highly unlikely that coda exchanges function in the transfer of factual information, as in the conversations of humans. Moreover, given both the overlap of codas in exchanges and the relatively close proximity of some whales in coda exchanges (see Chapter 8), it seems unlikely that coda exchanges function in the positional monitoring of social affiliates. Nevertheless, while Symmes and Biben (1988) suggest that conversational turn-taking in squirrel monkeys functions in the maintenance of social relationships, there is no reason why the overlapping non-antiphonal coda exchanges observed between close sperm whales cannot also serve a similar purpose. Instead of bonding occurring via the alternation of signal and response, however, bonding in sperm whales more likely occurs by the participation in duet-like sequences of overlapping coda exchanges.

CONCLUSIONS AND FUTURE RESEARCH

This analysis of sperm whale coda production using information theory and permutation tests has revealed that the communication system of this species, or at least of the social units studied here, is relatively less complex than it appears at first glance. Within the coda repertoires of these social units, a few coda types were produced very often while other coda types were produced only rarely, resulting in coda repertoires that are relatively unified or redundant and thus possess little communication capacity when compared to the vocal repertoires of humans and bottlenose dolphins. In contrast, the coda repertoire of the studied calf appeared to be relatively more diverse than that of the older animals as a whole, which may be a result of babbling behaviour similar to that observed in the infants of other species. A larger sample of calf codas would be useful to confirm the higher coda diversity of calf repertoires.

The redundancy in the coda repertoire of the Group of Seven social unit was perhaps an outcome of the observed tendency for whales to repeat particular coda types in sequences and match one another within and between overlapping exchanges, a behaviour also observed in the vocal exchanges of whales in Unit T. I suggest that the affinity for repeating or matching particular coda types within a unit might play a role in social bonding between unit members and perhaps function in broadcasting and/or reaffirming clan affiliation.

Finally, the lack of antiphonal turn-taking in sperm whale recordings suggests that sperm whale exchanges do not function in the transfer of factual information or in the maintenance of contact between individuals. Instead, given the social context of these exchanges and the tendency to overlap and match the codas of unit members, these exchanges most likely function in the establishment and reaffirmation of social relationships between vocalizing individuals.

Although this analysis provides a preliminary indication that sperm whale coda production is largely repetitive with little capacity for the transfer of complicated information, the analysis of larger data sets of individuals' coda sequences would allow the conclusive confirmation of these findings as well as permit the investigation of the presence of higher entropic orders in the sequential production of codas. Moreover, the collection of the coda repertoires from a variety of different individuals would permit the comparison of Zipf's slopes between different age and sex classes and so improve our understanding of the ontogenetic development and function of coda repertoires. Even so, despite the need for large amounts of codas to examine the finer complexities of coda communication, the capability to answer such research questions is now entirely possible given my finding that codas can quite easily be assigned to individuals within a recording. As a result, progress in this field is only limited by the collection of usable data sets and the time and resources available to analyze them.

Moreover, it should be added that even though the findings presented here suggest that there is no syntactic organization to the types of codas produced by sperm whales, research on other aspects of coda communication (e.g. absolute coda length, number of clicks in codas) and non-vocal communication could still reveal syntactic rules and suggest a higher capacity for communication than suggested here for coda types.

CHAPTER SIX

DIFFERENTIAL RATES OF CODA PRODUCTION OF INDIVIDUALS IN A WELL-STUDIED SPERM WHALE SOCIAL UNIT

INTRODUCTION

Different rates of vocal production between individuals within a species often result from the differential use of particular vocalization types by different age and sex classes (e.g. Bowyer and Kitchen 1987). As a result, observed differences in vocal rates that correlate with gender and/or age are often used by researchers to determine the presumed function of a vocalization type in a species. For example, because only male California gnatcatchers (*Polioptila californica*) produce 'churr' calls, it is believed that this vocalization serves a function in this species specific to males, such as mate attraction, the facilitation of nesting, or pair-bond maintenance (Preston et al. 1998). Likewise, because only infant European badgers (*Meles meles*) produce 'wails', it is hypothesized that these vocalizations provide a function that is specific to this age class (Wong et al. 1999).

However, individual animals may also produce the same call types at different rates, even within age and sex classes, such that variation in calling can be indicative of the function of the signal, depending on the identity, context, and behavioural state of the caller. Higher rates of vocal production can serve as an intensified form of the intended signal, indicating escalated levels of hunger (e.g. Leonard and Horn 2006), aggression (e.g. Falls 1969; Hau et al. 2000), anxiety (e.g. Marler et al. 1992), dominance (e.g. Tobias et al. 2004), or sexual states (e.g. Wetzel and Kelley 1983). For example, in the South African clawed frog (*Xenopus laevis*), sexually active males use vocal dominance to suppress the advertizement calling of other males, thereby distinguishing the vocally dominant frog from competitors and attracting gravid females (Tobias et al. 2004). Measuring differences in individual calling rates, however, is often more difficult than observing differences in call type production between age and sex classes due to the increased necessity to assess the vocal behaviour of individual animals rather than general classes. As a result, although the functions of gender-specific and class-specific calls may seem apparent for a species, the specific roles of calls within or across those classes may be uncertain without information on the rates at which individuals produce those calls.

Communication between conspecifics in social species may be particularly important in maintaining group cohesion and mediating social dynamics. In the African elephant (*Loxodonta africana*), adult females and their immature offspring live in matriarchal families, which combine with related families to form larger social units (Laws et al. 1975; Moss and Poole 1983; Poole et al. 1988). Consequently, because adult females display a more extensive vocal repertoire than males (Poole 1994), these calls likely play some role specific to female social behaviour such as communication with males, group coordination, reproduction, social bonding, or the mediation of social relationships (Poole 1994). However, while studies of the vocal rates of different social groups have found that vocal production increases with group size (Payne et al. 2003), because of the difficulty in assigning low-frequency elephant 'rumbles' to individuals (Payne et al. 1986) little information is available concerning the relative calling rates of individuals within a social group (but see Table 1 in Soltis et al. 2005a). As a result, although it has been suggested that elephant groups with older matriarchs have increased fitness due to the social knowledge of elder females (McComb et al. 2001), there is currently no information as to whether the matriarch vocalizes more often than other elephants in a social unit, thereby asserting dominance or conveying social knowledge (or ecological wisdom) to the group.

Likewise, our understanding of the communication system of the sperm whale (*Physeter macrocephalus*), an animal that exhibits a similar social structure (Weilgart et al. 1996) and sexual segregation in communication signals (Marcoux et al. 2006) to the elephant, also suffers from a lack of information on individual calling rates. Female sperm whales and immature animals of both sexes live in small social units (Christal et al. 1998; Whitehead et al. 1991; Whitehead and Weilgart 2000), and the production of codas (short stereotyped patterns of broadband clicks) is almost entirely dominated by adult females (Marcoux et al. 2006), suggesting that codas function in mediating social interactions between females. However, due to the difficulty of identifying the vocalizations and thus vocal rates of individual sperm whales, it is still unknown whether whales in social units produce codas at equal rates or whether particular animals are more vocal than others. While an analysis of the sizes of vocalizing sperm whales within a single social unit demonstrated that codas were produced by a variety of differently-sized animals, indicating that more than just one whale was vocalizing (Rendell and Whitehead 2004), it is difficult to compare the relative rates of coda production by different whales without knowledge of which whale produced which vocalizations.

The purpose of this study was to examine the rates of coda production by individual sperm whales in a well-studied social unit. I assigned recorded codas to individuals based on the similarity of their coda click and usual click IPIs (see Chapter 2) and used permutation tests to determine whether particular individuals vocalized more often than expected.

METHODS

A social unit of seven sperm whales (five adult females, one juvenile male, and one male calf) was observed for a total of 41 days between January 16 and March 26, 2005 off the coast of Dominica. This unit was termed the 'Group of Seven' (Gero 2005). The sexes and genetic relationships of these individuals were determined by genetic analysis using sloughed skin (see Gero et al. submitted). I made 15 recordings of this unit when codas were heard as well as recordings of their usual clicks (i.e. echolocation clicks) when solitary whales fluked at the start of a foraging dive (see Chapter 2). Recordings were made from a towed hydrophone and recorded on a Fostex VF-160 multi-track recorder (see Chapter 2) and labeled numerically according to month, day, and session of the day (e.g. #020703 was the third recording made on February 7th). Recordings were analyzed using Rainbow Click software (see Gillespie 1997; Leaper et al. 2000; Rendell and Whitehead 2004) and the IPIs of usual clicks and coda clicks were calculated using routines custom-written in MATLAB® (version 6.1; MathWorks Inc. 2001) and detailed elsewhere (see Chapter 2). Individual whales were identified as present during the time of recording using photo-identification of their flukes, or dorsal fin as in the case of the calf (see Gero 2005). The codas recorded of this unit were previously assigned to individuals based on the similarity of coda and usual click inter-pulse intervals (see Chapters 2 and 3).

Because I did not record all the time that animals were observed during the study period (cf. Soltis et al. 2005a) and did not record at regular sampling intervals, I could only compare the relative rates with which individuals produced vocalizations in these opportunistic recordings of different lengths. To determine whether a whale produced relatively more or less codas in recordings than expected (given the number of recordings for which it was present and the rates of coda production within each recording), I used permutation tests (see Manly 1997) that randomly reassigned the numbers of codas produced by whales within recordings, thereby keeping constant both the number of recordings in which each whale was present and the total number of codas produced in each recording (see Figure 6.1). Two recordings, although used in the analysis of individual repertoires (see Chapter 3), were excluded from this analysis of the relative rates of coda production. One recording (#030614) was excluded because only one whale was present at the time of the recording, thereby prohibiting tests of the relative rates of vocal production. Another recording (#021802) was excluded because a whale was present at the time of recording that was not photographed or visually identified, thereby precluding the certain assignment of particular codas to the identified whales. I used custom-written routines in MATLAB® to compare the observed mean number of codas produced by each whale in recordings for which it was present to the expected mean in 10,000 permutations. To control for recordings that may have high overall rates of coda production, I also repeated these permutation tests using the percentage of codas produced by a whale in a recording rather than the number of codas produced by a whale in a recording.

Whale I.D. number

Recording	#5703	#5727	#5130	#5563	#5722	#5561	#5560
012301	12	6		32		24	27
012601	0	9					
020101			22				23
020205			6			3	
020302	0	1				21	18
020703	0		4				5
020704		0	3				13
021101	0				2		
021501	0		1		7		
021705		0				7	11
022702	0				7	0	
030202		0					4
030901	0				20	7	
TOTAL	**12**	**16**	**36**	**32**	**36**	**62**	**101**
AVERAGE	**1.5**	**2.7**	**7.2**	**32.0**	**9.0**	**10.3**	**14.4**

Whale I.D. number

Recording	#5703	#5727	#5130	#5563	#5722	#5561	#5560
012301	27	6		12		24	32
012601	0	9					
020101			23				22
020205			6			3	
020302	21	1				0	18
020703	0		4				5
020704		0	13				3
021101	0				2		
021501	1		0		7		
021705		0				7	11
022702	0				0	7	
030202		4					0
030901	0				20	7	
TOTAL	**49**	**20**	**46**	**12**	**29**	**48**	**91**
AVERAGE	**6.1**	**3.3**	**9.2**	**12.0**	**7.3**	**8.0**	**13.0**

Figure 6.1. Depiction of a single permutation, randomizing the number of codas produced by each whale within a recording. The permutation maintains the number of codas produced within a recording and the number of recordings for which each whale was present. The numbers in the tables represent the number of codas in each recording assigned to each whale that was present at the time of recording. The total number and average number of codas produced by each whale over all the recordings for which it was present were calculated for both the observed data (on the left) and the randomized data (on the right).

RESULTS

When all the whales in the unit were included in the analysis, the calf (whale #5703) and juvenile (whale #5727) produced fewer codas in recordings than expected (see Methods) while its mother (whale #5722) and another female (#5560), the suspected mother of the juvenile male, produced more codas in recordings than expected (see Table 6.1). Moreover, even when the calf's mother was excluded, the calf produced fewer codas than expected (Observed mean = 2 codas/recording; Expected mean = 6.9 ± 2.5 codas/recording; *P* = 0.0452).

Table 6.1. The number of codas produced by each Group of Seven whale in each recording for which it was present. Also presented are the total and average number of codas produced by each whale, the expected average over 10,000 permutations, and the *P*-value for the difference between the observed and expected. Significant *P*-values are in bold and denoted by an asterisk.

Whale identification number

		#5703	**#5727**	**#5130**	**#5563**	**#5722**	**#5561**	**#5560**
	Recording	**Calf**	**Juvenile**					
	012301	12	6		32		24	27
	020101			22				23
	020205			6			3	
	020302	0	1				21	18
	020703	0		4				5
	020704		0	3				13
	021101	0				2		
	021501	0		1		7		
	021705		0				7	11
	022702	0				7	0	
	030202		0					4
	030901	0				20	7	
	TOTAL	**12**	**16**	**36**	**32**	**36**	**62**	**101**
	OBS. AVG	1.5	2.7	7.2	32.0	9.0	10.3	14.4
	EXP. AVG ± S.D.	6.6 ± 2.2	8.0 ± 2.7	7.6 ± 1.4	20.2 ± 9.7	3.7 ± 2.4	8.7 ± 2.8	9.9 ± 2.2
	P	**0.0074***	**0.0439***	0.892	0.203	**0.0195***	0.581	**0.0272***
Excluding Calf	OBS. AVG		1.4	7.2	32.0	11.3	10.3	14.4
	EXP. AVG ± S.D.		9.8 ± 3.0	8.2 ± 1.3	22.3 ± 9.8	7.0 ± 2.7	10.5 ± 2.7	10.8 ± 2.1
	P		**0.0042***	0.5258	0.2533	0.1246	0.9032	0.0562
Excluding Juvenile	OBS. AVG			7.2	32.0	11.3	10.3	16.2
	EXP. AVG ± S.D.			8.7 ± 1.2	27.6 ± 3.3	7.0 ± 2.7	13.0 ± 1.4	15.2 ± 1.1
	P			0.2706	0.3287	0.1239	0.0523	0.3848

When the calf was excluded from the analysis, the juvenile male (whale #5727) still produced fewer codas than expected but the calf's mother and whale #5560 did not produce more codas in recordings than expected (see Table 6.1). Finally, when limiting analysis to just the adult females, the hypothesis that all whales produced codas at the same rate was not rejected (see Table 6.1). When I repeated these tests but used percentage of total coda output produced by each whale in a recording instead of absolute number of codas, the results were qualitatively identical except that when the calf was excluded, not only did the juvenile still make fewer codas than expected but its most likely mother, whale #5560, made a greater percentage of the codas in recordings than expected (*P* = 0.0093).

DISCUSSION

These results confirm previous findings that adult females produce the majority of codas within a sperm whale social unit (Marcoux et al. 2006). Of the 283 codas made in the 13 analyzed recordings (excluding the calf), the adult females produced 94.3% of the recorded codas, a number that corresponds well with the finding by Marcoux et al. (2006) that adult females made 95% of codas in analyzed recordings. Moreover, the findings presented here also suggest that sperm whale calves are relatively quiet compared to other whales in the social unit. In the unit studied off Dominica, the calf produced far fewer codas than expected, apparently silent in 7 of the 8 recordings for which it was present. This demonstrates, as suggested by Marcoux et al. (2006), that adult females are more vocal in sperm whale social units than are younger animals. Although the automated IPI-analysis routines used by Marcoux et al. (2006) discarded codas with click IPIs less than 2 msec - thereby excluding the codas of calves (body length < 7.7 m) - it seems likely given their findings for juvenile whales, that had they analyzed coda clicks with small IPIs that they would have also found that calves produced relatively few codas.

While the calf and juvenile were relatively quiet in recordings, the calf's mother and the likely mother of the juvenile male (whale #5560) were relatively vocal in the recordings for which they were present. This finding, however, was a result of the relatively low rates of vocal production of their offspring since the exclusion of the calf and juvenile respectively reduced the average rates of coda production of the calf's mother and the juvenile's mother to levels that were not significantly different than those of the other adults. Moreover, given that the calf and juvenile produced relatively fewer codas than other whales even when their mothers were excluded, it is clear that the relative silence of these two whales compared to the adults was not solely a result of being in recordings with their mothers.

The fact that the calf and the juvenile produced codas at relatively lower rates than the adult females suggests that codas play a different role in adults than they do in the younger animals in this unit. This was also apparent when I examined the rates of coda overlapping between whales in this unit (see Chapter 4). While most of the adults in the unit engaged in overlapping exchanges with other adults more often than expected (see Chapter 4), the calf and juvenile did not. This suggests that the higher rates of coda production in adult females might function to permit the overlapping of codas between whales. Alternatively, the relatively higher rates of coda production observed in adult females could be a result of their participation in coda overlapping exchanges.

As discussed in Chapter 4, the function of coda overlapping is likely to reaffirm social bonds between individuals, a purpose that is seemingly unnecessary for the male juvenile or male calf in this unit. If codas function to permit overlapping to solidify social bonds, it is perhaps not surprising that male whales, which leave the social unit at around the age of six to form bachelor schools with other males (Whitehead and Weilgart 2000), do not engage in coda overlapping with adult females. A lack of necessity to bond with other whales via overlapping exchanges may thus explain the relative silence of the two males in this unit. To examine this bonding hypothesis further, it would be useful to study the rates of coda production in a unit with a female juvenile, which presumably will remain with her natal unit, to determine whether her vocal behaviour differs from that of the juvenile male observed here and involves overlapping exchanges with adult females.

The fact that the calf and juvenile produced codas at all and did not remain completely silent suggests that codas do have a function for these whales, although likely not to reaffirm social bonds with adult females by means of coda overlapping. As discussed in Chapter 3, the male calf produced a coda type repertoire that is different than those of the other whales and does not include the most common coda types in the unit repertoire, suggesting that coda production by the calf functions to permit individual identification in the unit. Moreover, the diversity of coda types produced by the calf could indicate that its coda production represents babbling, a behaviour observed in the young of other species (see Chapter 5).

In contrast to the calf, the coda type repertoire of the juvenile male is not significantly different from that of the adult females and is largely comprised of the two most common coda types of the social unit (Chapter 3). This suggests that coda production by the juvenile functions not to communicate individual identification but perhaps clan affiliation, a behaviour that is perhaps not required to occur often while socializing within one's social unit.

When the calf and juvenile were excluded, adult females produced codas at relatively equal rates, suggesting that adult females contribute equally to the coda production of a unit. Thus, while Freeberg (2001) and Tyack (2001) speculated that observed differences in coda repertoires between units might be an artifact of differences in coda production rates and repertoires between individuals, the equivalence in the rates with which adults produced codas in this unit and the general similarity in the coda repertoires of adults (see Chapter 3) suggest that recordings of social units represent a reasonable representation of the coda repertoire of the adults in the unit. Moreover, the lack of asymmetry in rates of coda production suggests that adults do not use vocal production to assert dominance (see Tobias et al. 2004) or aggression (see Falls 1969; Hau et al. 2000).

In conclusion, although all whales in the Group of Seven produced codas, the rates with which individuals produced them and the types that each whale produced provide information regarding their likely functions within the unit. Here, the higher rates of coda production by the adult females relative to the calf and juvenile, as well as the high rates of coda overlapping amongst adult females (Chapter 4) suggest that codas function amongst adult females in part to allow overlapping exchanges to occur between whales, most likely to solidify social bonds. In contrast, the lower rates of coda production by the calf and juvenile male, and the lack of coda overlapping exchanges involving the calf and juvenile, suggest that this function is not necessary for these whales and that codas serve some other function. In the case of the calf, its significantly different and diverse coda type repertoire suggests that it functions in individual identification or represents babbling behaviour. For the juvenile, its coda repertoire suggests that its codas function in communicating clan affiliation. Clearly additional research on the individual coda production rates of other units, particularly those with multiple calves and juveniles of different sexes will be useful in further understanding the functions of coda communication in this species.

CHAPTER SEVEN

A DYNAMIC PASSIVE ACOUSTIC ARRAY FOR STUDYING SPERM WHALE VOCAL BEHAVIOUR

The work presented in Chapter Seven also appears in:

Schulz, T. M., Whitehead, H., and Rendell, L. 2006. A remotely-piloted acoustic array for studying sperm whale vocal behaviour. Journal of the Canadian Acoustical Association 34: 54-55.

INTRODUCTION

A comprehensive understanding of vocal behaviour in a species requires knowledge of how individuals vocalize. Although studying the types and contexts of different vocalizations used by an animal population can provide some information on their function and use, a more detailed understanding of call function and the complexity of a species' communication system is not possible without knowledge of the way that vocalizations are exchanged between individual animals (Bradbury and Vehrencamp 1998). For example, variation in the vocal output of codas (short stereotyped click sequences) by sperm whales (*Physeter macrocephalus*) while socializing at the surface permits the allocation of social units into large, sympatric acoustic 'clans', which most likely result from the cultural transmission of vocal patterns (Rendell and Whitehead 2003b). Moreover, the tendency for units to preferentially socialize with other units of the same clan suggests that the clan represents a higher level of social structure (Rendell and Whitehead 2003b). However, without knowledge of the way that coda vocalizations are exchanged between individuals within a social unit, it is unclear whether coda production functions to identify members of the same social unit or clan, or if it serves some other communicative function. Furthermore, although sperm whales appear to produce codas within close proximity of one another (Watkins and Schevill 1977), the accuracy of previous findings is low. Therefore, the spatial scale of sperm whale coda exchanges and thus the likely function of these interactions are still unclear.

The difficulty in determining which individual in a group is vocalizing is a common problem in studying vocal communication in mammals that spend the majority of their time underwater (Costa 1993). While recent advances in the use of passive acoustic localization have provided important tools for studying the movement, foraging behaviour, and communication patterns of vocalizing marine mammal species (Miller and Tyack 1998; Hayes et al. 2000; Janik et al. 2000; Møhl et al. 2001; Miller et al.

2004), these systems do not easily permit the discrimination of vocalizations made by pelagic cetaceans in very close proximity to one another.

To study the vocal interactions between sperm whales socializing at the surface, I developed a dynamic acoustic array consisting of small, easily deployable remote-controlled vessels that can maintain array geometry around slow-moving or stationary whales. These remotely-piloted vessels (RPVs) log their GPS locations, collect acoustic signals, and transmit these signals to a research platform where they are simultaneously recorded. Subsequent synchronization and analysis of the GPS positions and acoustic recordings permit the *a posteriori* localization of vocalizations within and around the acoustic array.

METHODS

System Design

This localization system consists of several small RPVs (Figure 7.1) and one larger research platform from which they are launched. A 12-m auxiliary sailboat has been used previously as the primary research platform in field deployments (see Chapters 8 and 9). From the side of each recording platform is suspended a hydrophone (Vemco VHLF; frequency response: 200 Hz-20 kHz ±3dB; midband sensitivity: 147 dB re 1 V/μPa). On each RPV, acoustic signals from the hydrophone are amplified, high-pass filtered at 1 kHz, and broadcast by a FM transmitter (NRG Kits PLL PRO III). This signal is then received by a digital AM/FM PLL synthesized radio (SONY ICF-M260) onboard the deployment platform and digitally recorded on a multi-track recorder (FOSTEX VF-160; sampling rate: 44.1 kHz), which simultaneously records on separate tracks the acoustic signals detected by each of the hydrophones in the array.

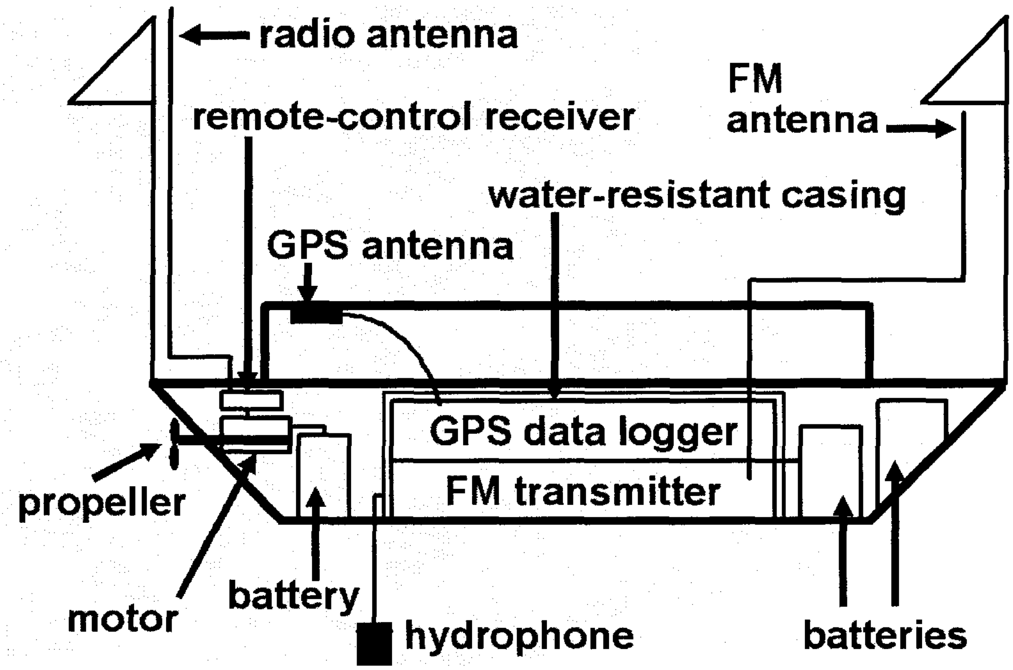


Figure 7.1. Schematic of a remotely-piloted vessel. Each vessel contains an instrument payload with a GPS receiver/logger and a FM transmitter, which broadcasts the acoustic data collected by the suspended hydrophone. For further explanation, see the text.

On each of the recording platforms, a GPS unit (Garmin GPS25-HVS) logs its position each second and saves the data (pseudorange and phase information) to a flashcard for later retrieval. A frequency shift keying (FSK) modulator transforms the stream of ASCII sentences from the GPS unit onboard the research platform to an amplitude-modulated tonal signal (see Møhl et al. 2001), which is recorded as an acoustic track on the multi-track recorder in synchrony with the hydrophone signals. Subsequent demodulation of the FSK timestamp during analysis allows for synchronization of the acoustic and positional data (Møhl et al. 2001).

Each RPV is 1 m in length, built of durable fiberglass by Scale Design Inc. (Barrie, Canada), and painted neon orange to improve its visibility while at sea. Coloured flags attached to plastic masts at the bow and stern of each RPV further improve visibility at sea, allow for visual discrimination between vessels at a distance, and provide a height for the attachment of the FM and remote-control antennas. Stainless-steel rings embedded in the bow and stern of the RPVs allow for easy deployment and retrieval using boat hooks. The motor and rudder of each RPV is powered by two 12-V batteries and controlled remotely by a radio transmitter onboard the deployment platform. The payload on each RPV (the FM transmitter, GPS receiver, and flashcard logger) is encased in a water-resistant housing and powered by an additional 12-V battery. The hydrophone on each RPV exits through the lid of the vessel and is attached to the hull so that it is suspended approximately 80 cm below the water surface.

On the deployment platform, the hydrophone is suspended over the side of the vessel approximately 80 cm below the water surface. The acoustic signal from this hydrophone is amplified and high-pass filtered at 1 kHz and fed directly to the multi-track recorder. The multi-track recorder is powered by a 12-V battery via a pure sine power inverter (PowerBright APS300) to minimize the detection of electrical noise on the sound recordings.

Deployment

In addition to the primary research platform, a minimum of two RPVs need to be deployed to localize a sound in two dimensions. Using boat hooks to lower the RPVs into the water, the vessels are deployed from the main platform around a group of socializing animals. The maximum array size possible with this system is limited by the range of the FM transmitters and is several hundred metres. Once deployed, the vessels can be piloted to establish and maintain favourable array geometry, provided focal animals are not moving too rapidly (approximately 1 knot). The maximum duration of a recording session (approximately 3 h) is limited by the length of time that the batteries powering the RPV payloads can last without requiring recharging. Estimates of sea surface temperature and salinity, obtained during deployment by a thermometer and refractometer, are used later in analysis to calculate the speed of sound. After the recording session, each deployed RPV is driven in turn alongside the research platform and recovered with boat hooks. The flashcards, containing GPS information, are retrieved from each payload and downloaded via a Compact Flashcard Reader to a laptop computer.

Analysis

In order to localize a vocalization detected on hydrophones in an acoustic array, one must have several pieces of information: the relative location of each recording platform when the sound was recorded, the time that the sound arrived at each recording platform, and the speed of sound in water. To localize a sound in two dimensions, the hydrophone receivers and vocalizing animal must all be at the same depth (Watkins and Schevill 1972).

Estimating the GPS positions of the recording platforms

The GPS information logged on each recording platform consists of two files: a text file containing the NMEA data and a binary file containing the phase data. The binary file is converted to a RINEX file and submitted to an online Precise Point Positioning processor (such as the Canadian Geodetic Service CSRS–PPP online processor) to improve the accuracy of the positions. Further exclusion of erroneous noise in GPS positions can be achieved by discarding fixes obtained by a low number of satellites and by independently smoothing the x-coordinates and y-coordinates for each GPS receiver by fitting quadratic equations to time segments spanning several seconds before and after each epoch in the record (see Christal and Whitehead 2001).

Thus, the position (x, y) of a receiver at a given second is estimated by quadratic regressions of the x- and y- coordinates of the neighbouring seconds on time (t):

$$x = a_1 + a_2t + a_3t^2 \tag{1}$$

$$y = b_1 + b_2t + b_3t^2 \tag{2}$$

Demodulation of the FSK timestamp (acoustic GPS output) recorded on the multi-track recorder allows the assignment of the GPS time to each second in the simultaneously recorded hydrophone tracks, thereby synchronizing the acoustic and positional data (Møhl et al. 2001). As a result, for a given vocalization recorded on each hydrophone, the GPS time and thus the GPS position of each recording platform at that moment are known.

Estimating time of arrival differences

When a sound is detected by several hydrophones, it reaches each hydrophone at slightly different times depending on the distance of each hydrophone from the sound source. It is these time-of-arrival-differences (TOADs) - along with knowledge of the relative positions of hydrophones and the speed of sound in water - that allow the determination of the most likely location of the vocalizing animal. Because sperm whales produce loud, abrupt, broadband clicks, TOADs are calculated as differences between hydrophones in the click onset, the time at which the click first becomes visible in the waveform of the recording.

Localization

Given the difference in the time of arrival of a sound at two hydrophones, the spatial distance between the two hydrophones, the speed of sound in water, and the assumption that the sound source and receivers are all at the same depth, a 2-D hyperbola can be calculated along which the vocalizing animal is expected to be positioned. The addition of a third hydrophone allows the calculation of three time differences (one for each hydrophone pair combination) and thus three hyperbolae, which intersect at the estimated location of the vocalizing animal. Because only two of the three TOADs are linearly independent, however, all three hyperbolae are expected to intersect at a single point. As a result, any imprecision in the intersection of these three hyperbolae represents localization error, particularly in estimating the time of arrival differences. The average of the three intersections provides the best estimate of the animal's location (see Janik et al. 2000). This localization method is similar to the MINNA (minimum number of receivers array) method described by Wahlberg et al. (2001) except that it repeats the MINNA method for each pair of intersecting hyperbolas and averages the intersections to give a solution that accounts for measurement error. The addition of a fourth hydrophone results in four possible hydrophone triads and thus a total of 12 hyperbolic intersections which can be averaged to estimate the animal's location while accounting for error (see Laurinolli et al. 2003).

Calibration

A series of calibration tests were conducted to determine the accuracy of this acoustic array. Three remotely-piloted vessels were deployed from a docked 40-foot sailboat and positioned so as to form a diamond approximately 25-50 m per side. Two metal pipes were suspended from a wood plank with a distance of 1.5 m between them and hung over the sides of an inflatable dinghy. The dinghy was rowed to the periphery of the array between two receivers and then rowed slowly through the centre of the array while a hammer struck the pipes in an alternating manner, thereby generating two loud sound sources of slightly different frequencies a known distance apart. The dinghy was than rowed to the periphery of the array very close to one receiver and one of the pipes struck in a repetitive manner. This was then repeated with the dinghy in an end-fire position outside of the array (i.e. directly in line with two receivers). Using measured sea surface temperature and salinity, the speed of sound in water was derived from the Leroy equation (Urick 1983). The sounds were recorded and localized by the method described above and the distances between localized bangs were compared to the known distance between pipes (either 1.5 m or 0 m). All acoustic analysis was conducted in a standard sound-editing program (Cool Edit, Syntrillium), a dedicated software package called Rainbow Click (see Gillespie 1997; Jaquet et al. 2001), and custom-written routines in MATLAB® (MathWorks). The TOADs, calculated as differences between hydrophones in bang onset, were calculated in Matlab routines written by Dr. Luke Rendell. The best estimate of each sound source position was calculated from the 12 hyperbolic intersections (that correspond to the four hydrophone triads) using Matlab routines written by myself and based on MINNA MATLAB® routines provided by Dr. Magnus Wahlberg.

The GPS data, once converted to RINEX format, were submitted to the CSRS–PPP online processor and subsequently processed in MATLAB® routines - written by myself - to provide the relative position of each receiver. To exclude erroneous jumps in positions, I omitted GPS fixes determined by less than 7 satellites. I also smoothed each GPS track using quadratic regressions for time segments spanning 60 s and 500 s on either side of each epoch for the RPVs and stationary research platform respectively. Averages of neighbouring x- and y- coordinates were used when gaps resulting from low satellite numbers prohibited quadratic regression.

RESULTS

Inside the array, the mean distance between the localized sound sources was 1.97 ± 0.3 m (*n* = 22), giving an overall mean absolute error of 0.48 m from the true distance (Figure 7.2). At the periphery of the array, this mean error increased to 0.83 ± 0.5 m (*n* = 7). The mean error for repeated bangs at the periphery of the array close to one receiver was 1.41 ± 0.8 m (*n* = 14), while the mean difference in localized positions of repeated bangs in the end-fire area (in line with two receivers) was 5.69 ± 3.6 m (*n* = 11).

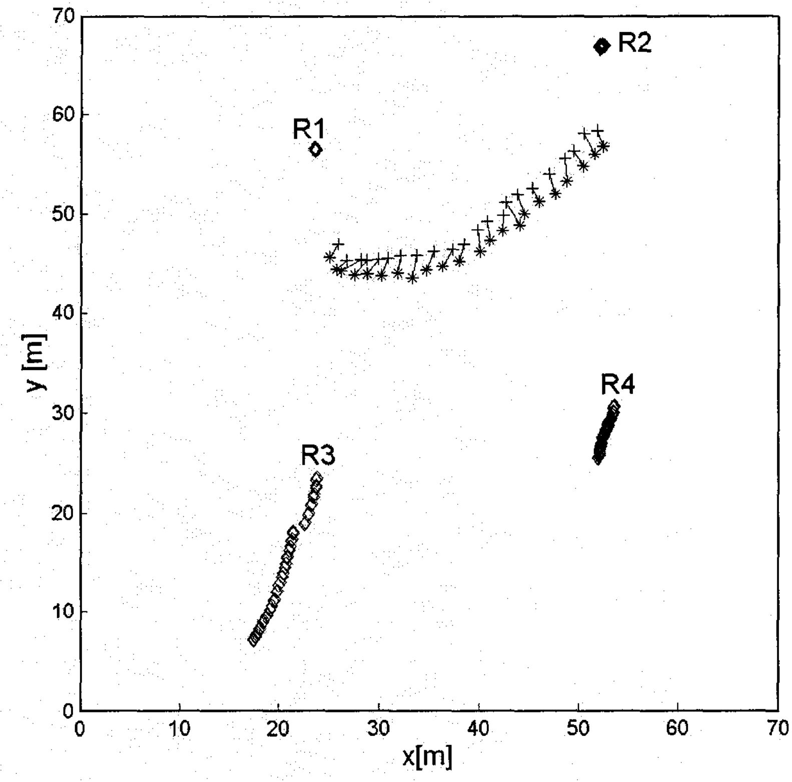


Figure 7.2. Calibrating localizations in a four-hydrophone array using three remotely-piloted vessels (R2-R4) and a stationary 40-ft sailboat (R1). The receiver positions throughout the calibration are represented in the figure by diamonds. During this calibration, two metal pipes a fixed distance of 1.5 m apart (represented here by × and ✳) were hung over the sides of a dinghy and struck with a hammer in an alternating manner as the dinghy was rowed through the array. The mean distance between the pipes as determined by acoustic localization (see text) was 1.97 ± 0.3 m (represented here by solid lines connecting the symbols representing the pipes). The GPS positions of the receivers in these localizations were smoothed by the methods outlined in the text.

The primary source of potential error with this localization system is the GPS positions of the hydrophone receivers. Despite processing the binary phase data with Precise Point Positioning software, erroneous jumps in GPS positions still resulted in positional error of approximately 6 m in both the x and y direction. When the described GPS improvement measures are not utilized, the mean distance between the localized sound sources inside the array was 4.16 ± 4.7 m (n = 22), giving an overall mean absolute error from the true distance of 2.67 m.

The utility of this acoustic array in studying sperm whales is proven by its successful field deployment around socializing sperm whales in the Sargasso Sea (see Chapters 8 and 9). Figure 7.3 shows the 2-D localization of nine codas produced by a sperm whale as it moved within the acoustic array towards the periphery. The certainty that the localized codas in Figure 7.3 were all produced by the same whale was confirmed by the fact that they all had calculated inter-pulse intervals of 2.95 msec (see Chapters 2 and 9).

DISCUSSION

This localization system was created to allow the recording and localization of individual sperm whales within a vocalizing and moving group and therefore permit a more thorough analysis of communication exchanges in this species than had been previously possible. The accuracy of this system, as determined by the calibration tests, is potentially high, about 0.5 m. As expected, the highest accuracy occurs for localizations in the centre of the array and the lowest accuracy occurs for localizations in an end-fire position outside the array (see Chapter 8 for location errors during field deployments).

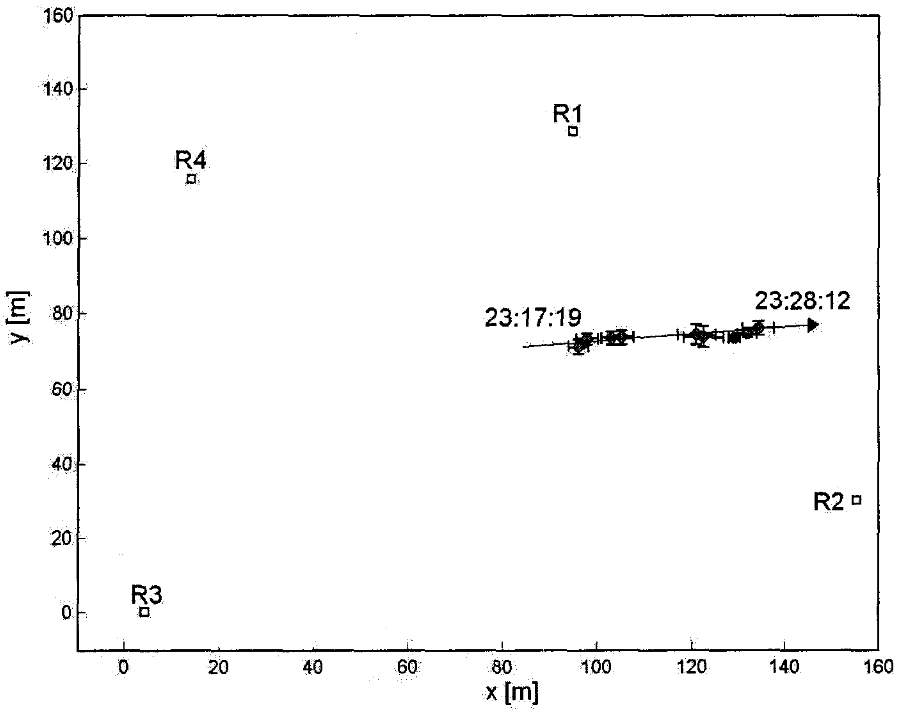


Figure 7.3. The GPS positions of four hydrophone receivers (R1-R4; □) and the estimated location solutions (•) for codas produced in a recording session on May 14th, 2005 in the Sargasso Sea. The error bars for each coda are the average zonal (ε_x) and meridional (ε_y) errors calculated from the standard deviation of the average location from the hyperbolae intersections for each click (see Chapter 9; Laurinolli et al. 2003). The arrow indicates the estimated direction of the vocalizing whale based on codas (inter-pulse intervals = 2.95 msec) localized between 23:27:19 and 23:28:12.

Despite the increase in error between localizations inside the array and those in the end-fire position, the estimated errors, both inside and outside of the array (relative to the array size), are less than those reported for other systems. Given the approximate array size of 40m per side, the estimated errors are approximately 1% and 14% the size of the array for within-array and end-fire localizations respectively. In comparison, in an array of drifting buoys in a triangle approximately 1.8 km per side, the reported errors relative to the size of the array are 4% inside the array and 32% outside the array (Hayes et al. 2000). Moreover, the within-array error of 0.48 m reported here is less than the 1 m error reported for a non-rigid array with a size of 30 m per side (Watkins and Schevill 1972). Because the array described here is similar in size to that used by

Watkins and Schevill (1972), it is assumed that the errors reported by Watkins and Schevill (1972) for localizations outside the array (25% of the maximum distance from the receiving hydrophones at a distance of 80 m and 50% at 300 m) are the maximum errors that would be experienced by this array at similar ranges.

An error of 0.48 m is more than acceptable in differentiating the coda vocalizations exchanged between sperm whales that are approximately 6.5 m (interquartile range: 3.9 -11.4 m) apart within a social cluster (Whitehead 2003a). However, assuming errors similar to those reported by Watkins and Schevill (1972) for whales vocalizing outside the array, the localization error at even 80 m from the array, while small enough to permit the differentiation of clicks made by different social groups, is too large to allow the confident differentiation of vocalizations made by different individuals located in close proximity to one another. Similarly, the estimated error of 6 m for sounds in end-fire positions complicates the differentiation of whales vocalizing in close proximity to one another in these regions. Therefore, the maintenance of favourable array geometry such that the vocalizing animals are either inside the array or very near it is extremely beneficial in reducing localization errors and allowing the attribution of vocalizations to specific whales in and around the array. Fortunately, the dynamic localization array described here is designed with the intention of addressing this problem and maintaining preferable array geometry by traveling with a group of slow-moving socializing sperm whales. Moreover, in combination with other techniques for assigning codas to individual whales (i.e. inter-pulse interval analysis; see Chapter 2), this array is useful in estimating the approximate distance between vocalizing whales, even when one whale in an interacting pair is located outside of the array (see Chapter 8).

Although previously described acoustic localization methods have proven useful in localizing marine mammals in a number of different contexts, each faces difficulties in studying the vocalizations of individual sperm whales moving in the open ocean. For example, the moored acoustic array designed by Janik et al. (2000), while practical in studying the exchange of coastal bottlenose dolphins whistles, is immobile and thus obviously only usable in the study of animals in a confined bay, lagoon, or cove. In the open ocean, Møhl et al. (2000, 2001) localized individual sperm whales several kilometres apart using a large-scale array consisting of several vessels. While this approach could certainly allow the maintenance of favourable array geometry around a group of moving sperm whales, the surrounding of a socializing whale group by several vessels may interfere with their natural behaviour. Furthermore, it is often impractical and economically unfeasible to employ several manned vessels in offshore waters for weeks at a time. Instead, the array described here, comprised of small battery-operated remotely-piloted vessels, presents little disturbance to socializing sperm whales and can be stored on and easily deployed from a relatively small research vessel, thus making this research logistically and economically viable.

The localization system proposed by Hayes et al. (2000), which utilizes independent sound-recording buoys in a drifting array, is likewise minimally invasive to both the environment and study animals and can be stowed on and deployed from small research vessels. The inability to control the movement of the drifting buoys once deployed, however, limits that system's capacity to travel with the whales and maintain favourable array geometry without the time-consuming retrieval and redeployment of the buoys. Furthermore, because the acoustic recordings are not acquired until after the buoys are recovered, it is impossible to determine during deployment if recording components are functioning properly or if the acoustic recorder is overloading. During field research, I found the ability to monitor and adjust the acoustic signal of each hydrophone throughout a deployment to be extremely useful in maintaining and improving sound recording quality.

Finally, while the towed beam-forming array developed by Miller and Tyack (1998) has proven to be extremely beneficial in studying the individual acoustic output of free-ranging killer whales, it only provides a bearing to the animals and the required distance between vocalizing whales (20 m at a 100 m distance from the array, 11° azimuthal separation) is too large to confidently assign codas to neighbouring sperm whales within a cluster. Rather, an array of several independent hydrophone receivers is required to localize sperm whales at accuracy great enough to allow individual discrimination.

Despite the discussed advantages of the dynamic acoustic array described here, there are also problems with this system. Although using FM frequencies to transmit sound signals is not a problem when conducting field research in the Sargasso Sea and other offshore areas, interference with local radio stations and requirements for licensing permits can restrict their use in coastal areas. And although the RPVs are capable of maintaining their positions around slow-moving whales in calm conditions, high winds, rough weather, or sperm whales traveling at speeds greater than 1.0 knot can make it difficult for the RPVs to maintain favourable array geometry. Faster, more powerful RPVs would thus be highly beneficial in keeping pace with the whales and permitting acoustic observation at the individual level during a variety of behavioural states. The vessels themselves, however, are highly robust and have been successfully deployed in conditions up to upper Beaufort Force 3. Finally, although smoothing of the GPS tracks improves accuracy of relative receiver positions and thus sound localization relative to the array, higher quality GPS receivers or a differential base station onboard the research platform could improve GPS accuracy to permit sound localization on a finer scale.

Nonetheless, this dynamic acoustic localization system has proven to be a useful tool in studying the vocalizations of individuals within groups of pelagic cetacean species and has recently been used to study the distance between sperm whales engaging in vocal exchanges (see Chapter 8) as well as the off-axis effects of sperm whale coda clicks (see Chapter 9).

CHAPTER EIGHT

USING PASSIVE ACOUSTIC LOCALIZATION TO ESTIMATE THE DISTANCE BETWEEN SPERM WHALES MAKING OVERLAPPING CODA EXCHANGES

INTRODUCTION

Animals exchange vocalizations with conspecifics to serve a number of different functions, including kin recognition (Gouzoules and Gouzoules 1990; Collins et al. 2005), mate attraction (Gerhardt et al. 2000), social bonding (Geissmann 1999), group cohesion (Miller et al. 2004), and territory defense (Hyman 2003). And while even within a given species vocal exchanges in different contexts and between different individuals can function in very different ways, studying the distance between vocalizing animals can often reveal information concerning the specific function of each type of vocal interaction.

This is particularly true for exchanges between conspecifics in mated pairs, social groups, or family units, for which there is usually less conflict of interest between individuals. For example, members of social groups or mated pairs separated by distance or by a visually dense environment often engage in loud vocal exchanges presumably to localize one another and maintain contact with the group (Snowdon and Cleveland 1984; Lamprecht et al. 1985; Miller et al. 2004). Loud vocal displays between pair-bond members in close proximity to one another, however, likely do not serve a localization function but are instead thought to play a role in the advertizement of joint territory defense (Hall and Magrath 2000) or of the bond between the calling animals (Haimoff 1984; Geissmann 1999), although they may also function to maintain or strengthen the pair bond (Armstrong 1973; Farabaugh 1982; Geissmann 1999; Geissmann and Orgeldinger 2000; Rogers et al. 2006). In contrast, low-amplitude vocal exchanges between pair-bond members likely disqualify an advertizing function and instead might indicate that they strengthen the pair bond or function in the exchange of information between vocalizing animals to the exclusion of eavesdroppers (Todt et al. 1981; Morton and Derrickson 1996). By examining the amplitude of vocal output and spatial arrangement of individuals engaged in vocal exchanges, researchers can gain insight into the probable function of the vocal interactions between social animals.

Sperm whales are highly social cetaceans that produce loud, stereotyped patterns of broadband clicks termed 'codas', which are generally produced during social periods at or near the water surface (Watkins and Schevill 1977). While male sperm whales leave their natal social unit at approximately age 6 to form bachelor schools with other males (Whitehead and Weilgart 2000), females tend to remain with their mother, forming highly stable (Whitehead et al. 1991; Whitehead and Weilgart 2000) and largely related - but not strictly matrilineal (Christal et al. 1988; Mesnick 2001) - social units of adult females, calves, and juveniles. The patterns of codas produced by sperm whales can be classified into discrete coda types (Weilgart and Whitehead 1993), which are generally shared among animals within social units (Chapter 3; Rendell and Whitehead 2004). Since social units demonstrate a preference to socialize and form larger, but temporary, social groups with units possessing similar coda dialects, coda repertoires have been suggested to function in the advertizement of a unit's affiliation to a higher social order, the 'acoustic clan' (Rendell and Whitehead 2003b).

Sperm whales do not produce codas erratically. Instead, they tend to produce them with temporal regularity and often engage in successive overlapping and type-matching coda exchanges with fellow social unit members (see Chapter 4). Previous research on two geographically disparate sperm whale units revealed that individual sperm whales tend to produce codas at regular intervals approximately every 3-5 s (Chapter 4). As a result of this temporal regularity in coda production, whales appear capable of coordinating their vocal output with other individuals, resulting in duet-like chains of overlapping coda exchanges (Chapter 4). While the overlapping nature of these exchanges suggest that they might function in social bonding (see Chapter 4), the fact that sperm whale coda clicks are apparently extremely loud (~190 dB//1 μPa;

P. Madsen, pers. comm.[3]) suggests that codas might function to maintain contact between separated whales or to broadcast information - such as clan affiliation - to eavesdroppers. However, because the distance between individuals within an encountered sperm whale group can vary (Best 1979; Whitehead 2003a), conclusions concerning the function of overlapping exchanges are limited without knowledge of the spatial scale at which these vocal interactions occur. If these exchanges do not occur between individuals immediately adjacent to one another but only between whales several hundred metres apart, then one might conclude that coda interactions serve a function in the coordination of group movement. Conversely, if coda exchanges only occur between individuals in close proximity to one another, then it could be assumed that they do not function in localization or group cohesion but instead in social bonding or in the advertizement of clan or pair affiliation.

Unfortunately, due to the difficulty of assigning vocalizations to free-ranging cetaceans (Costa 1993), knowledge of the spatial scale of sperm whale coda exchanges within social groups is limited. Although Watkins and Schevill (1977) reported that two sperm whales localized using a 3-D array exchanged codas from the same relative direction from the array, the whales were estimated to be approximately 1 km from the array and beyond the potential limits of precision for the system; a previous calibration of the array reported an error of 50% at 300 m from the array (Watkins and Schevill 1972), indicating that at a range of 1 km from the array it would be difficult to determine whether the whales in overlapping exchanges were several metres or several hundred metres apart. Therefore, to improve our understanding of the function of sperm whale coda overlapping exchanges, I used a dynamic passive acoustic localization system (see Chapter 7) to localize the codas of whales and estimate the distance between interacting individuals.

METHODS

Field Methods

The fieldwork for this research was conducted between May 5 – June 20, 2004 (38 days effort) in international waters between Bermuda and the east coast of the United States in the Sargasso Sea. Sperm whales encountered during this period were tracked visually during the day and acoustically at night using a directional hydrophone (see Whitehead and Gordon 1986). During the day, if whales at the surface were moving slowly (< 1 knot) and the weather conditions were favourable, the dynamic acoustic array described in Chapter 7 was deployed with the goal of attaining favourable array geometry around the observed whales.

Dynamic Acoustic Array

As described in Chapter 7, the acoustic array consisted of three small RPVs and one larger research platform, a 12-m auxiliary sailboat, from which the RPVs were deployed. Boat hooks were used to lower and raise the RPVs from the research platform during deployment and retrieval. An omnidirectional hydrophone (Vemco VHLF; frequency response: 200 Hz-20 kHz ± 3dB; midband sensitivity: 147 dB re 1 V/µPa) was suspended approximately 80 cm below the water surface from the side of each RPV.

On each RPV, acoustic signals from the hydrophone were amplified, high-pass filtered at 1 kHz, and broadcast by a FM transmitter (NRG Kits PLL PRO III). This signal was then received by a digital AM/FM PLL synthesized radio (SONY ICF-M260) onboard the deployment platform and digitally recorded on a multi-track recorder (FOSTEX VF-160; sampling rate: 44.1 kHz), which simultaneously recorded on separate tracks the acoustic signals detected by each of the hydrophones in the array. Recording sessions were labeled numerically according to month, day, and session of the day (e.g. #051403 was the third recording session on May 14th).

On each of the recording platforms, a GPS unit (Garmin GPS25-HVS) logged its position each second and saved the data (pseudorange and phase information) to a flashcard for later retrieval. A frequency shift keying (FSK) modulator transformed the stream of ASCII sentences from the GPS unit onboard the research platform to an amplitude-modulated tonal signal (see Møhl et al. 2001), which was recorded as an acoustic track on the multi-track recorder in synchrony with the hydrophone signals.

On the deployment platform, the directional hydrophone used in the tracking of whales at night (depth ~1 m) was also used in the recording of sperm whale clicks during array deployment. The acoustic signal from this hydrophone was amplified and high-pass filtered at 1 kHz and fed directly into the multi-track recorder. The multi-track recorder was powered by a 12-V battery via a pure sine power inverter (PowerBright APS300) to minimize the production of electrical noise on the sound recordings.

During the deployment of the array, the locations of the RPVs and whales relative to the primary research platform were recorded on a digital camcorder (SONY DCR-PC 105) from the sailboat's crow's nest. Sea surface temperature was measured using an onboard electronic thermometer and sea salinity was estimated using a refractometer.

Data Processing and Acoustic Localization

The binary file logged from each GPS receiver was converted to a RINEX file and submitted to an online Precise Point Positioning processor (Canadian Geodetic Service CSRS–PPP) to improve the accuracy of the positions. Further exclusion of erroneous noise in GPS positions was achieved by discarding fixes obtained by fewer than 7 satellites and by independently smoothing the x-coordinates and y-coordinates for each GPS receiver by fitting quadratic equations to time segments spanning 15 s before and 15 s after each epoch (see Chapter 7). Demodulation of the FSK timestamp (acoustic GPS output) recorded on the multi-track recorder permitted the synchronization of the acoustic and positional data (see Chapter 7; Møhl et al. 2001).

I inspected acoustic recordings for codas that were in overlapping exchanges and that were detected on at least three of the four hydrophones in the array. I marked clicks in codas that fit these two criteria using a dedicated software package, Rainbow Click (see Gillespie 1997; Jaquet et al. 2001), and the click data from each recording was output to a custom-written routine in MATLAB® (Mathworks) for the calculation of time of arrival differences (TOADs) between each pair of hydrophone receivers (see Chapter 7). Because sperm whales produce loud, abrupt, broadband clicks, TOADs were calculated as time differences between hydrophones in the click onset. For each click in each analyzed coda, the relative locations of the receivers, the TOADs between receivers, and the speed of sound in water (calculated using the sea surface temperature and salinity) were used to find the intersections of calculated hyperbolae of equal time difference. The average of the calculated intersections was taken as the best estimate of the location of the vocalizing whale (see Chapter 7; Laurinolli et al. 2003).

For clicks localized using four hydrophones, the error in the location was estimated from the standard deviation of the hyperbolae intersections in the zonal (ε_x) and the meridional (ε_y) directions, giving the root-mean-square (RMS) error $\varepsilon = (\varepsilon^2{}_x + \varepsilon^2{}_y)^{1/2}$ (as in Laurinolli et al. 2003). For localizations that yielded more than one solution (e.g. sound sources in end-fire positions), I selected the solution nearest to the least-squared-error fit (see Hayes et al. 2000) (i.e. the location in the 2-D array grid nearest the highest density of hyperbolae intersections). Where necessary, the validity for choosing this solution was corroborated by video footage of the location of whales at the surface relative to the acoustic array at the time of recording as well as the structure of click pulses on hydrophones at different aspects (see Chapter 9). Both the processing of GPS receiver positions and the localization of clicks were conducted in custom-written routines in MATLAB® (MathWorks).

For codas in which multiple clicks were successfully localized, the best estimate of the location of coda production was considered to be the mean of the average click locations, excluding click locations that were markedly dissimilar to the other click solutions in the coda. The zonal, meridional, and RMS errors for the location of each produced coda were calculated by taking the mean of each of these errors over the clicks in the coda.

The distance between average locations of codas in overlapping exchanges was calculated using the Pythagorean theorem. The error in estimating this distance was calculated as the square root of the sum of the squares of the zonal and meridional errors of the location solutions of the two codas.

Inter-pulse Interval and Coda Classification Analysis

Clicks in codas localized by acoustic localization were analyzed using a previously described inter-pulse interval (IPI) analysis method (see Chapter 2) to determine the IPIs of produced codas. Because the clarity of the pulse structure of coda clicks sometimes varies between acoustic channels depending on recording aspect (see Chapter 9), IPI analysis was conducted not just using the recording from one hydrophone receiver (as in Chapters 2-6) but repeated using recordings from several hydrophones in the array, thereby increasing the number of codas for which an IPI could be obtained. IPI assignment of codas, when possible, was consistent between hydrophone receivers.

Codas with assigned IPIs within 0.05 msec of one another were assumed to have been made by similarly-sized whales and thus likely the same whale (see Chapter

2). By assigning IPIs to codas, I was able to examine the range of distances between a given whale and its overlap exchange partners within a recording session.

The intervals between clicks within a coda ('inter-click intervals') were output from Rainbow Click, standardized by coda length, and classified into types using *k*-means cluster analysis (see Rendell and Whitehead 2004).

RESULTS

The criterion applied for the selection of the data presented in this chapter were that clicks in codas needed to be detected on at least three of the four hydrophones in the array. The clicks in 19 overlapping coda exchanges from three different recordings satisfied this criterion and were used to estimate the distance between whales in these vocal interactions. However, because localization errors calculated for codas localized in three-hydrophone arrays do not take into account all sources of error, localization errors for codas localized by a three-hydrophone array could not be validly compared to those for codas localized by a four-hydrophone array (see Laurinolli et al. 2003). The RMS localization error was therefore only calculated for the 22 codas localized by a four-receiver array (see Table 8.1).

An example of the localization of a single coda click produced within a four-receiver array is depicted in Figure 8.1. The mean RMS error ± SD for codas localized within the four-receiver array (with receivers positioned in a square with approximately 100 m per side) was 3.7 ± 1.3 m ($n = 10$). In contrast, the mean RMS error for codas localized outside the four-receiver array was 24.5 ± 14.6 m ($n = 12$) with RMS errors increasing with mean distance from the hydrophone receivers (Figure 8.2; $r = 0.905$, $P < 0.001$). The maximum observed RMS error for a coda outside the array was 51.7 m at a mean range of 364.6 m from the hydrophone receivers

The estimated distance between sperm whales in overlapping coda exchanges localized by a four-hydrophone array ranged from 1.2 ± 6.6 to 324.2 ± 51.8 m (see Table 8.2), indicating that this type of vocal interaction occurs at a variety of spatial scales (see Figures 8.3 and 8.4). Even within a given recording session (e.g. #051403), overlapping coda exchanges that occurred within a few seconds of one another - and thus likely within the same behavioural context - varied greatly in the estimated distance between the localized whales (see Table 8.2). Moreover, using the IPIs of coda clicks to assign codas to individuals indicated that a whale in recording session #051403 with an IPI of 2.95 msec engaged in an overlapping coda exchange at 23:27:19 UTC (Coordinated Universal Time) with a whale approximately 275 m away (Figure 8.3) and then with another whale at 23:27:52 UTC less than 6 m away (Figure 8.4), suggesting that coda overlapping serves a function for this whale at both spatial scales. Examination of the coda types produced by this whale (IPI = 2.95 msec) in overlapping exchanges indicated that the whale produced coda type '2+5' in two exchanges with a whale several metres away and coda types '6R' and '2+12' in two exchanges with a whale several hundred metres away (Table 8.2).

Although the codas in the nine overlapping coda exchanges in recording session #061002 were localized using only three hydrophone receivers, and thus were not calculated with any localization error, the estimated distances between whales in these exchanges still suggest that whales engaged in these vocal interactions with whales just a few metres away (see Table 8.2).

Table 8.1. Root-mean-square error for codas localized by a four-hydrophone acoustic array. The inter-pulse interval (IPI) of the localized coda is provided where available.

Recording number	**UTC time**	**IPI (msec)**	**Mean distance from receivers (m)**	**RMS Error (m)**
051403	23:27:19	2.95	inside array	2.6
051403	23:27:19	2.47	308.3	31.9
051403	23:27:28	2.95	inside array	2.6
051403	23:27:28	n/a	364.6	51.7
051403	23:27:32	2.95	inside array	2.9
051403	23:27:38	n/a	inside array	3.6
051403	23:27:38	2.49	340.5	34.0
051403	23:27:48	2.47	348.7	49.6
051403	23:27:48	n/a	inside array	5.3
051403	23:27:52	2.95	inside array	4.7
051403	23:27:52	3.45	inside array	4.6
051403	23:27:55	3.42	inside array	4.1
051403	23:27:55	2.95	inside array	4.9
051403	23:28:05	2.95	inside array	1.2
061703	13:10:48	2.00	130.8	7.7
061703	13:10:48	2.24	140.5	19.5
061703	13:10:50	2.00	138.2	24.1
061703	13:10:50	n/a	141.2	20.4
061703	13:10:53	2.54	135.7	17.5
061703	13:10:53	1.97	136.7	16.9
061703	13:10:58	2.72	155.5	10.8
061703	13:10:58	1.97	138.4	10.2

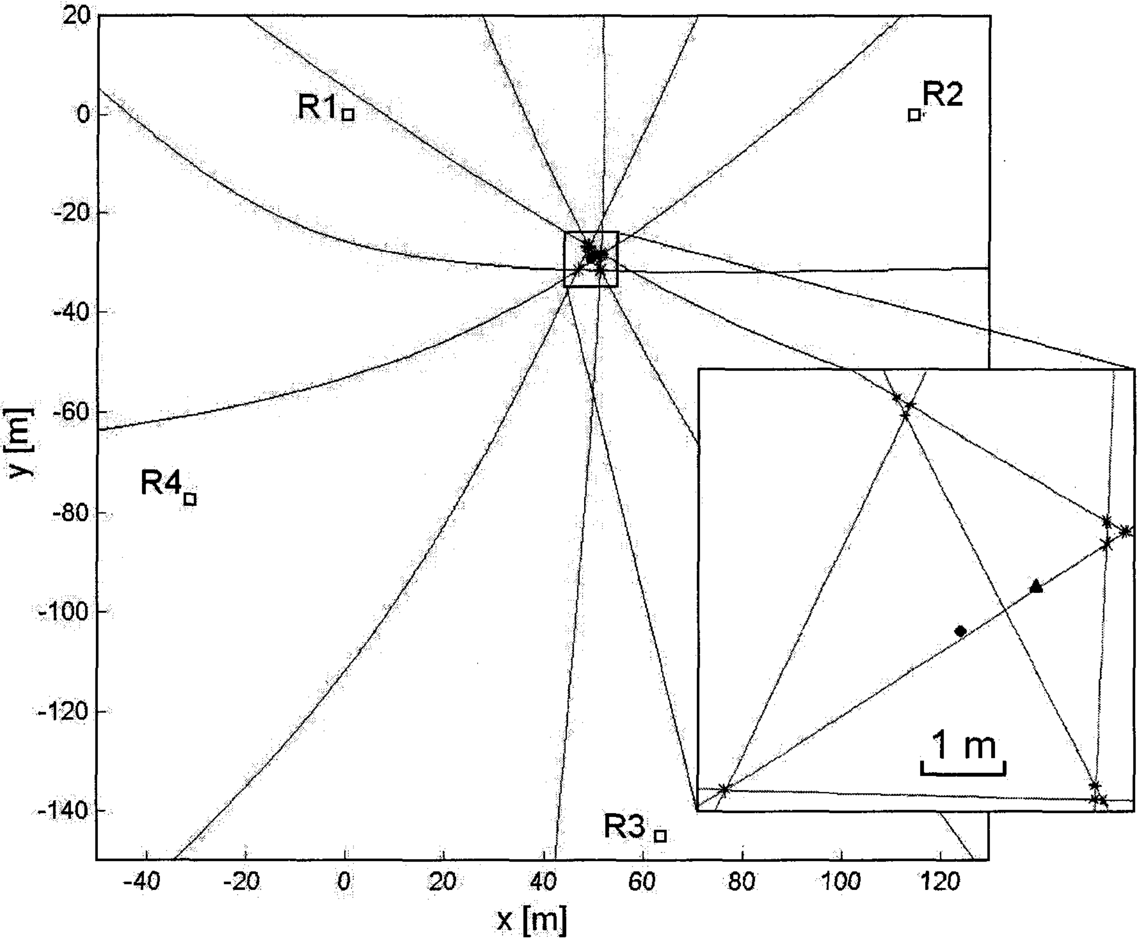


Figure 8.1. Example of a sperm whale click localization. The inset provides a more detailed illustration of the intersections of equal time difference hyperbolae. The asterisks represent intersections of the hyperbolae calculated relative to hydrophone positions (□) R1-R4. The average of the twelve intersections (•) is calculated as the best estimate of the sound source location. The solution of least-squared-error-fit is indicated by the triangle (▲).

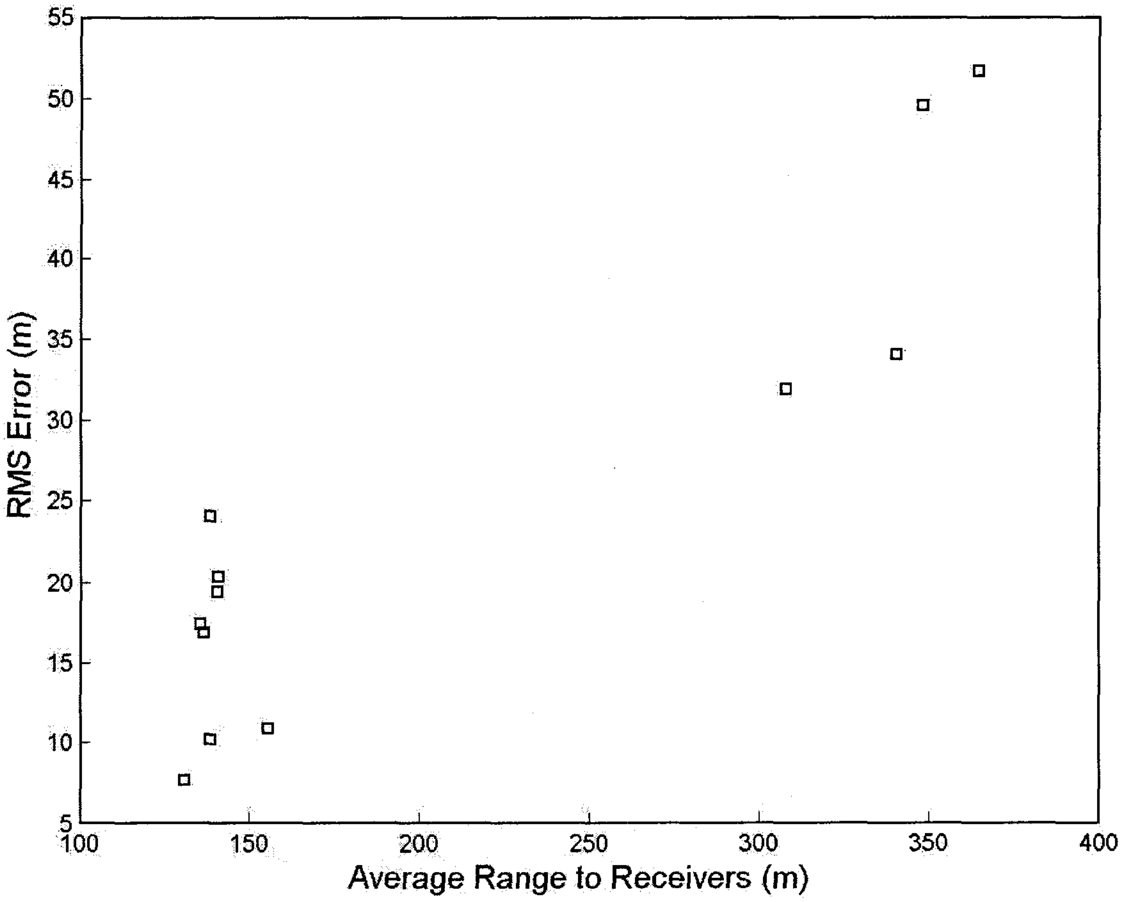


Figure 8.2. Average root-mean-square (RMS) error (m) in hyperbolae intersections vs average range (m) to the four hydrophone receivers used to estimate the location of sperm whale codas.

Table 8.2. Estimated distance (m) between whales in overlapping coda exchanges. The standard deviation of the estimated distance is provided only for overlap exchanges in which the codas were localized using a four-hydrophone receiver array. The inter-pulse intervals (IPIs) and types of codas produced by whales in the overlap exchanges are provided where available.

Rec. no.	Time	Distance (m)	IPI1 (msec)	Coda1	IPI2 (msec)	Coda2
051403	23:27:19	274.8 ± 32.0	2.95	6R	2.47	2+8
051403	23:27:28	324.2 ± 51.8	2.95	2+12	n/a	2+7
051403	23:27:38	290.5 ± 34.1	n/a	2+5	2.49	2+6
051403	23:27:48	290.9 + 49.9	n/a	2+4	2.47	2+5
051403	23:27:52	1.2 ± 6.6	2.95	2+5	3.45	5A
051403	23:27:55	1.5 ± 6.4	2.95	5R	3.42	2+5
061002	20:28:03	2.4	3.67	5R	3.24	9R
061002	20:28:11	0.8	3.65	7R	3.24	7R
061002	20:28:15	0.8	n/a	8R	3.24	6R
061002	20:28:19	6.5	3.67	5R	3.24	6R
061002	20:28:31	3.5	n/a	5R	3.24	4R
061002	20:29:36	2.9	3.67	9R	3.24	9R
061002	20:29:42	6	3.65	8R	3.24	7R
061002	20:29:47	0.5	3.67	9R	3.24	8R
061002	20:29:52	3.4	3.67	8R	3.24	11A
061703	13:10:48	10.5 ± 21.0	2.00	11R	2.24	9R
061703	13:10:50	5.4 ± 31.6	2.00	1+8	n/a	1+8
061703	13:10:53	7.9 ± 24.3	1.97	12A	2.54	1+9
061703	13:10:58	31.4 ± 14.8	1.97	11A	2.72	10R

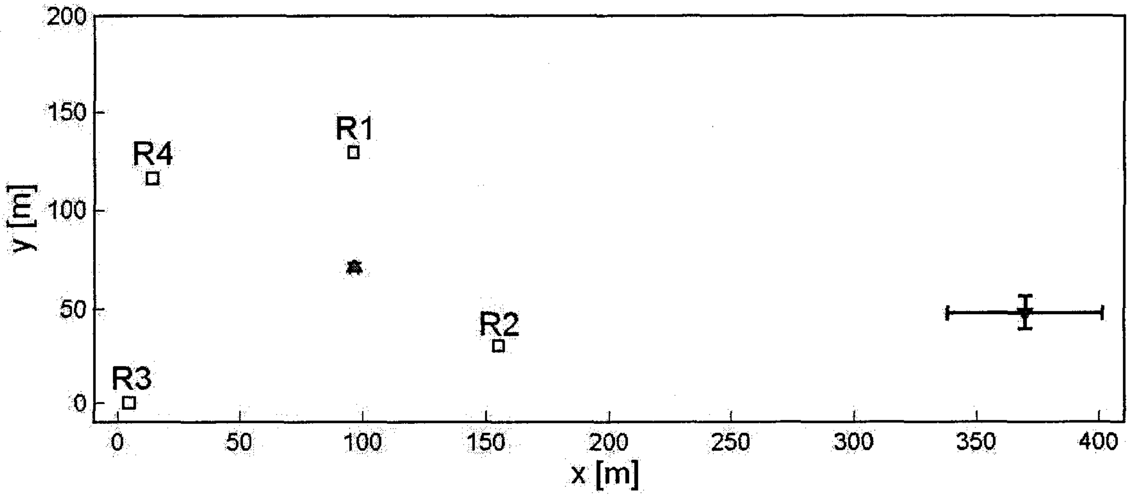


Figure 8.3. Estimated locations with standard deviation error bars in the zonal and meridional directions for two codas in an overlapping exchange at 23:27:19 UTC in recording #051403; one whale (▲) had an inter-pulse interval (IPI) of 2.95 msec and the other whale (▼) had an IPI of 2.47 msec. The estimated distance between the two whales is 274.8 ± 32.0 m. The four hydrophone receivers (R1-R4) are denoted by □.

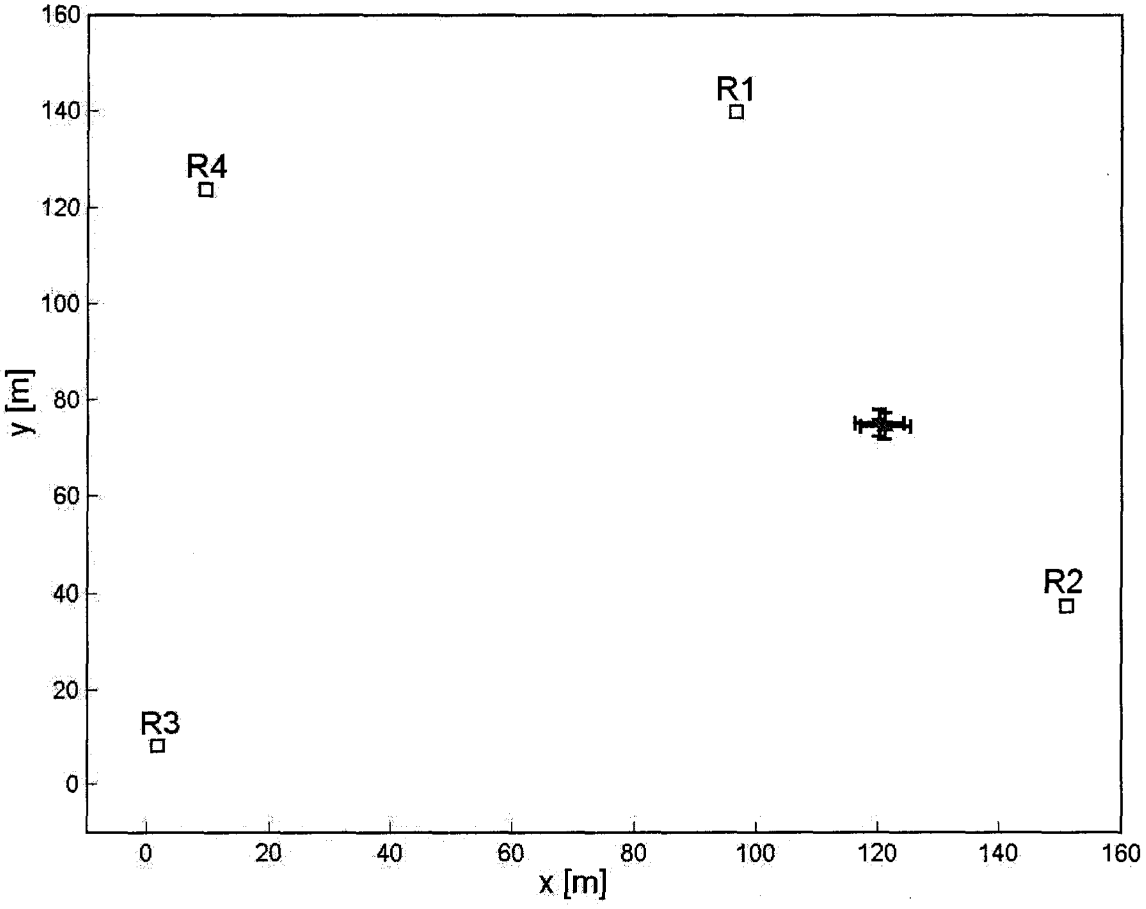


Figure 8.4. Estimated locations with standard deviation error bars in the zonal and meridional directions for two codas in an overlapping exchange at 23:27:52 UTC in recording #051403; one whale (▲) had an inter-pulse interval (IPI) of 2.95 msec and the other whale (▼) had an IPI of 3.45 msec. This IPI assignment indicates that the first whale (▲) is likely the same as the first whale (▲) localized in Figure 8.3 while the second whale (▼) is a different whale than that in the overlapping exchange with the first whale in Figure 8.3. The estimated distance between these two whales is 1.2 ± 6.6 m. The four hydrophone receivers (R1-R4) are denoted by □.

DISCUSSION

These results indicate that sperm whales exchange overlapping codas over a wide range of spatial separations, ranging from just a few metres to several hundred metres. If coda exchanges functioned in sperm whales in a manner similar to contact calls in other species to localize separated individuals (e.g. Masataka and Symmes 1986) or to coordinate group movement (e.g. Miller et al. 2004; Radford 2004), then they would likely occur only between individuals out of visual range of one another. Given that several localized vocal interactions occurred between whales in close proximity of one another (1-6m) - a range much smaller than the approximate underwater visibility in these waters (~20 m, S. Wong, pers. comm.[4]) - it seems doubtful that sperm whales use vocal exchanges to localize one another and coordinate group movement, a conclusion also supported by the fact that an overlapping coda would likely mask location information available in the responding coda. And although the binocular vision and tremendous size of these animals might hamper their ability to visually monitor even nearby conspecifics, sperm whale groups often travel at the water surface without any coda production (pers. obs.), further substantiating the conclusion that sperm whales do not use vocal exchanges to coordinate group movement. While one localized whale produced one coda type ('2+5') in overlapping coda exchanges with a nearby whale but two different coda types in overlapping coda exchanges with comparatively far whales (Table 8.2), the small sample size (*n* = 4 exchanges) precludes any useful conclusions concerning the function of different coda types in exchanges at different spatial scales.

Since coda exchanges occurred not only between adjacent individuals but also between whales several hundred metres apart, it appears that overlapping coda exchanges are not a phenomenon exclusive to individuals within visual contact of one another and therefore must function over a range of spatial scales. Given both the social context in which vocal exchanges are produced and the observed tendency for whales to sequence overlapping codas into duet-like exchanges (Chapter 5), the results presented here that overlapping coda exchanges occur at a variety of spatial scales strongly support the hypothesis that these vocal interactions function to reaffirm social bonds between unit members.

Many primates, as well as other animals, engage in social grooming, spending hours ruffling through each other's hair and removing ectoparasites, dead skin, leaves, and other foreign objects (Aureli et al. 1989; Thierry et al. 1990; Dunbar 1991; Cooper and Bernstein 2000). While this activity has obvious functions in achieving hygiene and good health (Tanaka and Takefushi 1993; Mooring and Hart 1997; Mooring and Samuel 1998), it can also be a reliable index of the closeness of the social bond between the grooming animals (Dunbar 1996) and so has been implicated for some species in the establishment and reinforcement of social ties. Moreover, the act of social grooming has been found to stimulate the release of beta-endorphins (Keverne et al. 1989), such that being groomed produces mildly narcotic effects (Terry 1970; Dunbar 1996) that may act to increase the feeling of attachment for the grooming animal. As a result, social grooming appears to be an effective means of reinforcing bonds and maintaining social structure in several animal species (Kimura 1998; Dunbar 1991; Cooper and Bernstein 2000).

As the group size of a social species increases, however, the extent of an individual's social alliances and thus the grooming time required to maintain them would eventually become unmanageable, thereby selecting for another means of achieving the same bonding effect (Dunbar 1996). Dunbar (1996) suggests that vocal grooming in primates, which likely evolved from contact calls that maintain group cohesion during dispersion, evolved to permit the maintenance of social structures without the time-consuming costs of physical social grooming. By maintaining social contact with group members even when physically separated, primates may use contact calls to 'groom at a distance' and bond with multiple individuals within a given interaction (Dunbar 1996). Moreover, if the localization of alliance members via vocal interactions came to be associated with kinship and a positive emotional response, then 'vocal grooming' would be functional in reinforcing social bonds even between individuals within close proximity. Although the evolution of vocal grooming has often been associated with an increase in group size, Dunbar (1996) notes that time constraints due to other factors could also select for vocal grooming as a surrogate to social grooming.

I suggest that sperm whales, which spend the majority (~75%) of their time at depth (Whitehead and Weilgart 1991; Gordon and Steiner 1992; Whitehead 2003a) foraging on mesopelagic squid and fish species (Kawakami 1980), engage in coda overlapping exchanges at the water surface as a form of vocal grooming to reaffirm social bonds between unit members after periods of separation at depth (see also Whitehead and Weilgart 1991). Although sperm whales sometimes engage in rubbing, touching and other forms of physical contact (Gordon 1991b, 1998) that resemble social grooming in horses (*Equus caballus*) (Kimura 1998) white-tailed deer (*Odocoileus virginianus*) (Forand and Marchinton 1989) and sheep (*Ovis aries*) (Wasilewski 2003), by utilizing vocal rather than physical interactions to reestablish contact and social connections after diving, whales would be capable of interacting with multiple individuals over a range of spatial scales with greater efficiency. And just as language in humans may have evolved from the vocal grooming benefits of contact calls (Dunbar 1996), coda exchanges may have likewise initially functioned to monitor the presence of unit members and subsequently evolved a vocal grooming function. This is especially conceivable if the coordinated exchange of vocalizations results in a positive emotional response (see Brown 2000; Kreutz et al. 2004; Mithen 2005), a sensation perhaps encouraged by the production of clan-identifying codas if they induce a feeling of inclusion.

As human groups grew larger and larger, it is hypothesized that this form of communication would have eventually exhausted its capacity to mediate the necessary social relationships, eventually selecting for signals to possess meaning so that individuals could communicate about other group members and therefore increase their sphere of social knowledge without the necessity of direct observation (Dunbar 1996). But for sperm whales, which tend to live in much smaller social units (~14 individuals) (Christal et al. 1998; Whitehead 2003a), it seems unlikely that codas would have been selected to evolve meaning, a fact corroborated by the overlapping of codas in exchanges (see Chapter 5) and the low communication capacity of coda production (see Chapter 6). Instead, it seems most probable that sperm whales exchange codas primarily as a surrogate to social grooming to reaffirm social connections with other individuals.

If coda overlap exchanges do function to reaffirm a social bond between exchange partners, one might expect the amplitude of produced codas to be relative to the distance between the vocalizing animals. Unfortunately, modifications to this recording system in the field after laboratory calibration prohibited study of the source levels of codas produced in exchanges. Nonetheless, I was able to examine whether a whale modified the amplitude of its codas depending on the distance between overlapping exchange partners by comparing the relative amplitude (average root-mean-square) of codas produced by the same whale (IPIs = 2.95 msec) in different overlapping coda exchanges within one recording session (#051403). The analysis indicated that the whale did not reduce the amplitude of its codas when engaging in a vocal interaction with a very near whale compared to when in overlapping exchanges with a comparatively far whale (Table 8.3). During these exchanges, the whale was seemingly traveling in one direction and thus presumably maintaining a constant acoustic axis relative to the hydrophone receivers (see Figures 9.4 and 9.5 in Chapter

9). This disqualifies any directionality effects in observed amplitude differences between codas. Therefore, these limited data suggest that whales do not modify the amplitude of their codas to suit the distance between vocal exchange partners. This finding, together with the observation that recorded coda clicks generally possess a noticeably high amplitude (P. Madsen, pers. comm.[3]), suggest that coda clicks are much louder than required to be detected by a conspecific within a few metres.

Table 8.3. Average root-mean-square (RMS) amplitude of codas produced by a whale in overlapping exchanges with both far whales (first two rows) and near whales (last two rows). The average RMS amplitude of each coda is presented for each of the recordings made from the four hydrophone receivers (R1-R4). The units of RMS amplitude are dimensionless sample units.

UTC Time	**Distance between whales (m)**	**Average RMS amplitude of coda**			
		R1	**R2**	**R3**	**R4**
23:27:19	274.8 ± 32.0	1547	815	2242	3383
23:27:28	324.2 ± 51.8	3305	2804	3681	4381
23:27:52	1.2 ± 6.6	2565	3533	4292	2060
23:27:55	1.5 ± 6.4	2114	3570	3366	2022

There are several possibilities that could explain why sperm whales appear to produce signals that are much louder than necessary to reach the apparent intended receiver. For example, perhaps the evolution of group living as a predator defense mechanism (Whitehead 2003a) alleviated the necessity to reduce the intensity of coda clicks and avoid detection by eavesdropping. Conversely, perhaps codas are produced louder than necessary as expensive, high-risk and therefore honest signals of the social bond between the vocalizing animals (Zahavi 1977; Zahavi and Zahavi 1997). Alternatively, or perhaps additionally, the intended signal receiver of the coda overlap may not be the overlapped whale (or not just the overlapped whale) but also other whales in the area either of the same or different units. In this way, coda overlap exchanges may function in a similar manner to duets in some other species to broadcast the social bond between exchanging individuals to eavesdroppers (Hall 2004). Furthermore, if whales primarily exchange codas that indicate clan affiliation, then the loud intensity of codas may also permit the broad advertizement of clan affiliation to both unit members and to whales from other social units. Finally, the seemingly excessive intensity of sperm whale coda clicks could simply be a byproduct of selection for the ability to produce highly intensive usual clicks such that whales are physiologically incapable of producing quiet clicks.

The localization results and errors presented here indicate that while this acoustic array would have difficulty in distinguishing between the vocalizations of whales within just a couple of metres of one another, because sperm whales are generally 6.5 m (interquartile range: 3.9 -11.4 m) apart within a social cluster (Whitehead 2003a), codas produced by different whales within the array could likely be differentiated using acoustic localization (see also Chapter 7). Moreover, this array can certainly be used to discriminate between individuals or clusters of whales several tens of metres apart as well as estimate the general distance between whales engaging in vocal exchanges. Not surprisingly, localization errors increased with distance from the array and were much smaller for sound sources localized within rather than outside of the four-receiver array. Clearly future deployments of this or similar array systems around stationary or slow-moving sperm whales will be fruitful in furthering our understanding of the spatial arrangement of individuals engaging in acoustic communication. Moreover, the deployment of a calibrated system would permit the study of the directionality of coda clicks, as has been achieved for sperm whale usual clicks (Møhl et al. 2000), and could be used to further examine the spatial arrangement of whales participating in vocal exchanges at the water surface. Nonetheless, the current study does indicate that the commonly observed phenomenon of coda overlapping (see Chapter 4), occurs over a range of spatial scales and thus is likely functional between whales that are both near and comparatively far from one another.

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CHAPTER NINE

OFF-AXIS EFFECTS ON THE MULTI-PULSE STRUCTURE OF SPERM WHALE CODA CLICKS

INTRODUCTION

The sperm whale (*Physeter macrocephalus*) is an animal of extremes. From its large body size and sexual dimorphism (Rice 1989; Whitehead 2003a) to its widespread geographic distribution and large-scale sexual segregation (Rice 1989; Whitehead 2003a), the largest odontocete demonstrates extreme differences in morphology and life-history both within the species and in comparison to other cetaceans. However, no feature of the sperm whale is perhaps as noticeably extreme and fascinating as the large nasal complex that characterizes the animal. Its large nose, which contains the spermaceti organ, junk bodies, and other organs associated with sound production in this species (Figure 9.1), makes up approximately 1/3 of the sperm whale's total body weight and body length (Rice 1989; Madsen 2002), giving this species the claim to the 'biggest nose on record' (Raven and Gregory 1933).

Although researchers had previously proposed battering ram (Carrier et al. 2002) and buoyancy regulation (Clarke 1970, 1978) functions for the hypertrophied nasal complex, Norris and Harvey (1972) were the first to advance a sound generating function, a function that has since been corroborated by experimental evidence. They suggested that an initial sound pulse generated by the forcing of air through the museau de singe (or phonic lips) (Figure 9.1) is reflected between air sacs at the anterior and posterior ends of the spermaceti organ (Norris and Harvey 1972), resulting in the multi-pulsed structure of sperm whale clicks first observed by Backus and Schevill (1966). Recently, this initial theory was revised as the 'bent horn' theory (Møhl et al. 2003) to explain the weak initial pulse (p0) and powerful subsequent pulse (p1) obvious in the recordings of usual clicks (echolocation clicks) recorded from in front of the vocalizing whale (Figure 9.2a). It is now believed that while a fraction of the initial sound energy in a usual click leaks directly into the water as the weak initial pulse (Møhl 2001), the majority of the sound energy is reflected backwards into the spermaceti organ (Figure

9.1). Subsequently, the sound energy reflects off the air-filled frontal sac at the posterior of the spermaceti organ and is focused in the junk complex before emission into the water as the powerful p1 pulse (Figure 9.1; Cranford 1999; Møhl et al. 2003), resulting in another extreme claim for this species - the loudest biologically produced sound (Møhl et al. 2000, 2003).

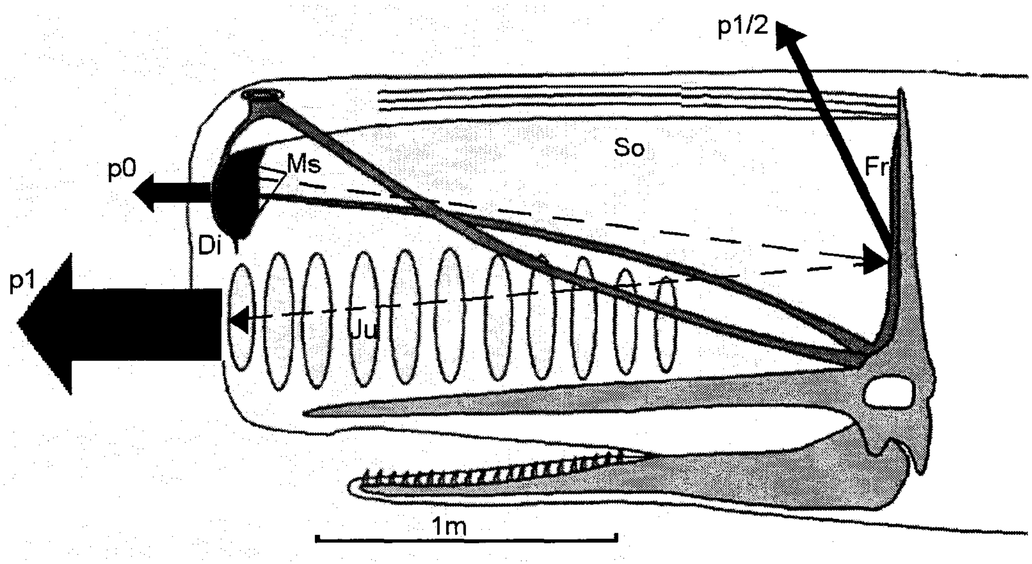

Figure 9.1. Schematic view of the head of a sperm whale depicting the bent-horn model of usual click sound generation (modified from Figure 1 of Madsen et al. 2002b). The dashed arrows indicate the primary sound path within the nasal complex according to the modified Norris and Harvey (1972) theory. The solid arrows indicate the emission of the weak pulse (**p0**) from the phonic lips/museau de singe (**Ms**), the emission of the highly directional sonar pulse (**p1**) from the junk (**Ju**), and the leakage of sound energy as the p1/2 pulse (**p1/2**) from the frontal air sac (**Fr**). **D**, distal air sac; **So**, spermaceti organ.

Recent research confirms this bent horn theory; sound is in fact produced at the museau de singe via a pressure differential (Madsen et al. 2003), the multi-pulsed structure of usual clicks is related to the two-way travel time between air sacs (Møhl 2001; Møhl et al. 2003), usual clicks are highly directional (Møhl et al. 2000, 2003) and the weaker p0 pulse has a broad backward-directed beam while the highly-directional p1 pulse has a forward-directed trajectory (Zimmer et al. 2005b). Moreover, research using far-field recordings in combination with acoustic and orientation recorder (DTAG) data confirms that the powerful p1 sonar pulse of usual clicks is indeed emitted from the junk surface, indicating that the junk is functionally homologous to the melon of smaller odontocetes in focusing the sound energy of echolocation clicks (Zimmer et al. 2005a).

In addition, this research by Zimmer et al. (2005a) also revealed that similar to the leakage of sound energy at the anterior end of the spermaceti organ when the initial p0 pulse is produced, the reflection of usual click sound energy on the frontal sac at the posterior end of the nasal complex also involves the leakage of sound energy into the water, resulting in the emission of a p1/2 pulse (Zimmer et al. 2005a). When a usual click is recorded on-axis directly in front of a vocalizing whale, the p1/2 pulse merges with the p1 pulse (Figure 9.2a) (Zimmer et al. 2005a). Conversely, when a usual click is recorded on-axis directly behind the vocalizing whale, the p1/2 pulse merges with the p0 pulse (Figure 9.2b) (Zimmer et al. 2005a).

In either case, the recorded waveform contains distinct and regular inter-pulse intervals (IPIs) that can be measured to estimate the length of the vocalizing whale (Gordon 1991b; Rhinelander and Dawson 2004) (see Figure 9.2a). However, when usual clicks are recorded off-axis, the p1/2 pulse will appear in the far field with a delay between 0 and the two-way-travel time of the nose, sometimes resulting in IPIs that cannot be distinguished (see Figure 9.2c) and thus the incorrect or impossible estimation of whale length (Zimmer et al. 2005a).

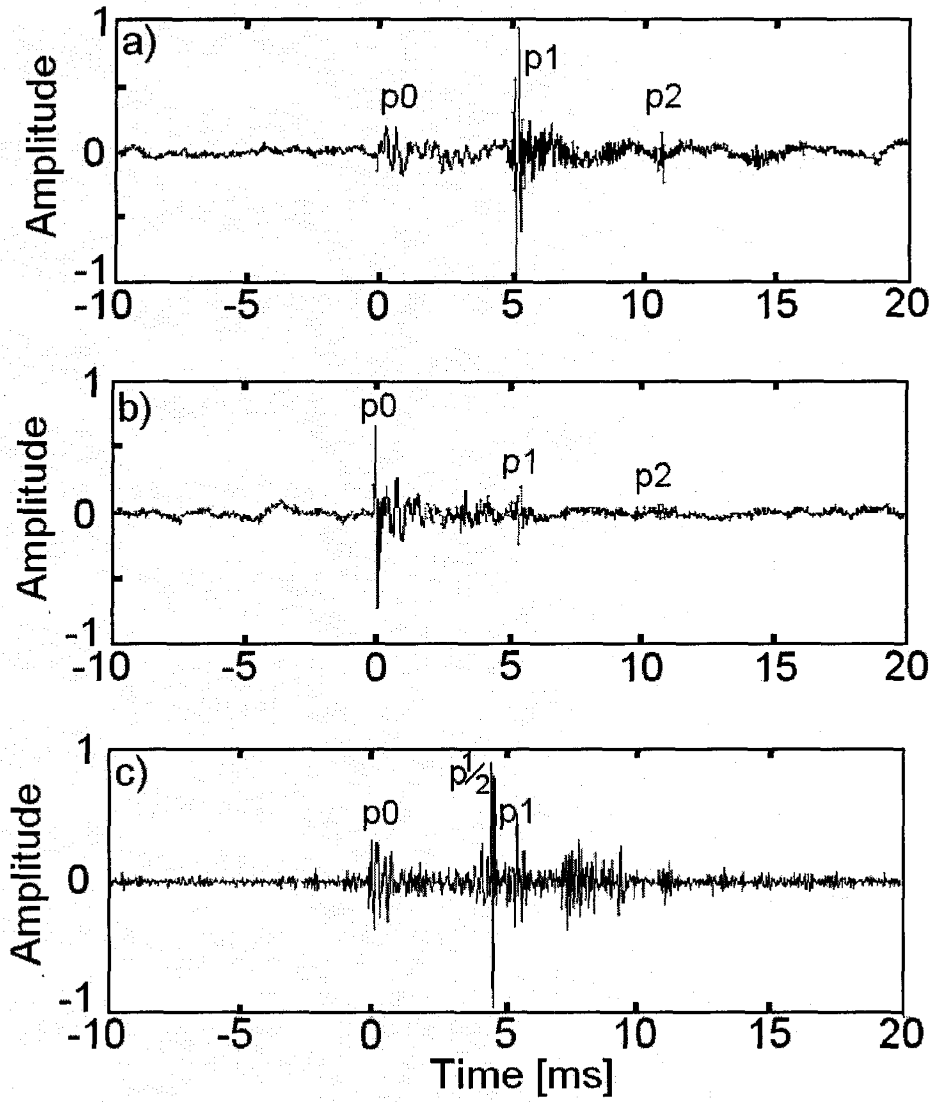

Figure 9.2. Usual clicks recorded from a remote receiver from in front **(a)**, behind **(b)**, and off the acoustic axis of a vocalizing whale **(c)** (modified from Zimmer et al. 2005a). The different component pulses in the clicks are denoted by p0, p1, and p2. Note that in **a)** and **b)** a single pulse by far dominates the energy content of the click. In the waveform recorded off-axis **(c)**, p1/2 denotes the click energy leaked from the spermaceti organ at the frontal sac.

While it is now accepted that usual clicks travel backwards through the spermaceti organ, reflect off the frontal sac, and are focused in the junk before emission as a highly powerful and directional echolocation click, the production of clicks observed in short stereotyped patterns termed ‘codas’ (Watkins and Schevill 1977), is presumed to follow a somewhat different trajectory (Madsen et al. 2002b). The structure of recorded coda clicks differs from usual clicks in that rather than almost all of the sound energy being allocated to a highly directional p1 pulse with relatively few and weak subsequent pulses (Figures 9.2a and 9.2b), coda clicks typically exhibit many successive pulses (Figure 9.3) and thus a longer overall click duration than usual clicks (Madsen et al. 2002b). The lower decay rate of coda clicks suggests that coda click sound energy is retained within the spermaceti organ to reverberate repeatedly between the air sacs rather than being redirected into the junk complex to be released as a powerful and directional pulse (Madsen et al. 2002b).

However, despite the inference from the multi-pulsed nature of coda clicks that the sound energy is maintained within the spermaceti organ, it is still unknown whether leakage of coda click sound energy also occurs at the frontal sac, as found for usual clicks. If coda click sound energy were only released at the anterior end of the spermaceti organ with no leakage of sound at the frontal sac, then the recorded pulse structure would be similar on each hydrophone receiver irrespective of recording aspect. However, if coda click energy leaks into the surrounding water upon reflection of the frontal sac, as in usual clicks, then they too would be affected by the aspect with which the click is recorded (Zimmer et al. 2005a). Although the waveforms of usual clicks have been examined from different recording aspects (Zimmer et al. 2005a; Madsen et al. 2002b), it remains to be seen whether the pulse structure of coda clicks also demonstrates off-axis effects indicative of sound energy leakage at the frontal sac.

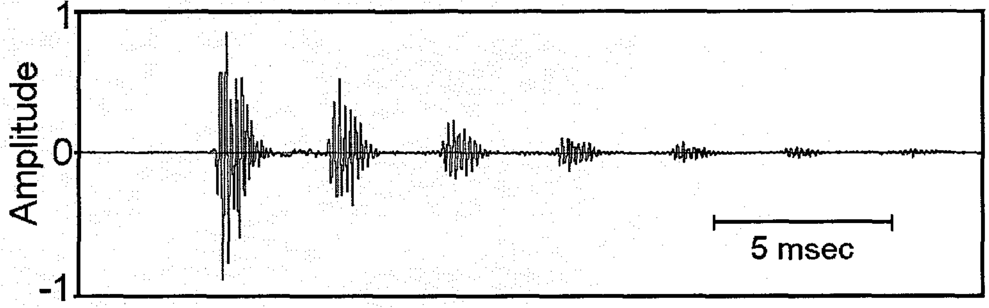

Figure 9.3. Waveform of a coda click recorded from behind a vocalizing whale. Note the multiple pulses with a low rate of decay compared to the nearly mono-pulsed waveform of usual clicks (see Figures 9.2a and 9.2b). Pulse numbers have not been assigned, as it is unclear whether the initial pulse in the waveform is p0 or p1.

Moreover, it is also unclear whether the initial, primary pulse in recorded coda clicks is a result of emission from the spermaceti organ directly into the water (as in the p0 pulse in usual clicks) or if the primary pulse first travels twice the length of the nasal complex before release into the water (as in the p1 pulse of usual clicks). If coda click production resembled usual click production in that the primary pulse travels twice the length of the spermaceti organ before release into the water, then one might expect similar emission or leakage of a small amount of sound energy at the distal sac, resulting in a weak p0 pulse similar to that observed in usual clicks. Although the recording of coda clicks on-axis from in front of a whale could potentially confirm the presence of a weak p0 pulse, most codas are recorded from an unknown recording aspect or from behind the vocalizing whale (see Marcoux et al. 2006) such that if leakage of sound energy at the frontal sac does occur for coda clicks, then the p1/2 pulse would merge with a p0 pulse and prohibit observation of the p0 pulse alone (see Figure 9.3). Clearly recording sperm whale coda clicks from in front of a vocalizing whale would be useful in determining whether the initial pulse observed in most coda click waveforms is a result of the direct emission of sound energy into the water.

To address these research gaps concerning the production of sperm whale coda clicks, I inspected and compared the waveforms of coda clicks recorded on different hydrophones in a passive dynamic acoustic array (see Chapters 7 and 8). To determine the trajectory and orientation of vocalizing whales relative to each hydrophone receiver, I assigned codas to individuals using IPI similarity (see Chapter 2) and localized successive codas using acoustic localization (see Chapter 7).

METHODS

Field Methods

The fieldwork for this research was conducted between May 5 – June 20, 2004 (38 days effort) in international waters between Bermuda and the east coast of the United States in the Sargasso Sea. Sperm whales encountered during this study were tracked visually during the day and acoustically at night using a directional hydrophone (see Whitehead and Gordon 1986). During the day, if whales at the surface were moving slowly (< 1 knot) and the weather conditions were favourable, the dynamic acoustic array described in Chapter 7 was deployed with the goal of attaining favourable array geometry around the observed whales.

Acoustic Array and Localization Analysis

The acoustic array used to localize and record sperm whale codas is described in detail in Chapters 7 and 8. The array consisted of three small remotely-piloted vessels (RPVs) and one larger research platform, a 12-m auxiliary sailboat, from which the RPVs were deployed. Each research platform was equipped with a hydrophone, GPS receiver and GPS logger. Clicks detected on each of the RPV hydrophones were transmitted by FM transmitter to the primary research platform, where all acoustic signals, including the FSK-modulated signal from the onboard GPS receiver, were recorded in synchrony on a multi-track recorder (FOSTEX VF-160; sampling rate: 44.1 kHz). Recording sessions were labeled numerically according to month, day, and session of the day (e.g. #051403 was the third recording session on May 14th).

During the deployment of the array, the locations of the RPVs and whales relative to the primary research platform were recorded on a digital camcorder (SONY DCR-PC 105) from the sailboat's crow's nest. Sea surface temperature was measured using an onboard electronic thermometer and sea salinity was estimated using a refractometer.

The methods used to process the logged GPS positions, localize the sound sources, and calculate location errors are described in detail in Chapter 7.

IPI Assignment of Codas

Codas localized by acoustic localization were analyzed using a previously described IPI analysis method (see Chapter 2) to determine the IPIs of produced codas. Because the clarity of the pulse structure of coda clicks sometimes varies between acoustic channels, IPI analysis was conducted not just using the recording from one hydrophone receiver (as in Chapters 2-6) but repeated using recordings from several hydrophones in the array, thereby increasing the number of codas for which an IPI could be obtained. IPI assignment of codas, when possible, was consistent between hydrophone receivers.

Codas with assigned IPIs within 0.05 msec of one another were assumed to have been made by similarly-sized whales and thus likely the same whale (see Chapter 2). The localized positions of successive codas presumed to have been made by the same whale were plotted with respect to the hydrophone receiver positions to estimate the trajectory and thus orientation of the vocalizing whale relative to the array. Using the GPS positions of the hydrophone receivers, the localized positions of successive codas likely produced by the same whale, and the estimated orientation of the vocalizing whale, I used the cosine rule to calculate the approximate angle between the whale and each hydrophone receiver relative to the whale's presumed body axis. The waveforms of clicks in these localized codas were then visually inspected in a standard sound-editing program (Cool Edit, Syntrillium) and qualitatively compared between hydrophone receivers to determine whether there were differences in pulse structure as a result of recording aspect.

To quantitatively describe the clarity in the multi-pulse structure of recorded coda click waveforms, I calculated the coefficient of variation (CV) in the squared amplitude over each sample in each recorded click within a 5 msec time interval beginning at click onset. A 5 msec (221 sample) time interval was used because the IPIs of all localized whales were estimated as less than 5 msec and because click durations were variable but generally longer than 5 msec. Because clicks with distinct initial pulses possessed high CVs and clicks with poorly defined pulse structures possessed low CVs, the CV provided a general measure of the clarity of the click structure while standardizing for the relative amplitude of the click.

RESULTS

In recording session #051403, a whale with an IPI of 2.95 msec was localized as it moved within the array toward the periphery (Figure 9.4). The structure of coda clicks produced while the whale was near the centre of the array was clearly multi-pulsed in recordings made on hydrophones positioned behind the vocalizing whale (R3 and R4; Figure 9.4). However, the pulse structure of the same clicks but recorded on a hydrophone receiver (R1) in an off-axis aspect was poorly defined (Figure 9.4). Moreover, the pulse structure of the same clicks but recorded slightly more on-axis in front of the vocalizing whale (hydrophone receiver R2) demonstrated a clear initial pulse but a less-defined succeeding pulse (Figure 9.4).

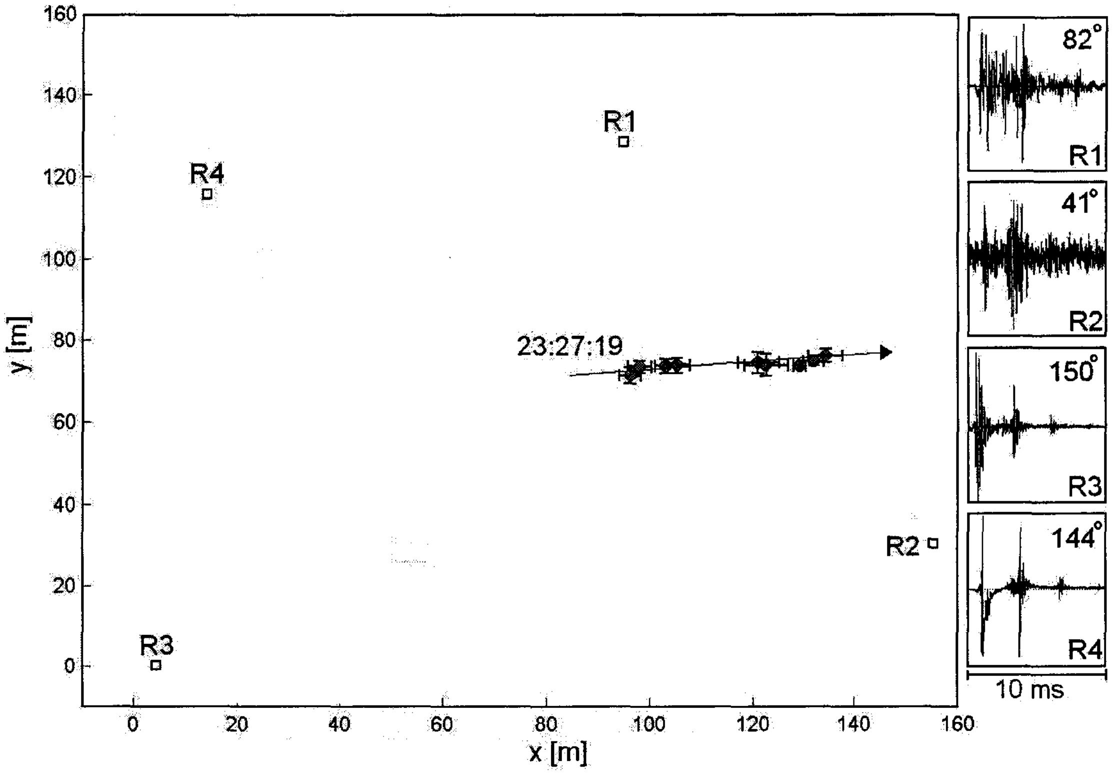

Figure 9.4. The GPS positions of four hydrophone receivers (R1-R4; □) at 23:27:19 UTC and the estimated location solutions (with standard deviation error bars in the zonal and meridional directions) for codas with inter-pulse intervals of 2.95 msec (•) produced throughout recording session #051403. The arrow indicates the estimated direction of the vocalizing whale based on codas localized between 23:27:19 and 23:28:12. The waveform of a coda click as received on each of the four hydrophone receivers at 23:27:19 is presented along the right side of the figure together with the calculated angle between the hydrophone receiver and the estimated acoustic axis of the whale.

Several seconds later at 23:28:12, after the whale had moved approximately 38 m toward the periphery of the array, the waveforms of coda clicks recorded on hydrophones from behind the whale still demonstrated a clear multi-pulsed structure (Figure 9.5). For hydrophone R1, which was now 111° behind the vocalizing whale, the waveforms of recorded coda clicks were slightly more multi-pulsed (Figure 9.5) than for the coda clicks recorded 53 s earlier when this hydrophone was at an angle of 82° in front of the animal (Figure 9.44). Conversely, for hydrophone R2, which was now 74° in front of the animal and thus at a more off-axis angle than 53 s earlier, the multi-pulsed structure of the click waveforms were much less discernible (Figure 9.5).

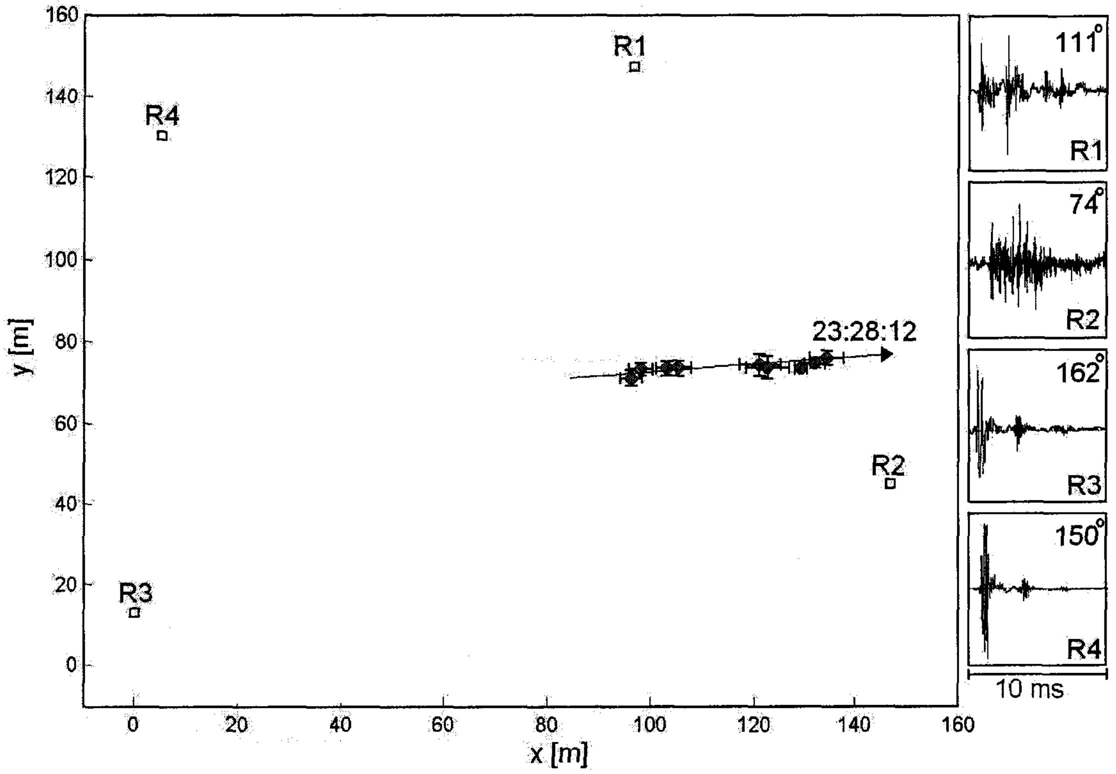

Figure 9.5. The GPS positions of four hydrophone receivers (R1-R4; □) at 23:28:12 UTC and the estimated location solutions (with standard deviation error bars in the zonal and meridional directions) for codas with inter-pulse intervals of 2.95 msec (•) produced throughout recording session #051403. The arrow indicates the estimated direction of the vocalizing whale based on codas localized between 23:27:19 and 23:28:12. The waveform of a coda click as received on each of the four hydrophone receivers at 23:28:12 is presented along the right side of the figure together with the calculated angle between the hydrophone receiver and the estimated acoustic axis of the whale.

Coda clicks produced during the same recording session but by a different whale (IPI = 2.49 msec) were localized several hundred metres from the array and demonstrated clear multi-pulsed waveforms on each of the four hydrophones, albeit slightly less distinct on the hydrophone receiver (R1) that was the least on-axis with the estimated orientation of the vocalizing whale (Figure 9.6).

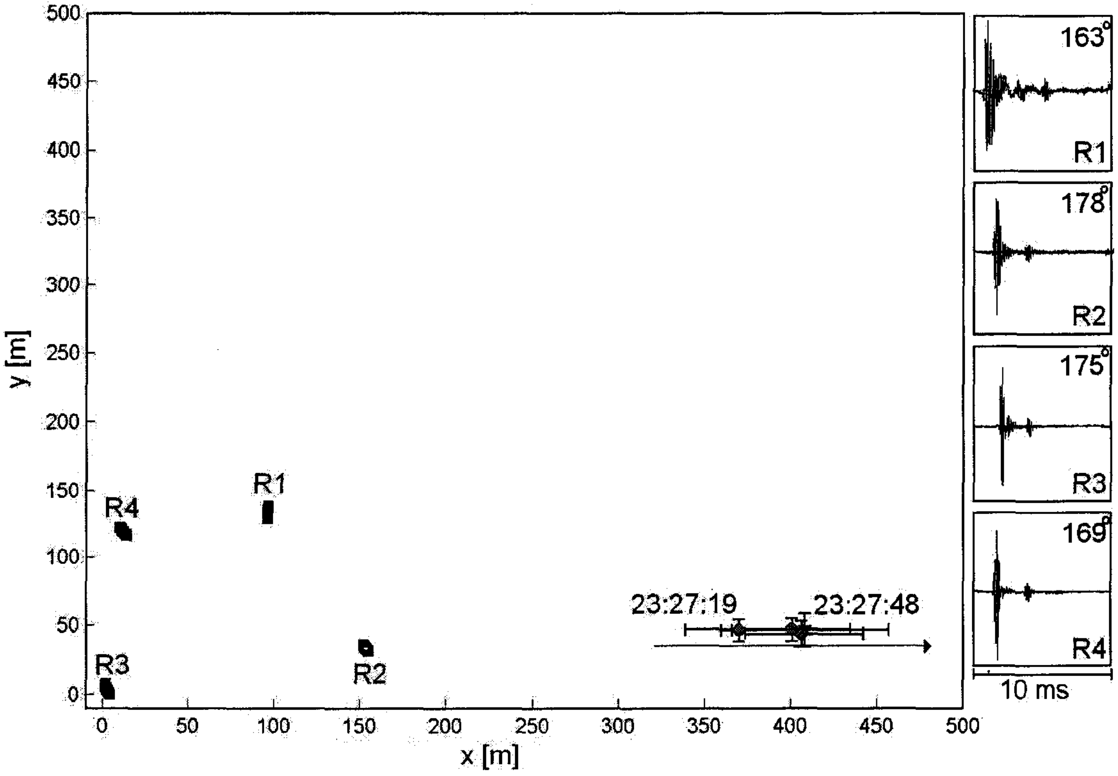

Figure 9.6. The GPS positions of four hydrophone receivers (R1-R4; □) and the estimated location solutions (with standard deviation error bars in the zonal and meridional directions) for codas with inter-pulse intervals of 2.49 msec (•) produced throughout recording session #051403. The arrow indicates the estimated direction of the vocalizing whale based on codas localized between 23:27:19 and 23:27:48. The waveform of a coda click as received on each of the four hydrophone receivers at 23:27:19 is presented along the right side of the figure together with the calculated angle between the hydrophone receiver and the estimated acoustic axis of the whale.

In recording session #060901, a whale with an IPI of 2.83 msec was localized moving toward the 3-receiver array (Figure 9.7). The three hydrophone receivers were estimated to be at approximately the same recording aspect to the vocalizing whale (21°-

26°) and all demonstrated well-defined pulse structures in recorded coda clicks with the majority of the sound energy allocated to the initial pulse (Figure 9.7).

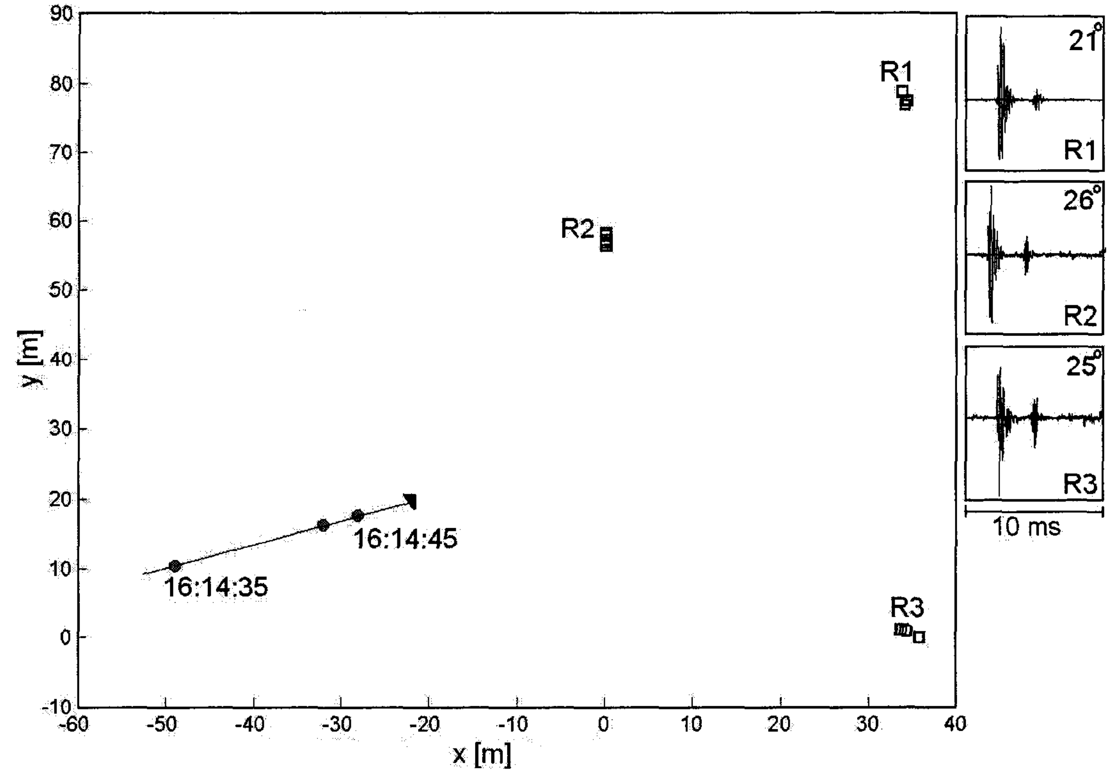

Figure 9.7. The GPS positions of three hydrophone receivers (R1-R3; □) and the estimated location solutions for codas with inter-pulse intervals of 2.83 msec (•) produced throughout recording session #060901. The arrow indicates the estimated direction of the vocalizing whale based on codas localized between 16:14:35 and 16:14:45. The waveform of a coda click as received on each of the three hydrophone receivers at 16:14:35 is presented along the right side of the figure together with the calculated angle between the hydrophone receiver and the estimated acoustic axis of the whale.

Finally, in recording session #061002, a whale with an IPI of 3.24 msec was localized moving away from the 3-receiver array, nearly inline with two hydrophone receivers (R1 and R2) while off-axis to the third hydrophone receiver (R3) (Figure 9.8). In the two recordings made from behind the vocalizing whale (R1: 172°; R2: 164°), the waveforms of coda clicks recorded at 20:27:55 possessed well-defined pulse structures, although the first pulse in the clicks was more elongated and less distinct than the subsequent pulses (Figure 9.8). In contrast, in the recording made from an off-axis aspect (107°) to the acoustic axis of the vocalizing whale, the waveforms of the same clicks demonstrated additional pulses between the primary pulses (Figure 9.8). Similar differences in waveforms on different hydrophone receivers were observed for a different whale in session #061002 with an IPI of 3.51 msec also localized moving away from the 3-receiver array.

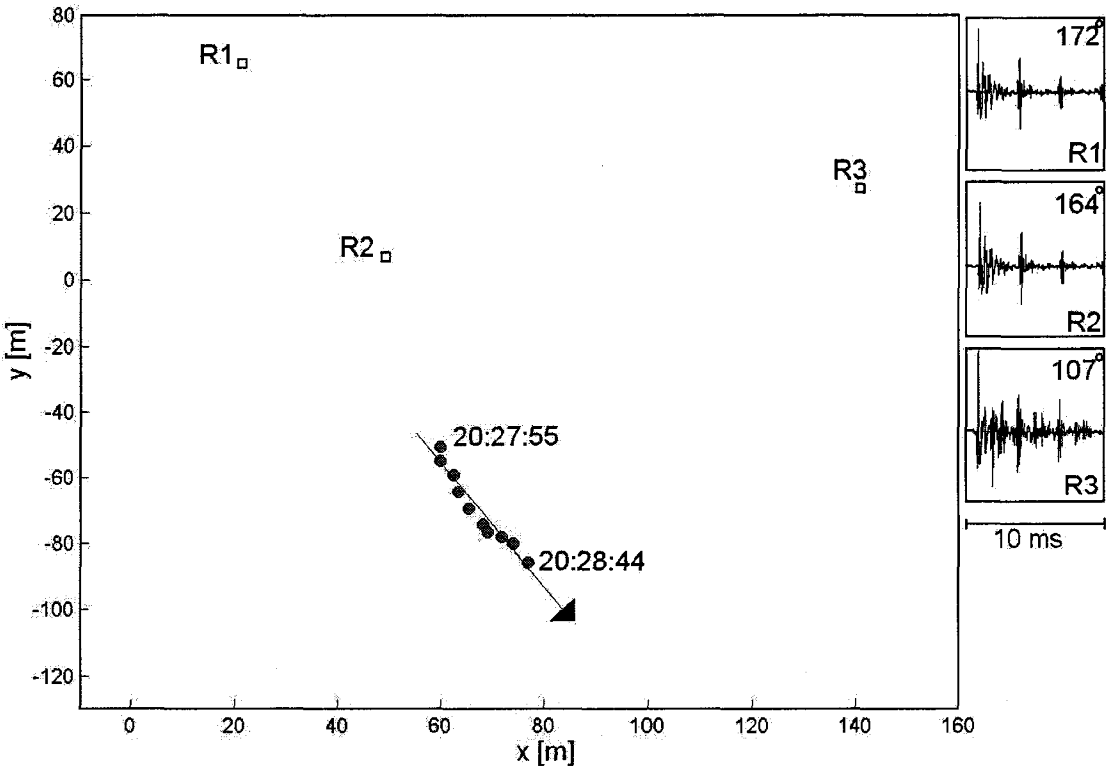

Figure 9.8. The GPS positions of three hydrophone receivers (R1-R3; □) at 20:27:55 and the estimated location solutions for codas with inter-pulse intervals of 3.24-3.27 msec (•) produced throughout recording session #061002. The arrow indicates the estimated direction of the vocalizing whale based on codas localized between 20:27:55 and 20:28:44. The waveform of a coda click as received on each of the three hydrophone receivers at 20:27:55 is presented along the right side of the figure together with the calculated angle between the hydrophone receiver and the estimated acoustic axis of the whale.

To examine the effect of recording angle on the clarity of pulse structure, I also plotted the CV in the squared amplitude of each localized click waveform on each hydrophone receiver against the estimated angle between the location of that hydrophone and the acoustic axis of the whale at the time at which the click was produced. Figure 9.9 quantitatively illustrates the qualitative observation described above that coda clicks recorded off-axis tended to possess less well-defined waveforms than those recorded closer to the acoustic axis. Although some click waveforms that were recorded on-axis possessed low CVs (see Figure 9.9), such waveforms possessed clear, well-defined pulse structures but poorly defined initial pulses (e.g. Figure 9.10), thereby resulting in a low CV during the initial 5 msec of the click. Poorly defined initial pulses in otherwise well-defined clicks may have been a result of the initial release of the sound energy into the water or the distortion of the initial pulse by the p1/2 pulse.

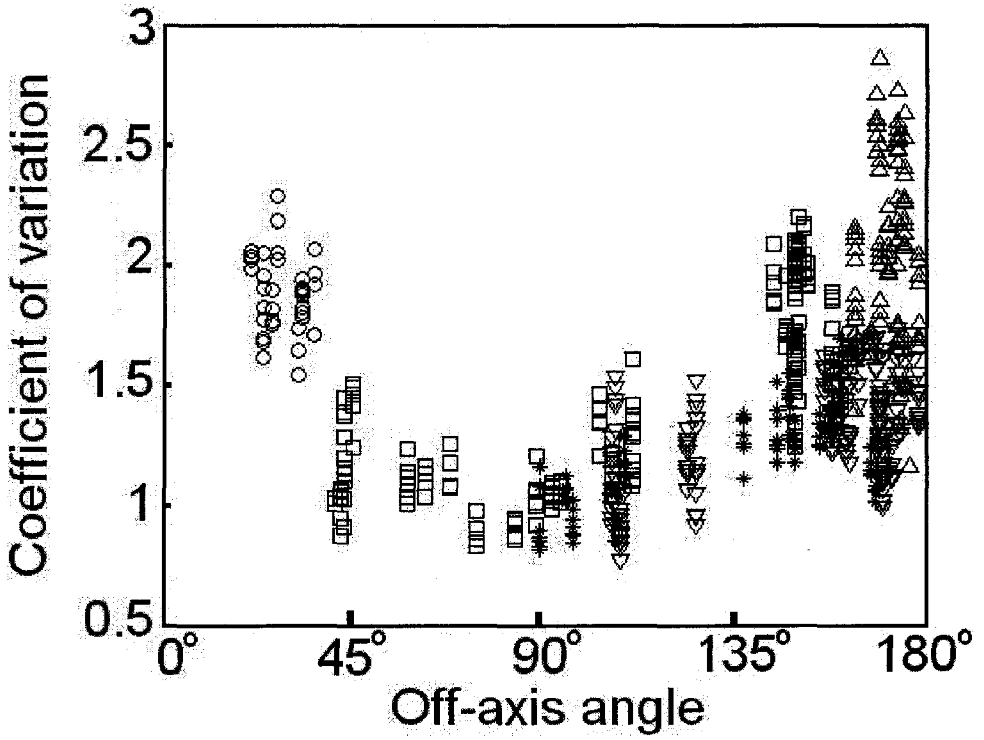

Figure 9.9. Scatterplot of the coefficient of variation (in the squared amplitude of the initial 221 samples) in coda click waveforms vs. the estimated angle between the hydrophone receiver and the acoustic axis of the whale. The coefficient of variation was calculated for 652 click waveforms from 33 different codas from five whales in three recording sessions (#051403, #060901, and #061002). Each whale is represented by a different symbol.

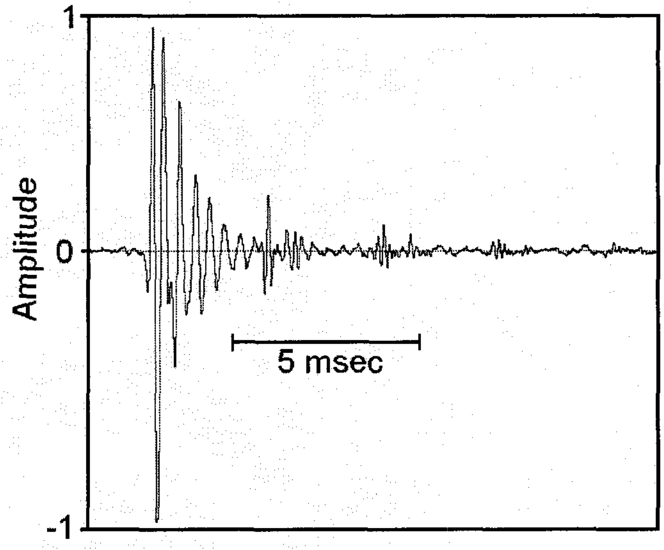

Figure 9.10. Waveform of a coda click recorded at an estimated angle of 178° between the hydrophone receiver and the acoustic axis of the whale. Although the pulse structure of the waveform is well-defined, it possesses a relatively low coefficient of variation in squared amplitude due to the indistinct initial pulse.

DISCUSSION

Examination of coda click waveforms recorded from different aspects indicates that sperm whale coda clicks, like usual clicks, are affected by recording orientation. For several different localized whales, waveforms of coda clicks recorded on or near the whale's estimated acoustic axis visually demonstrated a much more well-defined pulse structure than the same clicks recorded off-axis. Furthermore, plotting the coefficient of variation in amplitude of localized clicks against the estimated angle of recording indicated that clicks recorded off-axis (~90°) tended to have more poorly defined pulse structures than those recorded closer to the acoustic axis.

Differences in click waveforms between hydrophones are clearly due to differences in recording aspect and not an artifact of variation in recording quality between different hydrophones since recordings from receivers R1 and R2 in session #051403 demonstrated poor click waveforms for the clicks of one whale recorded off-axis within the array (Figure 9.5) but demonstrated distinct multi-pulsed waveforms for the clicks of another whale recorded on-axis out of the array (Figure 9.6). Moreover, there was also consistency within recording sessions in the clarity of pulse structure between recordings made from similar recording aspects, again indicating that the waveform of recorded coda clicks is dependent on the angle between the hydrophone receiver and the orientation of the vocalizing whale rather than the quality of the hydrophone recording.

If the sound energy of coda clicks were emitted only from the anterior end of the spermaceti organ, one would find the structure of recorded clicks to be similar at all recording aspects (Zimmer et al. 2005a). The results presented here that sperm whale coda clicks recorded off-axis are much less defined in pulse structure than clicks recorded on-axis indicate that the sound energy does not exit solely from the front of the spermaceti organ and must also be leaked as a p1/2 pulse from some other point, most likely upon reflection of the frontal sac as in usual clicks.

Zimmer et al. (2005a) mistakenly stated that field observations by Rendell and Whitehead (2004) suggest that codas recorded in the far-field have stable IPIs. The finding here of off-axis effects clearly indicates otherwise and partially explains the considerable number of coda clicks discarded in previous IPI analyses (Chapter 2; Rendell and Whitehead 2004; Marcoux et al. 2006). Moreover, the results of this chapter should encourage researchers to record sperm whale codas on-axis, most likely from behind the whale, and exclude from IPI analysis coda clicks recorded off-axis with poor pulse structure (see Chapter 2). Although ensuring on-axis recordings with a single hydrophone can be difficult, using a number of hydrophones in an acoustic array can increase the likelihood of recording coda clicks from an on-axis aspect and thus of obtaining clear IPIs for the estimation of body length or assignment to specific whales (see Chapter 2).

The waveforms of coda clicks recorded from different aspects also suggest that, unlike for usual clicks (Møhl et al. 2003; Zimmer et al. 2005a,b), the principal pulse is the p0 pulse. If coda click production resembled usual click production in that the bulk of the sound energy traveled backwards through the nasal complex and reflected off the frontal sac before release into the water, then one would likewise expect to observe a weak p0 pulse in the waveforms of coda clicks recorded from in front of the vocalizing whale, a result of the leakage of sound energy from the anterior end of the spermaceti organ. In array recordings made from receivers that appear to be nearly in front of a coda-producing whale (R1-R3 in session #060901), there was no observed weak p0 pulse before the large principal pulse (Figure 9.7 and Figure 9.11a), suggesting that the initial pulse is the p0 pulse and the result of sound energy released directly into the water. However, because no whale was observed at the water surface at the time that these codas were produced and because the codas were localized outside of a three-hydrophone array, estimates of the location and thus orientation of the vocalizing whale should be considered with caution.

On the other hand, assuming that the whale vocalizing in session #060901 was correctly localized moving toward the acoustic array, the lack of an observed weak p0 pulse could also be explainable if all – or nearly all – of the sound energy produced at the phonic lips was reflected backwards into the spermaceti organ rather than released directly into the water. This supposition is corroborated by the observation that some coda clicks recorded - but not localized - during the #051403 recording session possessed waveforms that are similar in structure to usual clicks recorded on-axis (i.e. weak p0 pulse followed by a very large p1 pulse) (Figures 9.11b and 9.11c). If coda click production involved the initial emission of a powerful p0 pulse directly into the water, then under no recording aspect could the coda click waveforms presented in Figures 9.11b and 9.11c possibly be observed.

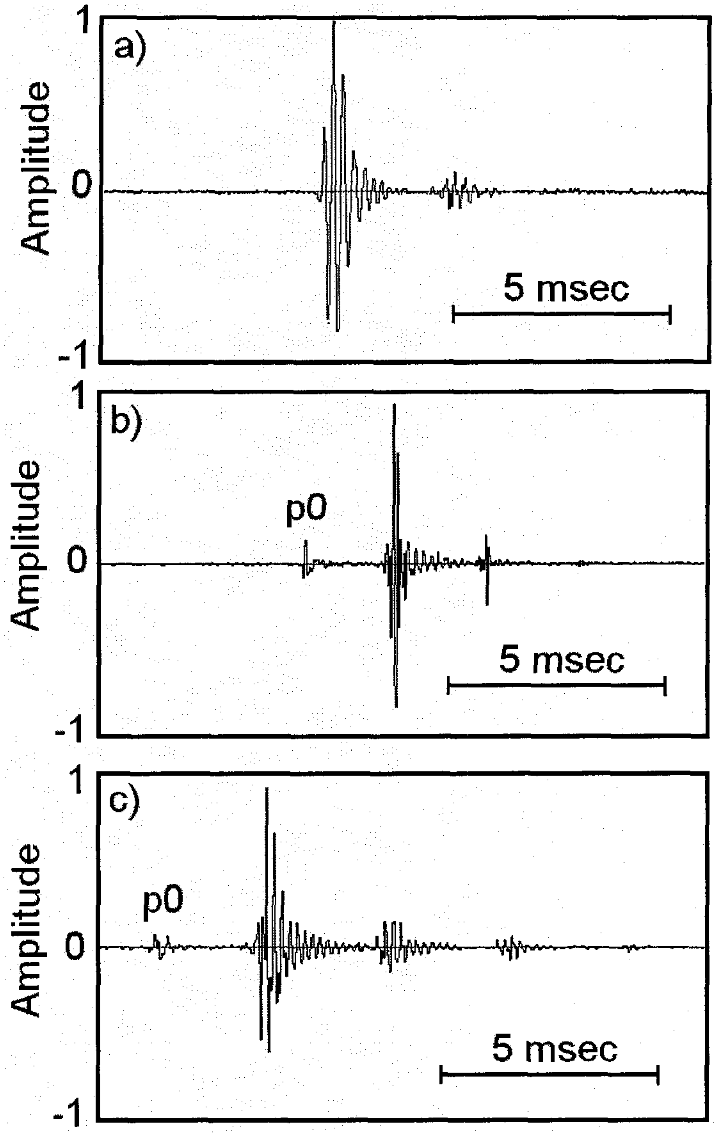

Figure 9.11a) A coda click recorded on hydrophone R2 in recording session #060901 as the localized whale appeared to be oriented toward the acoustic array; **b)** A highly mono-pulsed coda click with a weak initial pulse (p0) recorded in session #051403; **c)** Another coda click recorded in session #051403 with a weak initial pulse (p0) but with a less mono-pulsed waveform structure than b).

Rather, a more likely explanation for these click waveforms is that they were recorded on-axis in front of the vocalizing whale and produced in a manner similar to usual clicks with the majority of the sound energy reflected back into the spermaceti organ before emission into the water. Moreover, the highly mono-pulsed appearance of the waveform in Figure 9.11b compared to the multi-pulsed structure of most other coda clicks (Figure 9.3), suggests that the production of this click involved either the deflation of the distal sac after the emission of the p1 pulse (to greatly reduce the amount of sound energy reverberating within the spermaceti organ) or else the redirection of sound energy into the junk, as in usual click production, to produce a highly directional, mono-pulsed click. Nonetheless, these observed differences in the pulse structure of well-defined coda click waveforms suggest that sperm whales may be able to adjust their coda click production. If so, then coda click production may be more flexible than that of usual clicks, perhaps permitting sperm whales to produce both highly directional and powerful coda clicks as well as coda clicks with multiple pulses that more effectively advertize body length via inter-pulse intervals. Future research that examines the contexts in which multi-pulsed and essentially mono-pulsed coda clicks are produced would be useful not only in confirming this hypothesis but also in uncovering the functions of different coda click types if they do exist.

CHAPTER TEN

DISCUSSION

INTRODUCTION

The exchange of click patterns between sperm whales in long-term social units can give the impression that these large-brained animals engage in complex conversations using a Morse code-like language. While research at the level of the social unit has certainly improved our understanding of sperm whale coda production (see Whitehead and Weilgart 1991; Weilgart and Whitehead 1993; Rendell and Whitehead 2003b, 2004; Whitehead 2003a; Marcoux et al. 2006), the lack of knowledge of coda production at the individual level has left only speculation concerning the complexity and meaning of sperm whale coda communication. Likewise, the lack of information on bottlenose dolphin and killer whale vocal production at the level of the individual has allowed some artists, shamans, musicians, and other listeners to conclude that several cetacean species possess complicated languages that convey profound or spiritual information. Unfortunately without the ability to assign vocalizations of free-living cetaceans to individuals within a group, it has been difficult to refute, confirm, or even investigate these claims.

KEY FINDINGS AND SUGGESTED FUTURE RESEARCH

One of the most practical contributions of my thesis is the demonstration that recorded codas can be assigned to individuals using differences in their inter-pulse intervals (IPIs). In Chapter 2, I described how I used recordings in which only two whales were present to improve a previously developed routine – which calculated the IPIs of coda clicks – and find the criteria for assigning codas to whales within a recording. Although this method and criteria are most useful for discriminating between the codas of a few whales with highly dissimilar IPIs, its use should not be overlooked for analyzing recordings with many whales, some with similar IPIs. Even if several whales in a recording have similar IPIs (< 0.05 msec), adjacent codas with dissimilar IPIs (>0.10

msec) can be assumed to have been made by different whales, therefore still providing information on the production and exchange of codas between whales (see Chapters 4 and 5).

The application of this method to recordings of a well-studied social unit (the Group of Seven) not only allowed the detailed investigation of coda production at the individual level, but also revealed several interesting findings. First, the coda click IPIs of photo-identified whales were consistent in different recordings over several weeks, indicating that one can study the coda output of individuals in different contexts over time (Chapter 2). Second, each whale's modal usual click IPI was approximately 0.05 msec shorter than its coda click IPIs (Chapter 2). This suggests that usual clicks and coda clicks are produced differently within the nasal complex or that pressure at depth reduces the travel path of usual clicks. Analysis of recordings in which a whale produces both coda clicks and usual clicks at the surface would help to determine whether either of these hypotheses is true.

Not only did I develop a method to assign codas to individuals, but I also developed a passive acoustic array to localize sperm whales in the field (Chapter 7). Calibration tests indicated that this system is practical in discriminating between the codas produced by whales within the array (Chapter 7). Moreover, deployments of the array in the field demonstrated its utility at localizing sperm whales and addressing questions concerning the distance between coda exchanging whales (Chapter 8) as well as the physiology of coda click production (Chapter 9).

In Chapter 1, I outlined several possible hypotheses concerning the functions of coda production, many of which are not mutually exclusive (see Table 1.1). Making use of the modified IPI analysis method and the acoustic array described in chapters 2 and 7 respectively, I tested predictions that address these hypotheses. Here, I summarize the key findings of my thesis in as far as they support or reject these hypotheses (see Table

10.1) and discuss what these results mean in advancing our understanding of coda communication. Furthermore, I suggest priorities for future research based on the findings and methods presented here.

Table 10.1. Hypotheses for the functions of coda communication (rows) and the findings of predictive tests (columns). Within the table, hypotheses that are supported by a finding are indicated by **Y** and hypotheses that are rejected by a finding are indicated by **N**. Hypotheses that are neither supported nor rejected by a finding are left blank.

Function	Differences between whales in coda repertoires (Chapter 3)	Few differences between units in coda repertoires (Rendell 2003)	Differences between clans in coda repertoires (Rendell and Whitehead 2003b)	Little variation in coda repertoires within whales between recordings (Chapter 3)	Whales tend to overlap the codas of other whales (Chapter 4)	Coda overlapping is reciprocal between whales (Chapter 4)	Whales tend to match the codas of other whales (Chapter 4)	Coda matching is reciprocal between whales (Chapter 4)	Whales engage in duet-like coda exchanges (Chapter 4)	Redundancy in coda repertoire of unit (Chapter 5)	Whales do not alternate coda production with other whales (Chapter 5)	Few rules in the ordering of coda types within sequences (Chapter 5)	Coda production relatively equal amongst adult females in the unit (Chapter 6)	Coda exchanges occur between whales that are out of visual contact (Chapter 8)	Coda exchanges occur between whales that are in close proximity (Chapter 8)
Individual identification	Y	Y	Y	Y											
Unit identification	Y[1]	N	Y							Y					
Clan identification	Y[1]	Y	Y							Y					
Referential / contextual calling				N											
Contact calling					N	N	Y	Y	Y	Y	N		Y	Y	N
Affirmation of social bonds					Y	Y	Y	Y	Y	Y	Y		Y	Y	Y
Display of dominance or aggression					Y	N	Y	N	N	Y	Y		N		
Syntactic communication										N		N			

[1] Although the finding of some dissimilar coda repertoires within a social unit suggests that codas play some role in individual identification, because repertoires within a unit were generally similar, codas may still function in unit or clan identification.

The Role of Codas in Individual Identification

Codas were initially suggested to function as individual identifiers, with each whale producing one coda type to advertize its identity (Watkins and Schevill 1977; Watkins et al. 1985). However, the assignment of codas to individuals (or IPI classes) indicated that whales share several coda types within social units, thereby refuting this hypothesis (Chapter 3; Rendell and Whitehead 2004). Moreover, my analysis in Chapter 3 indicated that, for the most part, whales within a unit produced different coda types at similar rates. This suggests that in general, whales do not possess individual-specific coda repertoires to advertize identity and that any observed differences in repertoires between units or clans likely cannot be attributed to differences between individuals. This finding therefore rejects the hypothesis that codas or coda repertoires function exclusively in individual identification but still permits consideration of the hypotheses that coda types function in unit or clan identification (see Table 10.1).

Nevertheless, the analysis presented in Chapter 3 also revealed that two animals – the calf and its mother - did possess coda repertoires that were dissimilar to those of the other whales, including each other. Given that these repertoire differences were not correlated with genetic relatedness, the individual repertoires of these two animals are likely functional and related to their increased necessity to locate one another and ensure the efficient transfer of milk. Therefore, codas likely do play a role in broadcasting individual identification (see Table 10.1), but only for those animals with an increased need to do so. However, further research on this social unit, as well as units consisting of multiple mothers and calves, is necessary to determine whether mothers possess individual-specific or mother-specific repertoires. Continued research on the repertoires of the Group of Seven whales will be particularly useful now that the mother has lost its calf and another unit member, which was the calf's principal babysitter (Gero 2005), appears to have a calf (S. Gero pers. comm.[5]).

The Role of Codas in Unit and Clan Identification

Because coda repertoires differ between units in different clans (Rendell and Whitehead 2003b) – but differ little between units within clans (Rendell 2003) – and because units preferentially associate with units with similar repertoires (Rendell and Whitehead 2003b), it seems likely that coda types function in advertizing clan – but not unit – identity (Table 10.1). Moreover, the tendency for social units to favour a few coda types and produce others only rarely (Chapter 5) also suggests that codas function to broadcast clan affiliation at least on some occasions (Table 10.1). Nonetheless, future analysis of the types of codas produced by units when alone and when socializing with other units will be important in determining whether unit repertoires function specifically in communicating clan affiliation for the purpose of identifying other clan members, or whether clan-specific repertoires are purely the result of cultural drift.

The Role of Codas in Referential / Contextual Communication

Another proposed function of sperm whale codas is to refer to external referents or contexts. However, the analysis of Group of Seven whales in Chapter 3 indicated that the coda repertoires of whales were as varied within recordings as they were between them. Assuming that recordings made on different days over several weeks represent different contexts, this suggests that codas differ little between recording contexts. In fact, several whales in the unit – particularly the calf's mother – favoured only one or two coda types in several recordings made over several weeks. While these findings tentatively reject the hypothesis that codas function to refer to context-specific cues or referents (see Table 10.1), the role of coda types in this function could become more apparent when comparing very different recording contexts. Therefore, future research on the variation in coda types produced in markedly different contexts (e.g. presence of mature males or predators) is needed to fully reject this hypothesis.

The Role of Coda Exchanges as Contact Calls

Vocal exchanges between highly related and social animals often function as cohesion calls (to maintain contact between separated group members) or isolation calls (to locate and reunite isolated individuals). While the loud intensity of sperm whale coda clicks (Watkins 1980; P. Madsen pers. comm.[6]), the tendency to coda match (Chapter 4), the redundancy in the coda repertoires of social units (Chapter 5), and the observation of coda exchanges between whales several hundred metres apart (Chapter 8) all suggest that vocal exchanges could function as contact calls, several other findings conflict with this hypothesis. First, whales do not alternate coda production in a turn-taking fashion (Chapter 5), as has been observed in animals that maintain acoustic contact during physical separation (e.g. Snowdon and Cleveland 1984; Oda 2002). Second, coda exchanges occur not only between distant whales but also between whales that are in very close proximity and certainly within visual contact (Chapter 8). Third, most coda exchanges occur as coda overlaps (Chapter 4). This was true in recordings made of the Group of Seven, Unit T, and pairs of sperm whales recorded in the Sargasso Sea (Chapter 4). Therefore, while the observation of coda exchanges between both near and far whales could imply that exchanges function as contact calls between distant whales but have some other purpose between close whales, because overlapping exchanges likely mask the location information available to the signaler and receiver, this hypothesis is rejected (Table 10.1). And while the dissimilarity between the calf and mother's coda repertoires with those of other whales in the Group of Seven suggest that their codas function to advertise individual identity (and thus reunite the pair after periods of separation), additional research on coda production by mother-calf pairs during separation and reunion is necessary before concluding that they function as contact calls.

The Role of Coda Exchanges in Social Bonding

Overlapping coda exchanges between whales both in close proximity and several hundred metres apart could function in advertizing, establishing, or reaffirming social bonds between unit members. Because vocalizing sperm whales tend to produce codas every 3-5 s (Chapter 4), listening whales likely anticipate the timing of subsequent coda production and produce a coda that results in an overlapping coda exchange (see Richman 1978). The tendency for whales to produce codas in sequences and overlap other whales therefore results in sequences of overlapping coda exchanges that resemble the duets of mated birds and primates (Chapter 4). Given that duets function in several species to advertize and/or affirm a social bond (see Armstrong 1973; Richman 1978; Wickler 1980; Farabaugh 1982; Haimoff 1984; Geissmann 1999; Geissmann and Orgeldinger 2000; Hall 2004; Rogers et al. 2006), the overlapping exchange sequences of sperm whales likely serve to broadcast the pair bond to other whales and/or to confirm the social relationship between the vocalizing whales (Table 10.1). In this way, coda overlapping may function as a form of vocal grooming (Dunbar 1996) to maintain the social structure of units.

The analysis of sperm whale coda exchanges in Chapter 4 not only revealed that whales engage in overlapping exchanges, but also indicated that whales often match the coda that they overlap. However, further analyses also revealed that whales match a previous coda in an overlapping exchange sequence even more often than the coda that they overlap. Together with the short time onset between some overlapping codas, this suggests that whales respond to the *previous* coda rather than directly to the coda that they overlap. This resembles the duetting behaviour of Gelada monkeys (see Richman 1978).

In both social units studied, only one coda type in each unit was matched more often than expected (Chapter 4), suggesting that whales do not match a variety of coda types but simply respond in kind to a specific type. If a specific coda type functions within a unit to signify clan affiliation (see Chapter 3), then the matching of that type might function to further bond together those whales that share that affiliation. Given the success of playback experiments in improving our understanding of song overlapping and matching in songbirds (e.g. Burt et al. 2001), playback experiments that produce sequences of codas at regular intervals and overlap/match the codas of other whales may be useful in further examining this behaviour and its function in sperm whales.

The Role of Codas in Communicating Dominance and Aggression

Although overlapping exchanges function in some species to signify dominance or aggressive intentions (e.g. Verner 1975; Kroodsma 1979; Dabelsteen et al. 1997; Burt et al. 2001), the results in Chapter 4 indicate that coda overlapping was reciprocal between whales and not biased towards animals with larger IPIs. Moreover, coda overlapping occurred during social periods and was not associated with any noticeable displays of aggression (pers. obs.), suggesting that overlapping does not play a dominance or aggression function (Table 10.1). Similarly, coda matching was also reciprocal, suggesting that this behaviour is mutually beneficial and does not have a dominance or aggressive function (Table 10.1).

A comparison of the rates of vocal output amongst adult females in the Group of Seven indicated that whales vocalized at roughly equal rates (Chapter 6), rejecting the possibility that sperm whales use vocal output to assert dominance over other adult females (Table 10.1). However, the two males within the unit – the calf and the juvenile – vocalized much less frequently than the adult females (Chapter 6), which could indicate that they are subordinate to the more vocal adult females. More likely, this indicates that while codas serve some function even for young males, coda production in adult females serves some additional function, such as social bonding via coda overlapping and matching.

The Role of Codas in Syntactic Communication

Finally, the assignment of codas to individuals permitted the examination of the relative communication capacity and possible syntactic structure of coda communication (Chapter 5). The unit repertoires of both the Group of Seven and Unit T were highly redundant, meaning that a few coda types were produced very often while others were produced only rarely. Therefore, the repertoires of these social units differ from those of human languages and bottlenose dolphins - which balance redundancy and diversity for the optimal transfer of information (Zipf 1949, 1968; McCowan et al. 1999) - and suggest that coda production does not function in syntactic communication (see Table 10.1). In contrast to the repertoire of the adults as a whole, however, the calf's repertoire in the Group of Seven was more diverse, and therefore could represent babbling as observed in bottlenose dolphin and human infants (Zipf 1949, 1968; McCowan et al. 1999).

Whales in both social units tended to repeat themselves in coda sequences, indicating that not only was coda production in these units highly redundant but also that they are highly repetitious temporally (Chapter 5). Again, this suggests that coda production provides little capability of generating meaningful syntactic sentences (see Table 10.1). Instead, whales may repeat themselves to ensure that a coda type and its communicative significance are effectively conveyed to the intended receiver(s). Moreover, since coda transitions between whales (both within and between overlapping coda exchanges) also tended to be coda matches (Chapter 5), it is possible that production of a particular coda type – perhaps a coda that denotes clan affiliation – provokes the repetition of that type, possibly as a result of opiate production. As a result, the high proportion of particular coda types in the coda repertoires of a social unit might not be an adaptation to advertize clan affiliation but rather a byproduct of the repetition and matching of specific coda types that function in social bonding within the unit.

The rejection of the hypothesis that codas function to convey meaningful information is further supported by the observation that whales did not exchange codas in a conversational turn-taking fashion (Chapter 5) and most exchanges were overlapping exchanges (Chapter 4), which would mask the signal content of the overlapped and overlapping codas.

CONCLUSIONS

The results presented in this thesis suggest that the primary purpose of coda production by adult females within a sperm whale social unit is to affirm social bonds between unit members, a function achieved by the overlapping and matching of codas. Because vocalizing sperm whales tend to produce codas at regular 3-5 s intervals, whales are likely able to anticipate and subsequently overlap and match another whale's codas, resulting in duet-like overlapping and matching sequences that sometimes include highly synchronized echocodas. Given the tendency for whales to overlap other codas, the variable distance between exchanging whales, the reciprocity in overlapping and matching, and the little communication capacity within sequences and between whales, these exchanges likely do not function as contact calls, as displays of dominance, or in the syntactic exchange of meaningful information. Instead, these observations suggest that sequences of overlapping exchanges resemble duets in other social species or mated pairs and therefore function as vocal grooming to reaffirm social bonds. This is likely important in maintaining the structure of long-term social units.

If coda production does function largely for social bonding, this would explain the relative lack of coda production – and coda overlapping – by the male calf and juvenile in the Group of Seven, since these animals would eventually leave their natal unit to join bachelor schools. However, since these males still produced codas within the unit – although not as overlaps – codas probably serve some function for these whales other than social bonding. Furthermore, the variety of coda types produced by adult females also suggests that codas serve some additional function besides social bonding for these whales as well. The data suggest that this additional function is individual and clan identification.

The juvenile male's repertoire within the Group of Seven is similar to that of other adult females within the unit – excluding the calf's mother – suggesting that the types of codas that it produces function in a manner similar to the types produced by the other adult females. Given that the repertoires of the juvenile and adult females – excluding the calf's mother - were dominated by the most prevalent codas in the unit repertoire and given that units tend to associate with units with similar unit repertoires, the function of these coda types is likely to communicate clan affiliation. If so, then this could explain the repetition and matching of these types within units, perhaps to ensure the efficacy of signal reception or perhaps as a result of the release of endorphins from producing a coda that communicates belonging to a particular clan. However, whether codas function to signal clan affiliation within units or between units when forming groups is still not clear. Therefore, there is a need to examine the coda repertoires of individuals and units both when in isolated units and when units meet with other units to form groups.

Not only might coda types function to identify clan affiliation, but they may also function in individual identification, at least for some whales. The markedly dissimilar coda repertoire of the calf's mother in the Group of Seven and its consistency between recordings made over several weeks suggests that its coda types do not function in context-specific calling but instead in advertizing individual identity, although further research is needed to determine whether the mother's codas function as contact calls to facilitate reunion with the calf. While the calf's repertoire was also dissimilar to the other whales in the Group of Seven, this could be a result of its greater coda diversity, which could indicate babbling and the development of its coda repertoire. Longitudinal studies of the coda repertoires of individuals are needed to examine the development of calves' coda repertoires as well as the individuality of adult females' coda repertoires before, during, and after periods as a nursing mother.

A social bonding function for coda communication is to be expected given the stable nature of social units. Because whales within a unit are separated a great deal during alternating foraging dives, social grooming in the form of vocal exchanges likely plays an important role in maintaining social relationships between animals that cooperatively provide allomaternal care and communal protection from predators. Since it is from close-contact vocal grooming that it is suggested that human language first evolved (Dunbar 1996), one might also expect to find similar syntactic rules or referential communication in sperm whale coda production. However, coda communication appears to be rather simple and devoid of complicated syntax, which might be related to the apparent inability of sperm whales to point, since pointing may be associated with the development of symbolic and syntactic language (see Steels et al. 2002; Számadó and Szathmáry 2006). Without the ability to point at external referents and associate these referents with particular codas, sperm whale communication may remain at the vocal grooming and social bonding stage.

Despite the advances made here in improving our understanding of coda communication, several questions remain. If only a few coda types function to identify clan affiliation, then why do whales produce a variety of different coda types? Why not produce one or two clan-specific coda types and exchange these types in social bonding overlap exchanges? Although whales certainly favour one or two coda types within a unit, the reason for producing other coda types, even rarely, is still unclear. Future longitudinal studies on the coda output of individuals in different recording contexts and in the presence of different unit members would be useful to examine this question. Likewise, long-term studies with repeated recordings of the same individuals are needed to examine the ontogeny of coda repertoires and changes in coda repertoires during different life stages. With these objectives in mind, research off the coasts of Dominica and Guadeloupe, where social units tend to remain in the area for extended periods of time (Gero et al. in press), would likely be most fruitful in addressing these questions. Now that it is evident that codas can be assigned to individuals, our understanding of sperm whale communication is only limited by the collection of usable data and the time and resources available to analyze them.

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APPENDIX ONE

Publications

The work presented in Chapter 7 also appears in:

Schulz, T. M., Whitehead, H., and Rendell, L. 2006. A remotely-piloted acoustic array for studying sperm whale vocal behaviour. Journal of the Canadian Acoustical Association 34: 54-55.

REFERENCES

Adler-Fenchel, H. S. 1980. Acoustically derived estimate of the size distribution for a sample of sperm whales (*Physeter catodon*) in the Western North Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 37: 2358-2361.

Aitchison, J. 1998. The articulate mammal: An introduction to psycholinguistics, 4th edition. Routledge, London.

Anderson, R. C., Searcy, W. A., and Nowicki, S. 2005. Partial song matching in an eastern population of song sparrows, *Melospiza melodia*. Animal Behaviour 69: 189-196.

Arak, A. 1983. Vocal interactions, call matching and territoriality in a Sri Lankan treefrog, *Philautus leucorhinus* (Rhacophoridae). Animal Behaviour 31: 292-302.

Armstrong, E. A. 1973. A study of bird song, 2nd edition. Dover, New York.

Arnbom, T. 1987. Individual identification of sperm whales. Reports of the International Whaling Commission 37: 201-204.

Aureli, F., van Schaik, C., and van Hooff, J. 1989. Functional aspects of reconciliation among captive long-tailed macaques (*Macaca fascicularis*). American Journal of Primatology 19: 39-51.

Backus, R. H. and Schevill, W. E. 1966. *Physeter* clicks. In Whales, dolphins and porpoises. Edited by K. S. Norris. University of California Press, Berkeley. pp. 510-527.

Beecher, M. D., Stoddard, P. K., and Loesche, P. 1985. Recognition of parents' voices by young cliff swallows. Auk 102: 600-605.

Beecher, M. D., Campbell, S. E., Burt, J. M., Hill, C. E., and Nordby, J. C. 2000. Song-type matching between neighbouring song sparrows. Animal Behaviour 59: 21-27.

Bejder, L., Fletcher, D., and Bräger, S. 1998. A method for testing association patterns of social animals. Animal Behaviour 56: 719-725.

Bérubé, M. and Palsbøll, P. 1996. Identification of sex in cetaceans by multiplexing with three ZFX and ZFY specific primers. Molecular Ecology 5: 283-287.

Best, P. B. 1979. Social organization in sperm whales, *Physeter macrocephalus. In* Behavior of marine mammals, vol. 3. *Edited by* H. E. Winn and B. L. Olla. Plenum Press, New York. pp. 227-289.

Biben, M. 1993. Recognition of order effects in squirrel monkey antiphonal call sequences. American Journal of Primatology 29: 109-124.

Biben, M., Symmes, D., and Masataka, N. 1986. Temporal and structural analysis of affiliative vocal exchanges in squirrel monkeys (*Saimiri sciureus*). Behaviour 29: 259-273.

Bildstein, K. L. 1983. Why white-tailed deer flag their tails. The American Naturalist 121: 709-715.

Bowyer, R. T. and Kitchen, D. W. 1987. Sex and age-class differences in vocalizations of Roosevelt elk during rut. American Midland Naturalist 118: 225-235.

Bradbury, J. W. and Vehrencamp, S. L. 1998. Principles of Animal Communication. Sinauer Associates, Inc., Sunderland, Massachusetts.

Broadbent, D. E. and Gregory, R. L. 1962. Reaction time. Journal of Experimental Psychology 63: 575-584.

Brown, S. 2000. The ‘musilanguage’ model of music evolution. *In* The origins of music. *Edited by* N. L. Wallin, B. Merker, and S. Brown. MIT Press, Cambridge. pp. 271-300.

Burt, J. M. and Vehrencamp, S. L. 2005. Dawn chorus as an interactive communication network. *In* Animal communication networks. *Edited by* P. K. McGregor. Cambridge University Press, Cambridge. pp. 320-343.

Burt, J. M., Campbell, S. E., and Beecher, M. D. 2001. Song type matching as threat: a test using interactive playback. Animal Behaviour 62: 1163-1170.

Cairns, S. J. and Schwager, S. J. 1987. A comparison of association indices. Animal Behaviour 35: 1454-1469.

Caldwell, M. C., Caldwell, D. K., and Tyack, P. L. 1990. A review of the signature whistle hypothesis for the Atlantic bottlenose dolphin, *Tursiops truncatus*. *In* The bottlenose dolphin. *Edited by* S. Leatherwood and R. R. Reeves. San Diego: Academic Press.

Carrier, D. R., Deban, S. M., and Otterstrom, J. 2002. The face that sunk the *Essex*: Potential function of the spermaceti organ in aggression. Journal of Experimental Biology 205: 1755-1763.

Catchpole, C. K. and Slater, P. J. B. 1995. Bird song. Cambridge University Press, Cambridge.

Chaiken, M. 1990. The ontogeny of antiphonal calling in European starlings. Developmental Psychobiology 23: 233-46.

Cheney, D. L. and Seyfarth, R. M. 1980. Vocal recognition in free-ranging vervet monkeys. Animal Behaviour 28: 362-367.

Cheney, D. L. and Seyfarth, R. M. 1990. How monkeys see the world: Inside the mind of another species. University of Chicago Press, Chicago.

Chomsky, N. 1965. Aspects of the theory of syntax. M.I.T. Press, Cambridge, Massachusetts.

Chomsky, N. 1968. Language and mind. Harcourt, Brace & World, New York.

Christal, J. and Whitehead, H. 2001. Social affiliations within sperm whale (*Physeter macrocephalus*) groups. Ethology 107: 323-340.

Christal, J., Whitehead, H., and Lettevall, E. 1998. Sperm whale social units: Variation and change. Canadian Journal of Zoology 76: 1431-1440.

Clark, C. W. 1983. Acoustic communication and behavior of the southern right whale. *In* Communication and behavior of whales. *Edited by* R. Payne. Westview Press, Boulder. pp. 163-198.

Clark, C. W., Ellison, W. T., and Beeman, K. 1986. Acoustic tracking of migrating bowhead whales. IEEE Oceans Conference Proceedings, Washington D.C.

Clarke, M. R. 1970. The function of the spermaceti organ of the sperm whale. Nature 238: 405-406.

Clarke, M. R. 1978. Buoyancy control as a function of the spermaceti organ in the sperm whale. Journal of the Marine Biological Association of the United Kingdom 58: 27-71.

Clarke, M. R. 1980. Cephalapoda in the diet of sperm whales of the southern hemisphere and their bearing on sperm whale biology. Discovery Reports 37: 1-324.

Collins, K. T., Rogers, T. L., Terhune, J. M., McGreevy, P. D., Wheatley, K. E., and Harcourt, R. G. 2005. Individual variation of in-air female 'pup contact' calls in Weddell seals, *Leptonychotes weddellii*. Behaviour 142: 167-189.

Connor, R. C., Wells, R. S., Mann, J. and Read, A. J. 2000. The bottlenose dolphin: social relationships in a fission-fusion society. *In* Cetacean societies: field studies of dolphins and whales. *Edited by* J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead. Chicago University Press, Chicago. pp. 91-126.

Cooper, M. A. and Bernstein, I. S. 2000. Social grooming in assamese macaques (*Macaca assamensis*). American Journal of Primatology 50: 77-85.

Costa, D.P. 1993. The secret life of marine mammals. Oceanography 6: 120-127.

Cranford, T. W. 1999. The sperm whale's nose: Sexual selection on a grand scale? Marine Mammal Science 15: 1133-1157.

Dabelsteen, T., McGregor, P. K., Shepherd, M., Whittaker, X. and Pedersen, S. B. 1996. Is the signal value of overlapping different from that of alternating during matched singing in great tits? Journal of Avian Biology 27: 189-194.

Dabelsteen, T., McGregor, P. K., Holland, J., Tobias, J. A., and Pedersen, S. B. 1997. The signal function of overlapping singing in male robins. Animal Behaviour 53: 249-256.

Dittus, W. P. G. 1984. Toque macaque food calls: Semantic communication concerning food distribution in the environment. Animal Behaviour 32: 470-477.

Donders, F. F. 1868. Archives of Anatomy and Physiology. pp. 657-701.

Drouot, V., Gannier, A. and Goold, J. C. 2004. Diving and feeding behavior of sperm whales (*Physeter macrocephalus*) in the northwestern Mediterranean Sea. Aquatic Mammals 30: 419-426.

Dufault, S. and Whitehead, H. 1993. Assessing the stock identity of sperm whales in the eastern equatorial Pacific. Reports of the international Whaling Commission 43: 469-475.

Dunbar, R. 1991. Functional significance of social grooming in primates. Folia Primatologica 57: 121-131.

Dunbar, R. 1996. Grooming, Gossip, and the Evolution of Language. Harvard University Press, Cambridge, Massachusetts.

Falls, J. B. 1969. Functions of territorial song in the White-throated Sparrow. *In* Bird vocalizations. *Edited by* R. A. Hinde. Cambridge University Pres, Cambridge, England. pp. 207-232.

Farabaugh, S. M. 1982. The ecological and social significance of duetting. *In* Acoustic communication in birds, vol. 2. *Edited by* D. E. Kroodsma and E. H. Miller. Academic Press, New York. pp. 85-124.

Fitch, W. T. 2004. Evolving honest communication systems: Kin selection and "mother tongues". *In* Evolution of communication systems: A comparative approach. *Edited by* D. K. Oller and U. Griebel. MIT Press, Cambridge, Massachusetts. pp. 50-76.

Fitch, W. T. 2007. Evolving meaning: The roles of kin selection, allomothering and paternal care in language evolution. *In* Emergence of communication and language. *Edited by* C. Lyon, C. Nehaniv, and A. Cangelosi. Springer, New York. pp 29-51.

Forand, K. J. and Marchinton, R. L. 1989. Patterns of social grooming in adult white-tailed deer. American Midland Naturalist 122: 357-364.

Ford, J. K. B. 1991. Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. Canadian Journal of Zoology 69: 1454-1483.

Freeberg, T. M. 2001. Communicative cultures in cetaceans: big questions are unanswered, functional analyses are needed. Behavioral and Brain Sciences 24: 334.

Geberzahn, N. and Hultsch, H. 2004. Rules of song development and their use in vocal interactions by birds with large repertoires. Anais da Academia Brasileira de Ciências 76: 209-218.

Geissmann, T. 1999. Duet songs of the siamang, *Hylobates syndactylus*: II. Testing the pair-bonding hypothesis during a partner exchange. Behaviour 136: 1005-1039.

Geissmann, T. and Orgeldinger, M., 2000: The relationship between duet songs and pair bonds in siamangs, *Hylobates syndactylus*. Animal Behaviour 60: 805-809.

Gerhardt, H. C. Roberts, J. D., Bee, M. A., and Schwartz, J. J. 2000. Call matching in the quacking frog (*Crinia georgiana*). Behavioral Ecology and Sociobiology 48: 243-251.

Gero, S. 2005. Fundamentals of sperm whale societies: Care for calves. M.Sc. dissertation. Dalhousie University, Halifax, Nova Scotia.

Gero. S., Engelhaupt, D., and Whitehead, H. Submitted. Heterogenous associations within a sperm whale social unit reflect pairwise relatedness. Ethology.

Gero, S., Gordon, J., Carlson, C., Evans, P., and Whitehead, H. In press. Population estimate and inter-island movement of sperm whales, *Physeter macrocephalus*, in the Eastern Caribbean. Journal of Cetacean Research and Management.

Gillespie, D. 1997. An acoustic survey for sperm whales in the Southern Ocean sanctuary conducted from the R/V Aurora Australia. Reports of the International Whaling Commission. 47: 897-908.

Goold, J. C. 1996. Signal processing techniques for acoustic measurement of sperm whale body lengths. Journal of the Acoustical Society of America 100: 3431-3441.

Gordon, J. C. D. 1991a. Evaluation of a method for determining the length of sperm whales (*Physeter catodon*) from their vocalizations. Journal of Zoology, London 224:301-314.

Gordon, J. C. D. 1991b. The World Wildlife Fund's Indian Ocean Sperm Whale Project: An example of cetacean research within the Indian Ocean Sanctuary. *In* Cetaceans and cetacean research in the Indian Ocean Sanctuary. *Edited by* S. Leatherwood and G. P. Donovan. UNEP Technical Report Number 3, Nairobi, Kenya. pp. 219-239.

Gordon, J. C. D. 1998. Sperm whales. Colin Baxter, Grantown-on-Spey, Scotland.

Gordon, J. C. D. and Steiner, L. 1992. Ventilation and dive patterns in sperm whales, *Physeter macrocephalus*, in the Azores. Reports of the International Whale Commission 42:561-565.

Gouzoules, H. and Gouzoules, S. 1990. Matrilineal signatures in the recruitment screams of pigtail macaques, *Macaca nemestrina*. Behaviour 115: 327-347.

Gouzoules, S., Gouzoules, H., and Marler, P. 1984. Rhesus monkey (*Macaca mulatta*) screams: Representational signaling in the recruitment of agonistic aid. Animal Behaviour 32: 182-193.

Green, S. and Marler, P. 1979. The analysis of animal communication. *In* The handbook of behavioral neurobiology, vol. 3, Social behavior and communication. *Edited by* P. Marler and J. G. Vandenbergh. Plenum Press, New York. pp. 73-158.

Hailman, J. P. 1994. Constrained permutation in 'chick-a-dee'-like calls of the black-lored tit, *Parus xanthogenys*. Bioacoustics 6: 33-50.

Hailman, J. P. and Ficken, M. S. 1986. Combinatorial animal communication with computable syntax: 'chick-a-dee' calling qualifies as 'language' by structural linguistics. Animal Behaviour 34: 1899-1901.

Hailman, J. P., Ficken, M. S., and Ficken, R.W. 1985. The 'chick-a-dee' calls of *Parus atricapillus*: A recombinant system of animal communication compared with written English. Semiotica 56: 191-224.

Hailman, J. P., Ficken, M. S., and Ficken, R. W. 1987. Constraints on the structure of combinatorial 'chick-a-dee' calls. Ethology 75: 62-80.

Hailman, E. D. and Hailman, J. P. 1993. UNCERT: Analyses of sequential events by Markov chains (version alpha). A DOS-compatible software.

Haimoff, E. H. 1984. Acoustic and organizational features of gibbon songs. *In* The lesser apes. Evolutionary and behavioural biology. *Edited by* H. Preuschoft, D. J. Chivers, W. Y. Brockelman and N. Creel. Edinburgh University Press, Edinburgh. pp. 333-353.

Hall, M. L. 2004. A review of hypotheses for the functions of avian duetting. Behavioral Ecology and Sociobiology 55: 415-430.

Hall, M. L. and Magrath, R. D. 2000. Duetting and mate-guarding in Australian magpie-larks (*Grallina cyanoleuca*). Behavioral Ecology and Sociobiology 47: 180-187.

Hall, M. L., Illes, A., and Vehrencamp, S. L. 2006. Overlapping signals in banded wrens: long-term effects of prior experience on males and females. Behavioral Ecology 17: 260-269.

Halliday, T. 1983. Information and communication. *In* Animal behaviour communication. *Edited by* T. R. Halliday and P. J. B. Slater. Blackwell Scientific, Oxford. pp. 43-81.

Hau, M. Wikelski, M., Soma, K. K., Wingfield, J.C. 2000. Testosterone and year-round territoriality in a tropical bird. General and Comparative Endocrinology 117: 20-33.

Hauser, M. D. 2000. The sound and the fury: Primate vocalizations as reflections of emotion and thought. *In* The origins of music. *Edited by* N. Wallin, B. Merker, and S. Brown. M.I.T. Press, Cambridge. pp. 77-102.

Hauser, M. D. and Marler, P. 1993. Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors. Behavioral Ecology 4: 194-205.

Hayes, S. A., Mellinger, D. K., Croll, D. A., Costa, D. P., and Borsani, J. F. 2000. An inexpensive passive acoustic system for recording and localizing wild animal sounds. Journal of the Acoustical Society of America 107: 3552-3555.

Hemelrijk, C. K. 1990. Models of, and tests for, reciprocity, unidirectionality and other social interaction patterns at a group level. Animal Behaviour 39: 1013-1029.

Hinde, R. A. 1958. Alternative motor patterns in chaffinch song. Animal Behaviour 6: 211-218.

Hultsch, H. and Todt, D. 1986. Zeichenbildung durch mustergleiches Antworten. Zeitschrift für Semiotik 8: 233-244.

Hyman, J. 2003. Countersinging as a signal of aggression in a territorial songbird. Animal Behaviour 65: 1179-1185.

Jäckel, M. and Trillmich, F. 2003. Olfactory individual recognition of mothers by young guinea-pigs (*Cavia porcellus*). Ethology 109: 197-208.

Janik, V. M. 2000. Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). Science 289: 1355-1357.

Janik, V. M. 2005. Underwater acoustic communication networks in marine mammals. *In* Animal communication networks. *Edited by* P. K. McGregor. Cambridge University Press, Cambridge. pp. 390-415.

Janik, V. M. and Slater, P. J. B. 1998. Context-specific use suggests that bottlenose dolphin signature whistles are cohesion calls. Animal Behaviour 56: 829-838.

Janik, V. M., van Parijs, S. M., and Thompson, P. M. 2000. A two-dimensional acoustic localization system for marine mammals. Marine Mammal Science 162: 437-447.

Janik, V. M., Sayigh, L. S. and Wells, R. S. 2006. Signature whistle shape conveys identity information to bottlenose dolphins. Proceedings of the National Academy of Sciences of the United States of America. 103: 8293-8297.

Jaquet, N., Dawson, S., and Douglas, L. 2001. Vocal behavior of male sperm whales: Why do they click? Journal of the Acoustical Society of America 109: 2254-2259.

Jehle, R. and Arak, A. 1998. Graded call variation in the Asian cricket frog *Rana nicrobariensis*. Bioacoustics 9: 35-48.

Jones, I. L., Falls, J. B., and Gaston, A. J. 1987. Vocal recognition between parents and young of Ancient murrelets, *Synthliboramphus antiquus* (Aves: Alcidae). Animal Behaviour 35: 1405-1415.

Kawakami, T. 1980. A review of sperm whale food. The Scientific Reports of the Whales Research Institute. 6 :49-72.

Keverne, E., Martensz, N., and Tuite, B. 1989. Beta-endorphin concentrations in *cerebrospinal fluid on monkeys are influenced by grooming relationships.* Psychoneuroendocrinology 14: 155-161.

Kimura, R. 1998. Mutual grooming and preferred associate relationships in a band of free-ranging horses. Applied Animal Behaviour Science 59: 265-276.

Krebs, J. R., Ashcroft, R. and van Orsdol, K. 1981. Song matching in the great tit *Parus major* L. Animal Behaviour 29: 918-923.

Kreutz, G., Bongard, S., Rohrmann, S., Hodapp, V., and Grebe, D. 2004. Effects of choir singing or listening on secretory immunoglobin A, cortisol, and emotional state. Journal of Behavioral Medicine 27: 623-635.

Kroodsma, D. E. 1979. Vocal dueling among male marsh wrens: evidence for ritualized expressions of dominance/subordinance. Auk 96: 506-515.

Lamprecht, J., Kaiser, A., Peters, A., and Kirchgessner, C. 1985. Distance call duets in bar-headed geese (*Anser indicus*): co-operation through visual relief of the partner? Zeitschrift für Tierpsychologie. 70: 211-218.

Lambrechts, M. M. and Dhondt, A. A. 1995. Individual voice discrimination in birds. Current Ornithology 12: 115-139.

Langemann, U., Tavares, J. P., Peake, T. M., and McGregor, P. K. 2000. Response of great tits to escalating patterns of playback. Behaviour 137: 451-471.

Laurinolli, M. H., Hay, A. E., Desharnais, F., and Taggart, C. T. 2003. Localization of North Atlantic right whale sounds in the Bay of Fundy using a sonobuoy array. Marine Mammal Science 19: 708-723.

Laws, R. M., Parker, I. S. C. and Johnstone, R. C. B. 1975. Elephants and Their Habitats: the Ecology of Elephants in North Bunyoro, Uganda. Oxford: Clarendon.

Leaper, R., Chappell, O. and Gordon, J. 1992. The development of practical techniques for surveying sperm whale populations acoustically. Reports of the International Whaling Commission 42: 549-560.

Leaper, R., Gillespie, D. and Papastavrou, V. 2000. Results of passive acoustic surveys for odontocetes in the Southern Ocean. Journal of Cetacean Research and Management 2: 187-196.

Lemasson, A. and Hausberger, M. 2004. Patterns of vocal sharing and social dynamics in a captive group of Campbell's monkeys (*Cercopithecus campbelli campbelli*). Journal of Comparative Psychology 118: 347-359.

Lengagne, T., Jouventin, P., and Aubin, T. 1999. Finding one's mate in a king penguin colony: efficiency of acoustic communication. Behaviour 136: 833-846.

Leonard, M. L. and Horn, A. G. 2006. Age-related changes in signaling of need by nestling tree swallows (*Tachycineta bicolor*). Ethology 112: 1020-1026.

Leong, K. M., Ortolani, A., Graham, L. H., and Savage, A. 2003a. The use of low-frequency vocalizations in African elephant (*Loxodonta africana*) reproductive strategies. Hormones and Behavior 43: 433-443.

Leong, K. M., Ortolani, A., Burks, K. D., Mellen, J. D. and Savage, A. 2003b. Quantifying acoustic and temporal characteristics of vocalizations for a group of captive African elephants, *Loxodonta africana*. Bioacoustics 13: 213–231.

Lilly, J. C. and Miller, A. M. 1961. Vocal exchanges between dolphins; bottlenose dolphins "talk" to each other with whistles, clicks, and a variety of other noises. Science 134: 1873-1876.

Macedonia, J. 1991. What is communication in the anti-predator calls of lemurs: Evidence from playback experiments with ring-tailed and ruffed lemurs. Ethology 86: 177-190.

Madsen, P. T. 2002. Sperm whale sound production. Ph.D. dissertation. Aarhus University, Aarhus, DK.

Madsen, P. T., Wahlberg, M., and Møhl, B. 2002a. Male sperm whale (*Physeter macrocephalus*) acoustics in a high latitude habitat: implications for echolocation and communication. Behavioral Ecology and Sociobiology 53: 31-41.

Madsen, P. T., Payne, R., Kristiansen, N. U., Wahlberg, M., Kerr, I., and Møhl, B. 2002b. Sperm whale sound production studied with ultrasound time/depth-recording tags. Journal of Experimental Biology 205: 1899-1906.

Manly, B. F. J. 1994. Multivariate statistical methods. Chapman & Hall, New York.

Manly, B. F. J. 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology. 2nd edition. Chapman & Hall, London.

Mantel, N. 1967. The detection of disease clustering and generalized regression approach. Cancer Research 27: 209-220.

Marcoux, M., Whitehead, H., and Rendell, L. 2006. Coda vocalizations recorded in breeding areas are almost entirely produced by mature female sperm whales (*Physeter macrocephalus*). Canadian Journal of Zoology 84: 609-614.

Marler, P. 1959. Developments in the study of animal communication. *In* Darwin's Biological Work. *Edited by* P. R. Bell. Cambridge University Press, Cambridge. pp. 150-206.

Marler, P., Evans, C. S., and Hauser, M. D. 1992. Animal signals. Reference, motivation, or both? *In* Nonverbal vocal communication: Comparative and developmental approaches. *Edited by* H. Papoušek, U. Jürgens, and M. Papoušek. Cambridge University Press, Cambridge, England. pp. 66-86.

Masataka, N. and Biben, M. 1987. Temporal rules regulating affiliative vocal exchanges of squirrel monkeys. Behaviour 101: 311-319.

Masataka, N. and Symmes, D. 1986. Effect of separation distance on isolation call structure in squirrel monkeys (*Saimiri sciureus*). American Journal of Primatology 10: 271-278.

Mathevon, N. 1996. What parameters can be used for individual acoustic recognition by the greater flamingo? Comptes Rendus de l Academie des Sciences. Serie III, Sciences de la Vie (Paris) 319: 29-32.

MathWorks Inc. 2001. MATLAB®. Version 6.1.450, release 12.1, with Signal Processing Toolbox [computer program]. The MathWorks Inc., Natick, Mass.

Matsumura, S. 1981. Mother-infant communication in a horseshoe bat (*Rhinolophus ferrumequium nippon*): Vocal communication in three-week-old infants. Journal of Mammalogy 62: 20-28.

McArthur, P. D. 1982. Mechanisms and development of parent-young vocal recognition in the pinon jay (*Gymnorhinus cyanocephalus*). Animal Behaviour 30: 62-74.

McComb, K., Moss, C., Durant, S. M., Baker, L., and Sayialel, S. 2001. Matriarchs as repositories of social knowledge. Science 292: 491-494.

McCowan, B. and Reiss, D. 2001. The fallacy of 'signature whistles' in bottlenose dolphins: a comparative perspective of 'signature information' in animal vocalizations. Animal Behaviour 62: 1151-1162.

McCowan, B., Hanser, S. F., and Doyle, L. R. 1999. Quantitative tools for comparing animal communication systems: Information theory applied to bottlenose dolphin whistle repertoires. Animal Behaviour 57:409-419.

McCowan, B., Doyle, L. R., Jenkins, J. M., and Hanser, S. F. 2005. The appropriate use of Zipf's law in animal communication studies. Animal Behaviour 69: F1-F7.

McCulloch, S. and Boness, D. J. 2000. Mother-pup vocal recognition in the grey seal (*Halichoerus grypus*) of Sable Island, Nova Scotia, Canada. Journal of Zoology 251: 449-455.

McGregor, P. K. 1993. Signalling in territorial systems: A context for individual identification, ranging and eavesdropping. Philosophical Transactions: Biological Sciences 340: 237-244.

McGregor, P. K. and Falls, J. B. 1984. The response of western meadowlarks (*Sturnella neglecta*) to the playback of degraded and undegraded songs. Canadian Journal of Zoology 62: 2125-2128.

McGregor, P. K., Dabelsteen, T., Shepherd, M., and Pedersen, S. B. 1992. The signal value of matched singing in great tits: evidence from interactive playback experiments. Animal Behaviour 43, 987–998.

McShane, L. J., Esters, J. A., Riedman, M. L., and Staedler, M. M. 1995. Repertoire, structure, and individual variation of vocalizations in the sea otter. Journal of Mammalogy 76: 414-427.

Mennill, D. J. and Ratcliffe, L. M. 2004. Overlapping and matching in the song contests of black-capped chickadees. Animal Behaviour 67: 441-450.

Mesnick, S. L. 2001. Genetic relatedness in sperm whales: evidence and cultural implications. Behavioral and Brain Sciences 24: 346-347.

Miller, P. J. and Tyack, P. L. 1998. A small towed beamforming array to identify vocalizing resident killer whales (*Orcinus orca*) concurrent with focal behavioral observations. Deep-Sea Research 45: 1389-1405.

Miller, P. J. O, Shapiro, A. D., Tyack, P. L., and Solow, A. R. 2004. Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*. Animal Behaviour 67: 1099-1107.

Mitani, M. 1986. Voiceprint identification and its application to sociological studies of wild Japanese monkeys (*Macaca fuscata yakui*). Primates 27: 397-412.

Mithen, S. 2005. The Singing Neanderthals: The Origins of Music, Language, Mind and Body. Weidenfeld and Nicolson, London.

Møhl, B. 2001. Sound transmission in the nose of the sperm whale *Physeter catodon*. A post mortem study. Journal of Comparative Physiology [A] 187: 335-340.

Møhl, B., Wahlberg, M., Madsen, P. T., Miller, L. A., and Surlykke, A. 2000. Sperm whale clicks: Directionality and source level revisited. Journal of the Acoustical Society of America 107: 638-648.

Møhl, B., Wahlberg, M., and Heerfordt, A. 2001. A large-aperture array of nonlinked receivers for acoustic positioning of biological sound sources. Journal of the Acoustical Society of America 109: 434-437.

Møhl, B., Wahlberg, M., Madsen, P. T., Heerfordt, A., and Lund, A. 2003. The monopulsed nature of sperm whale clicks. Journal of the Acoustical Society of America 114: 1143-1154.

Molles, L. E. and Vehrencamp, S. L. 1999. Repertoire size, repertoire overlap, and singing modes in the banded wren (*Thryothorus pleurostictus*). The Auk 116: 677-689.

Mooring, M. S. and Hart, B. L. 1997. Reciprocal allogrooming in wild impala lambs. Ethology 103: 665-680.

Mooring, M. S. and Samuel, W. M. 1998. Tick-removal grooming by elk (*Cervus elaphus*): Testing the principles of the programmed-grooming hypothesis. Canadian Journal of Zoology 76: 740-750.

Morton, E. S. and Derrickson, K. C. 1996. Song ranging by the dusky antbird, *Cercomacra tyrannica* – ranging without song learning. Behavioral Ecology and Sociobiology 39: 195-201.

Moss, C. J. and Poole, J. H. 1983. Relationships and social structure of African elephants. *In* Primate Relationships: an Integrated Approach. *Edited by* R. A. Hinde. Blackwell Scientific, Oxford. pp. 315–325.

Myrberg, A. A., Jr. 1980. Ocean noise and the behavior of marine animals: relationships and implications. *In* Advanced concepts in ocean measurements for marine biology. *Edited by* F. P. Diemer, F. J. Vernberg, and D. Z. Mirkes. University of South Carolina Press, Columbia. pp. 461-491.

Naguib, M. 2005. Singing interactions in songbirds: implications for social relations and territorial settlement. *In* Animal communication networks. *Edited by* P. K. McGregor. Cambridge University Press, Cambridge. pp. 300-319.

Naguib, M. and Wiley, R. H. 2001. Estimating the distance to a source of sound: mechanisms and adaptations for long-range communication. Animal Behaviour. 62: 825-837.

Norris, K. S. and Harvey, G. W. 1972. A theory for the function of the spermaceti organ of the sperm whale (*Physeter catodon* L.). *In* Animal orientation and navigation. *Edited by* S. R. Galler, K. Schmidt-Koenig, G. J. Jacobs, and R. E. Belleville. NASA, Washington, D.C. pp. 397-417.

Nowak, M. A., Plotkin, J. B., and Jansen, V. A. A. 2000. The evolution of syntactic communication. Nature 404: 495-498.

Oda, R. 2002. Individual distinctiveness of the contact calls of ring-tailed lemurs. Folia Primatologica 73: 132-136.

Okayasu, N. 1987. Coo sound communication. Kikan Jinruigaku 19: 12-30.

Otter, K. A., Ratcliffe, L., Njegovan, M., and Fotheringham, J. 2002. Importance of frequency and temporal song matching in black-capped chickadees: Evidence from interactive playback. Ethology 108: 181-191.

Pallett, J. R. and Passmore, N. I. 1988. The significance of multi-note advertisement calls in a reed frog, *Hyperolius tuberilinguis*. Bioacoustics 1: 13-23.

Parr, L. A. and de Waal, F. B. M. 1999. Visual kin recognition in chimpanzees. Nature 399: 647-648.

Pavan, G., Hawyard, T. J., Borsani, J. F., Priano, M., Manghi, M., Fossati, C., and Gordon, J. 2000. Time patterns of sperm whale codas recorded in the Mediterranean Sea 1985-1996. Journal of the Acoustical Society of America 107: 3487-3495.

Payne, K. B., Langbauer, W. R. and Thomas, E. M. 1986. Infrasonic calls of the Asian elephant (*Elephus maximus*). Behavioral Ecology and Sociobiology 18: 297-301.

Payne, K., Thompson, M., and Kramer, L. 2003. Elephant calling patterns as indicators of group size and composition: the basis for an acoustic monitoring system. African Journal of Ecology 41: 99-107.

Pitman, R. L., Balance, L. T., Mesnick, S. L., and Chivers, S. 2001. Killer whale predation on sperm whales: observations and implications. Marine Mammal Science 17: 494-507.

Poole, J. H. 1994. Sex differences in the behaviour of African elephants. *In* The differences between the sexes. *Edited by* R. V. Short and E. Balaban. Cambridge University Press, New York. pp. 331-346.

Poole, J. H., Payne, K., Langbauer, W. R. and Moss, C. 1988. The social contexts of some very low frequency calls of African elephants. Behavioral Ecology and Sociobiology 22: 385-392.

Preston K. L., Grishaver, M. A., and Mock, P. J. 1998. California Gnatcatcher vocalization behavior. Western Birds 29: 258-268.

Radford, A. N. 2004. Vocal coordination of group movement by green woodhoopoes (*Phoeniculus purpureus*). Ethology 110: 11-20.

Raven, H. C. and Gregory, W. K. 1933. The spermaceti organ and nasal passages of the sperm whale (*Physeter catodon*) and other odontocetes. American Museum Novitates 677: 1-18.

Rendell, L. E. 2003. Cultural variation and usage of coda vocalisations by sperm whales, *Physeter macrocephalus*. Ph.D. thesis, Dalhousie University.

Rendell, L. E. and Whitehead, H. 2003a. Comparing repertoires of sperm whales: a multiple methods approach. Bioacoustics 14: 61-81.

Rendell, L. E. and Whitehead, H. 2003b. Vocal clans in sperm whales (*Physeter macrocephalus*). Proceedings of the Royal Society of London, Series B. 270: 225-232.

Rendell, L. E. and Whitehead, H. 2004. Do sperm whale share coda vocalizations? Insights into coda usage from acoustic size measurements. Animal Behaviour 67: 845-874.

Rhinelander, M. Q. and Dawson, S. M. 2004. Measuring sperm whales from their clicks: Stability of inter-pulse intervals and validation that they indicate whale length. Journal of the Acoustical Society of America 115: 1826-1831.

Rice, D. W. 1989. The Sperm Whale (*Physeter macrocephalus* Linnaeus, 1758). *In* Handbook of marine mammals Vol. 4. *Edited by* S. H. Ridgway and R. Harrison. Academic Press, London. pp. 177-233.

Richard, D. G., Wolz, J. P., and Herman, L. M. 1984. Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. Journal of Comparative Psychology 98: 10-28.

Richard, K. R., Dillon, M. C., Whitehead, H., and Wright, J. M. 1996. Patterns of kinship in groups of free-living sperm whales (*Physeter macrocephalus*) revealed by multiple molecular genetic analyses. Proceedings of the National Academy of Sciences of the United States of America 93: 8792- 8795.

Richman, B. 1978. Synchronization of voices by gelada monkeys. Primates 19: 569-581.

Robinson, J. G. 1984. Syntactic structures in the vocalizations of wedge-capped capuchin monkeys, *Cebus olivaceus*. Behaviour 90:46-79.

Rogers, A. C., Mulder, R. A., and Langmore, N. E. 2006. Duet duels: sex differences in song matching in duetting eastern whipbirds. Animal Behaviour 72: 52-61.

Santos, M. B., Clarke, M. R., and Pierce, G. J. 2001. Assessing the importance of cephalopods in the diets of marine mammals and other top predators: problems and solutions. Fisheries Research 52: 121-139.

Sayigh, L. S., Tyack, P. L., Wells, R. S., Solow, A. R., Scott, M. D., and Irvine, A.B. 1998. Individual recognition in wild bottlenose dolphins: a field test using playback experiments. Animal Behaviour 57: 41-50.

Schleidt, W. M. 1973. Tonic communication: Continual effects of discrete signs in animal communication systems. Journal of Theoretical Biology 42: 359-386.

Schnell, G. D., Watt, D. J. and Douglas, M. E. 1985. Statistical comparison of proximity matrices: applications in animal behaviour. Animal Behaviour 33: 239-253.

Schusterman, R. J., Reichmuth, C. J. and Kastak, D. 2000. How animals classify friends and foes. Current Directions in Psychological Science 9:1-6.

Schwartz, J. J. 1986. Male calling behavior and female choice in the neotropical treefrog *Hyla microcephala*. Ethology 73: 116-127.

Searcy, W. A., Anderson, R., and Nowicki, S. 2006. Bird song as a signal of aggressive intent. Behavioral Ecology and Sociobiology 160: 234-241.

Seyfarth, R. M., Cheney, D. L., and Marler, P. 1980. Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. Science 210: 801-803.

Sibly, R. H., Nott, H. M. R., and Fletcher, D. J. 1990. Splitting behaviour into bouts. Animal Behaviour 39: 63-69.

Slater, P. J. B. and Lester, P. 1982. Minimising errors in splitting behaviour into bouts. Behaviour 79: 153-161.

Smolker, R. A., Mann, J., and Smuts, B. B. 1993. Use of signature whistles during separations and reunions by wild bottlenose dolphin mothers and infants. Behavioral Ecology and Sociobiology 33: 393-402.

Snowdon, C. T. and Cleveland, J. 1984. "Conversations" among pygmy marmosets. American Journal of Primatology 7: 15-20.

Soltis, J., Leong, K., and Savage, A. 2005a. African elephant vocal communication I: antiphonal calling behaviour among affiliated females. Animal Behaviour 70: 579-587.

Soltis, J., Leong, K., and Savage, A. 2005b. African elephant vocal communication II: rumble variation reflects the individual identity and emotional state of callers. Animal Behaviour 70: 589-599.

Steels, L., Kaplan, F., McIntyre, A., and van Looveren, J. 2002. Crucial factors in the origin of word-meaning. *In* The transition to language. Edited by A. Wray. Oxford University Press, Oxford. pp. 252-271.

Stoddard, P. K. 1996. Vocal recognition of neighbours by territorial passerines. *In* Ecology and evolution of acoustic communication in birds. *Edited by* D. E. Kroodsma and E. H. Miller. Cornell University Press, New York. pp. 356-374.

Stoddard, P. K., Beecher, M. D., Campbell, S. E. and Horning, C. L. 1992. Song-type matching in the song sparrow. Canadian Journal of Zoology 70: 1440-1444.

Stokes, A. W. and Williams, H. W. 1968. Antiphonal calling in quail. Auk 85: 83-89.

Sugiura, H. 1998. Matching of acoustic features during the vocal exchange of coo calls by Japanese macaques. Animal Behaviour 55: 673-687.

Suzuki, R., Tyack, P. L., and Buck, J. R. 2005. The use of Zipf's law in animal communication analysis. Animal Behaviour 69: F9-F17.

Symmes, D. and Biben, M. 1988. Conversational vocal exchanges in squirrel monkeys. *In* Primate vocal communication. *Edited by* D. Todt, P. Goedeking, and D. Symmes. Springer-Verlag, Berlin. pp. 123-132.

Számadó, S. and Szathmáry, E. 2006. Selective scenarios for the emergence of natural language. Trends in Ecology and Evolution 21: 555-561.

Tanaka, I. and Takefushi, H. 1993. Elimination of external parasites (lice) is the primary function of grooming in free ranging Japanese macaques. Anthropological Science 101: 187-193.

Teichner, W. H. 1954. Reaction time: a review. Psychological Bulletin 51: 128-174.

Teloni, V. 2006. Bioacoustic study of clicks from diving sperm whales. Ph.D. dissertation. Aarhus University, Aarhus, Denmark.

Terry, R. L. 1970. Primate grooming as a tension reduction mechanism. Journal of Psychology 76: 129-136.

Thierry, B., Gauthoer, C., and Peignot, P. 1990. Social grooming in Tonkean macaques (*Macaca tonkeana*). International Journal of Primatology 11: 357-375.

Tobias, M. L., Barnard, C., O'Hagan, R., Horng, S. H., Rand, M., and Kelley, D. B. 2004. Vocal communication between male *Xenopus laevis*. Animal Behaviour 67: 353-365.

Todt, D. 1981. On functions of vocal matching: effect of counter-replies on song post choice and singing. Zeitschrift für Tierpsychologie 57: 73-93.

Todt, D. and Naguib, M. 2000. Vocal interactions in birds: the use of song as a model in communication. *In* Advances in the study of behavior. Vol. 29*. Edited by* P. J. B. Slater, J. S. Rosenblatt, C. T. Snowdon, and T. J. Roper. Academic Press, San Diego. pp. 247–296.

Todt, D. Hultch, H., and Duvall, F. P. 1981. Behavioural significance and social function of vocal and non-vocal displays in the monogamous duet-singer *Cossypha heuglini*. Bonner Zoologische Beitraege 27: 421-448.

Tooze, Z. T., Harrington, F. H., and Fentress, J. C. 1990. Individually distinct vocalizations in timber wolves, *Canis lupus*. Animal Behaviour 40: 723-730.

Tyack, P. L. 1986a. Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles? Behavioral Ecology and Sociobiology 18: 251-157.

Tyack, P. 1986b. Population biology, social behavior and communication in whales and dolphins. Trends in Ecology and Evolution 1: 144-150.

Tyack, P. L. 1998. 'Acoustic communication under the sea. *In* Animal acoustic communication. *Edited by* S. L. Hopp, M. J. Owren, and C. S. Evans. Springer, Berlin. pp. 163–220.

Tyack, P. 1999. Communication and cognition. *In* Biology of marine mammals. *Edited by* J. E. Reynolds III and S. A. Rommel. Smithsonian Institution Press, Washington, D.C. pp. 287-323.

Tyack, P. 2001. Cetacean culture: humans of the sea. Behavioral and Brain Sciences 24: 358-359.

Tyack, P. L. and Sayigh, L. S. 1997. Vocal learning in cetaceans. *In* Social influences on vocal development. *Edited by* C. T. Snowdon and M. Hausberger. Cambridge University Press, Cambridge. pp. 208-233

Urick, R. J. 1983. Principles of Underwater Sound, 3rd ed. McGraw Hill, New York.

van Parijs, S.M., Lydersen, C., and Kovacs, K.M. 2003. Vocalizations and movements suggest alternative mating tactics in male bearded seals. Animal Behaviour 65: 273-283.

Vehrencamp, S. L., Ritter, A. F., Keever, M., and Bradbury, J. W. 2003. Responses to playback of local vs. distant contact calls in the orange-fronted conure, *Aratinga canicularis.* Ethology 109: 37-54.

Verner, J. 1975. Complex song repertoire of male Long-billed Marsh Wrens in eastern Washington. Living Bird 14: 263-300.

von Frisch, K. 1967. The dance language and orientation of bees. Harvard University Press, Cambridge, Massachusetts.

Wahlberg, M., Møhl, B., and Madsen, P. T. 2001. Estimating source position accuracy of a large-aperture hydrophone array for bioacoustics. Journal of Acoustical Society of America 109: 397-406.

Wasilewski, A. 2003. “Friendship” in ungulates? – Sociopositive relationships between non-related herd members of the same species. Ph.D. dissertation. Philipps-Universität, Marburg, Germany.

Watkins, W. A. 1980. Acoustics and the behavior of sperm whales. *In* Animal sonar systems. *Edited by* R. Busnel and J. F. Fish. Plenum Press, New York. pp. 291-297.

Watkins, W. A. and Schevill, W. E. 1972. Sound source location by arrival times on a non-rigid three-dimensional hydrophone array. Deep-Sea Research 19: 691-706.

Watkins, W. A. and Schevill, W. E. 1977. Sperm whale codas. Journal of the Acoustical Society of America 62: 1486-1490.

Watkins, W. A., Moore, K. E., and Tyack, P. 1985. Sperm whale acoustic behaviors in the southeast Caribbean. Cetology 49: 1-15.

Weilgart, L. S. 1990. Vocalizations of the sperm whale (*Physeter macrocephalus*) off the Galápagos Islands as related to behavioral and circumstantial variables. Ph.D. dissertation, Dalhousie University, Halifax, Canada.

Weilgart, L. and Whitehead, H. 1993. Coda vocalizations in sperm whales (*Physeter macrocephalus*) off the Galápagos Islands. Canadian Journal of Zoology 71: 744-752.

Weilgart, L. and Whitehead, H. 1997. Group-specific dialects and geographical variation in coda repertoire in South Pacific sperm whales. Behavioral Ecology and Sociobiology 40: 277-285.

Weilgart, L., Whitehead, H., and Payne, K. 1996. A colossal convergence. American Scientist 84: 278-287.

Wetzel, D. and Kelley, D. 1983. Androgen and gonadotropin control of the mate calls of male South African clawed frogs, *Xenopus laevis*. Hormones and Behavior 17: 388-404.

Whitehead, H. 1990. Computer assisted individual identification of sperm whale flukes. Reports of the International Whaling Commission (Special Issue) 12: 71-77.

Whitehead, H. 1996a. Babysitting, dive synchrony, and indications of alloparental care in sperm whales. Behavioral Ecology and Sociobiology 38: 237-244.

Whitehead, H. 1996b. Variation in the feeding success of sperm whales: Temporal scale, spatial scale and relationship to migrations. Journal of Animal Ecology 65: 429-438.

Whitehead, H. 2003a. Sperm whale societies; social evolution in the ocean. University of Chicago Press, Chicago.

Whitehead, H. 2003b. Society and culture in the deep and open ocean: the sperm whale. *In* Animal social complexity. Intelligence, culture and individualized societies. *Edited by* F. B. M. de Waal and P. L. Tyack. Harvard University Press, Cambridge, Massachusetts. pp. 444-464.

Whitehead, H. and Gordon, J. 1986. Methods of obtaining data for assessing and modelling sperm whale populations which do not depend on catches. Reports of the International Whaling Commission (Special Issue) 8: 149-166.

Whitehead, H. and Weilgart, L. 1991. Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. Behaviour 118: 275-296.

Whitehead, H. and Weilgart, L. 2000. The sperm whale: social females and roving males. *In* Cetacean societies: Field studies of whales and dolphins. *Edited by* J. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead. University of Chicago Press, Chicago. pp. 154-172.

Whitehead, H., Gordon, J., Mathews, E. A. and Richard, K. R. 1990. Obtaining skin samples from living sperm whales. Marine Mammal Science 6: 316-326.

Whitehead, H., Waters, S., and Lyrholm, T. 1991. Social organization of female sperm whales and their offspring: constant companions and casual acquaintances. Behavioral Ecology and Sociobiology 29: 385-389.

Whitehead, H., Dillon, M., Dufault, S., Weilgart, L., and Wright, J. 1998. Non-geographically based population structure of South Pacific sperm whales: dialects, fluke-markings and genetics. Journal of Animal Ecology 67: 253- 262.

Whitehead, H., Bejder, L., and Ottensmeyer, C. 2005. Testing association patterns: issues arising and extensions. Animal Behaviour 69: e1-e6.

Wickler, W. 1980. Vocal duetting and the pair bond. I. Coyness and partner commitment. A hypothesis. Zeitschrift für Tierpsychologie 52: 201-209.

Wong, J., Stewart, P. D., and MacDonald, D. W. 1999. Vocal repertoire in the European badger (*Meles meles*): Structure, context, and function. Journal of Mammalogy 80: 570-588.

Zahavi, A. 1977. The testing of a bond. Animal Behaviour 25: 246-47.

Zahavi, A. and Zahavi, A. 1997. The handicap principle: a missing piece of Darwin's puzzle. Oxford University Press, Oxford.

Zimmer, W. M. X., Madsen, P. T., Teloni, V., Johnson, M. P., and Tyack, P. L. 2005a. Off-axis effects on the multi-pulse structure of sperm whale usual clicks with implications for sound production. Journal of the Acoustical Society of America 118: 3337-3345.

Zimmer, W. M. X., Tyack, P. L., Johnson, M. P., and Madsen, P. T. 2005b. Three-dimensional beam pattern of regular sperm whale clicks confirms bent-horn hypothesis. Journal of the Acoustical Society of America 117: 1473-1485.

Zipf, G. K. 1949. Human Behavior and the Principle of Least Effort. Addison-Wesley, Reading, Massachusetts.

Zipf, G. K. 1968. The Psycho-Biology of Language: An Introduction to Dynamic Philology. M.I.T. Press, Cambridge, Massachusetts.

Zuberbühler, K. 2000. Referential labeling in Diana monkeys. Animal Behaviour 59: 917-927.

Zuberbühler, K., Noe, R., and Seyfarth, R. M. 1997. Diana monkey long-distance calls: Messages for conspecifics and predators. Animal Behaviour 53: 589-604.